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Snow crab (*Chionoecetes opilio*) in the Barents Sea

Diet, biology and management

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Abstract

This thesis seeks to develop a better understanding of snow crab (*Chionoecetes opilio*), a non-native species that has established in the Barents Sea. Very little is known about the species role in the ecosystem, but it can be perceived both as a pest and as a goldmine. It is expected that the population will accommodate a significant fishery. As a non-native benthic crustacean spreading throughout a continental shelf shared between Norway and Russia, snow crab is legally a challenging management object. This thesis attempts to predict probable future distribution of the Barents Sea snow crab as well as ecosystem effects, and discuss management challenges. The research subject has been approached with a combination of a literature review and a diet study. Snow crab can potentially colonize most of eastern, central and northern Barents Sea. As an omnivorous benthic feeder it will likely affect important ecosystem processes, but the severity of snow crabs impact is unknown. It might in fact strengthen the pelagic-benthic coupling in the Barents Sea. As it seems that snow crab is a sedentary species, most of the commercial stock is currently Russian, but it is likely that it will spread into Norwegian zones soon. Two potential management strategies for the Barents Sea snow crab are discussed; "the pest strategy" and "the ecosystem based fishery strategy".

Key-words: Snow crab, *Chionoecetes opilio*, non-native species, invasive species, pest, transformer, immigrant, sedentary, Barents Sea, Loophole, Svalbard fishery protection zone, fisheries management, diet study, stomach analysis

Sammendrag

Denne masteroppgaven søker å bedre forståelsen av snøkrabbe (*Chionoecetes opilio*), en fremmed art som har etablert seg i Barentshavet. Lite er kjent om artens rolle i økosystemet, men den kan bli sett både som en pest og en gullgruve. Det er ventet at populasjonen vil bli et gjenstand for et betydelig fiskeri. Som et fremmed krepsdyr som sprer seg over en kontinentalsokkel delt mellom Norge og Russland, er snøkrabbe et juridisk utfordrende forvaltningsobjekt. Denne oppgaven forsøker å predikere snøkrabbas framtidige utbredelse så vel som økosystemeffektene, og diskutere forvaltningsutfordringene. Tilnærmingen til temaet har vært en kombinasjon av litteraturstudium og diettstudium. Som en bunnlevende alteter er det sannsynlig at snøkrabba vil påvirke viktige økosystemprosesser, men alvorlighetsgraden er ukjent. Det kan tenkes at snøkrabbe vil forsterke den pelagisk-bentiske koblingen i Barentshavet. Snøkrabba virker å være en sedentær art, og dermed er mesteparten av den nåværende kommersielle bestanden russisk, men det er sannsynlig at det snart kommer en større spredning inn i norske soner. To potensielle forvaltningsstrategier for snøkrabba i Barentshavet blir diskutert; "pest" og "økosystembasert fiskeri".

Preface // Acknowledgements

This is a highly curiosity driven thesis, reflective of my interdisciplinary background as well as my interest for the intersection between ecology and society. Being interdisciplinary is both a blessing and a curse, as I can address subjects from different angles and connect threads, but not fully indulge in details. It that essence it sometimes feels like only scratching the surface of important subjects, but at the end of this process it feels like the scratching has resulted in something meaningful.

I want to thank Bjørnar S. Kolflaath for proposing snow crab as the subject for a term paper we wrote together in early 2014. Through that work I met what would come to be my co-supervisor Jan H. Sundet at the Institute of Marine Research (IMR). Jan suggested snow crab as the subject of my thesis and has given critical and useful advice throughout the process. In addition he facilitated for me to get hands-on experience on a research vessel and collect my own data through stomach analysis. Maria Jenssen at the IMR has shown patience and great knowledge in helping me to conduct the stomach analysis. In addition Maria made her own data available for my statistical analysis. Thank you Jan, Maria and the rest of the IMR in Tromsø.

I wish to express gratitude towards my supervisor Einar Nilssen that has not only contributed significantly to the statistical analysis; he has also made himself available and patiently provided constructive feedback. In addition I am thankful towards Alf Håkon Hoel (IMR) and Tore Henriksen (UiT) for being available to discuss resource rights in the Barents Sea.

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At last I want to thank the inspiring staff I have learned to know during our courses at the Norwegian College of Fishery Science, especially Roger B. Larsen who let me come aboard R/V Helmer Hanssen in the Barents Sea for three weeks during November 2014.

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Harald Sakarias Brøvig Hansen

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1. Introduction

During the last two decades snow crab (*Chionoecetes opilio*), a non-native species of significant commercial interest, has established in the Barents Sea. The populations seem to be rapidly increasing, while the ecosystem consequences as well as the nationality of the commercial part of the population are in the unknown. This thesis treats the apparent paradox of snow crab being a potential pest species as well as a potential goldmine, and how it can be managed.

1.1 Geographical distribution

The presence of snow crab in the Barents Sea was discovered in 1996 when a few individuals were caught at the Goose Bank in the southeastern part of the sea (marked by * in fig. 1) (Kuzmin et al., 1999). Snow crab is natively distributed on deep mud bottoms in the Northwest Atlantic Ocean, the North Pacific Ocean, the Arctic Ocean, the Bering Sea and the Sea of Japan (Squires, 1990; Slizkin, 1998) (figure 1). Norwegian fishers caught two snow crabs in Norwegian waters first time in 2003 (Alvsvåg et al., 2009).

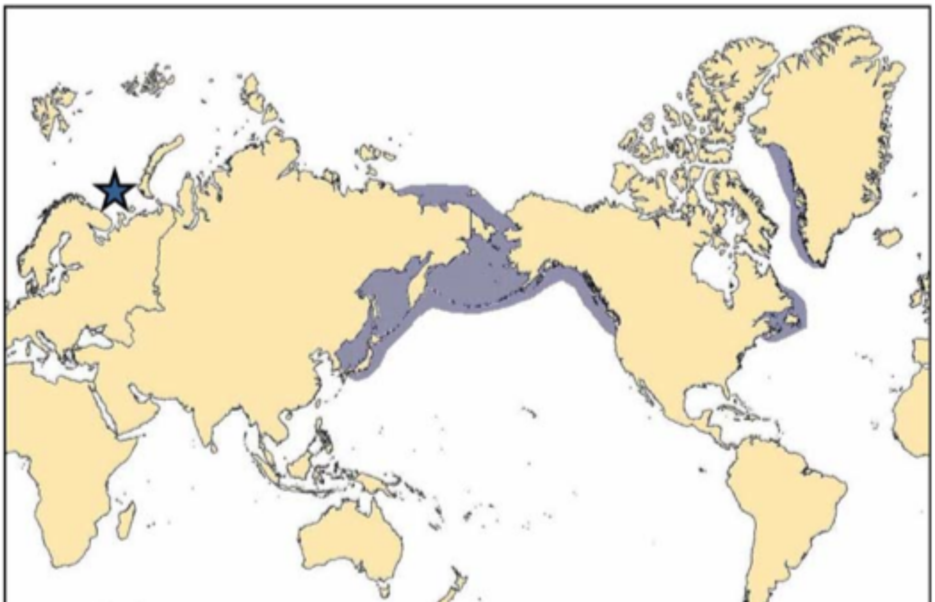

Figure 1 Natural distribution range of snow crab *Chionoecetes opilio*. * Indicates the observations of a new population in the northeastern Atlantic (from Alvsvåg et al., 2009).

It is not clear how the species have entered the Barents Sea, or if it involves direct or indirect human actions. It is also not known which areas of the Barents Sea snow crab will colonize. Snow crab larvae have multiple planktonic stages that constitute three to five months in total, such a relatively long planktonic phase may facilitate long distance dispersal between widely distributed populations (Hardy et al., 2011), which can contribute to the understanding of snow crab dispersal to and in the Barents Sea. It is not impossible that larvae hatched in the Pacific can enter the Polar region and the Barents Sea (Agnalt et al., 2014). Evidence for a self-reproducing population of snow crab in the Barents Sea was provided by Alvsvåg et al. (2009) and later research has shown that the population is rapidly increasing and spreading. In some locations in the southeastern Barents Sea, 41% of the benthic biomass consist of snow crab (Jørgensen et al., 2014). Total stock size is considerable, and new areas further to the north and west are likely to be invaded (Sundet and Bakanev, 2014). It is of interest to investigate how limiting environmental factors control the distribution of the species, such as temperature, depth and food availability.

1.2 Ecosystem effects

In 2012 snow crab was listed as a species with "severe ecological risk" (SE), the highest impact category on the Norwegian blacklist of alien species (Gederaas et al., 2012). Ecosystems are dynamic and constantly changing. How the Barents Sea ecosystem reacts to snow crab and if it triggers major changes depends on the resilience of the system. The establishment of snow crab is in some ways comparable to that of the red king crab (*Paralithodes camtschaticus*), which is also a rather novel invasive crustacean in the Barents Sea. The red king crab is said to represent an important source of income, but also a potential threat to the highly productive fisheries in the region through its ecosystem impacts (Falk-Petersen et al., 2011). The invasion of red king crab has lead to markedly reduced fauna, loss of structural and functional diversity as well as fundamental changes in sediment integrity in Varangerfjorden (Oug et al., 2011).

It has been observed in several ecosystems how what appear to be small changes lead to major shifts, as the reintroduction of a few wolves (*Canis lupus*) to Yellowstone national park in the USA. Wolves lead to decreased elk (*Cervus elaphus*) population, increased canopy cover and increased numbers of beaver (*Caster canadensis*) and bison (*Bison bison*) (see e.g. Ripple and Beschta, 2012). Wolves even impacted river morphology (Beschta and Ripple, 2012). Another example is an urchin fishery that developed in the Gulf of Maine in the 1980s; within a decade urchin populations crashed and kelp forests recovered. Kelp act as an important habitat for juvenile crabs (Cancer spp.), and with the loss of fish predators, crabs have settled in large numbers to Gulf of Maine kelp beds. These crabs now serve as an apex predator with functionally the same impact cod and other fish predators had had in the past (Mangel and Levin, 2005).

Chionoecetes crabs are generalist feeders known to feed on algae, mollusks, crustaceans, polychaets, echinoderms and fish (Lovvorn, 2010). The benthic community in the Barents Sea is of vital ecological importance, as a significant portion of the primary production pass through epibenthos, which thus play an important role for energy flow and trophodynamics (e.g. Piepenburg and Schmid, 1996). Changes in the benthic community may therefore heavily affect the ecosystem. For now, the environmental carrying capacity of snow crab in the Barents Sea ecosystem is unknown and in general, little is known about how snow crab interacts as predator or prey with other species in the Barents Sea. Thus, it is of interest to ascertain the diet of the Barents Sea snow crab and discuss potential ecosystem effects.

With the knowledge that snow crab might impair the Barents Sea ecosystem, a relevant question is which obligations the coastal states have towards a novel organism such as snow crab. The question very much boils down to if snow crab should be viewed legally as an alien invasive species or not. Several international treaties deal with the protection of ecosystems from marine alien invasive species. In this regard UNCLOS and the Convention on Biological Diversity (CBD) are the most relevant.

1.3 Fisheries and management

Snow crab has been fished commercially in eastern Canada since the 1960s and is now among the most valuable fisheries in Canada. It was the most valuable crab fishery in the United States of America until the Eastern Bering Sea population collapsed in 1999. The fishing season varies between areas, as well as from year to year. In Canadian Gulf of St. Lawrence fishing takes place from spring to early summer, which has the advantage of avoiding mating season as well as soft-shelled and white crab. In other areas of Canada the fishing season deviate somewhat from this (Anon., 2005a).

The Barents Sea snow crab population is viewed as a great economic opportunity. The front page of Kystavisa Fiskeribladet Fiskaren (August 4th 2014) stated that “the snow crab fishery may become as valuable as the cod fishery” (my translation), which is the most valuable fishery in the Norwegian exclusive economic zone (EEZ) today. A fishery for snow crab started in the Barents Sea in 2013 (Sundet and Bakanev, 2014) and in 2014 more than 4,000 tons were landed in Norway (Anon., 2015a) exceeding NOK 100 million in value (Anon., 2014a). Nine Norwegian boats participated in the fishery in 2014, however there are currently four Norwegian vessels actively participating in the snow crab fishery. In addition vessels from Spain, Lithuania and Latvia have landed Barents Sea snow crab in Norwegian ports. Most of what is landed in Norway comes from the Loophole[1], although some catch is registered in the Svalbard Fishery Protection Zone (Anon., 2015a). So far in 2015 the catches in the Loophole seem to be about 50% of what they were in the same period in 2014 (Anon., 2015b). The Norwegian Ministry of Trade, Industry and Fisheries has currently put a total ban on snow crab harvesting within the Norwegian EEZ, the Svalbard fishery protection zone, as well as on all Norwegian vessels in international waters, with the exception of vessels that receive a dispensation from the Directorate of Fisheries (Anon., 2014b). Such a ban is standard protocol when a stock is put under management, and in this case as a precursor to the management process. In 2014 Russia set a total allowable catch (TAC) for fishing within the Russian EEZ and continental shelf (Anon., 2014c).

As snow crabs are spreading across the Barents Sea continental shelf that is shared between the Kingdom of Norway and the Russian Federation (fig. 1.2), it must be clarified which zones and legal rules adhere to the species. Such regulations are founded in the United Nations Convention on Law of the Sea (UNCLOS). Legally the Barents Sea snow crab is a special case, as the crab is currently primarily fished outside exclusive economic zones, but inside the continental shelf (the Loophole).

Snow crab is primarily found within the Russian continental shelf; however, the population is shared with Norway. Currently Norwegian vessels (with dispensation from the Directorate of Fisheries) are allowed to harvest snow crab in the Loophole, which is high seas and (for the most part) Russian continental shelf, although they are not allowed to harvest snow crab within the Russian EEZ (Anon., 2014d).

If the species is legally defined as sedentary, Russia can exclude Norwegian boats from harvesting snow crab within (most of) the Loophole. If it is a sedentary species, the countries are neither bound by the UN Fish Stocks Agreement to manage in cooperation. The legal definition of "sedentary" is unclear, thus it is of interest to pursue this question. In addition

[1] The Loophole is an area of the Barents Sea not covered by exclusive economic zones as illustrated by figure

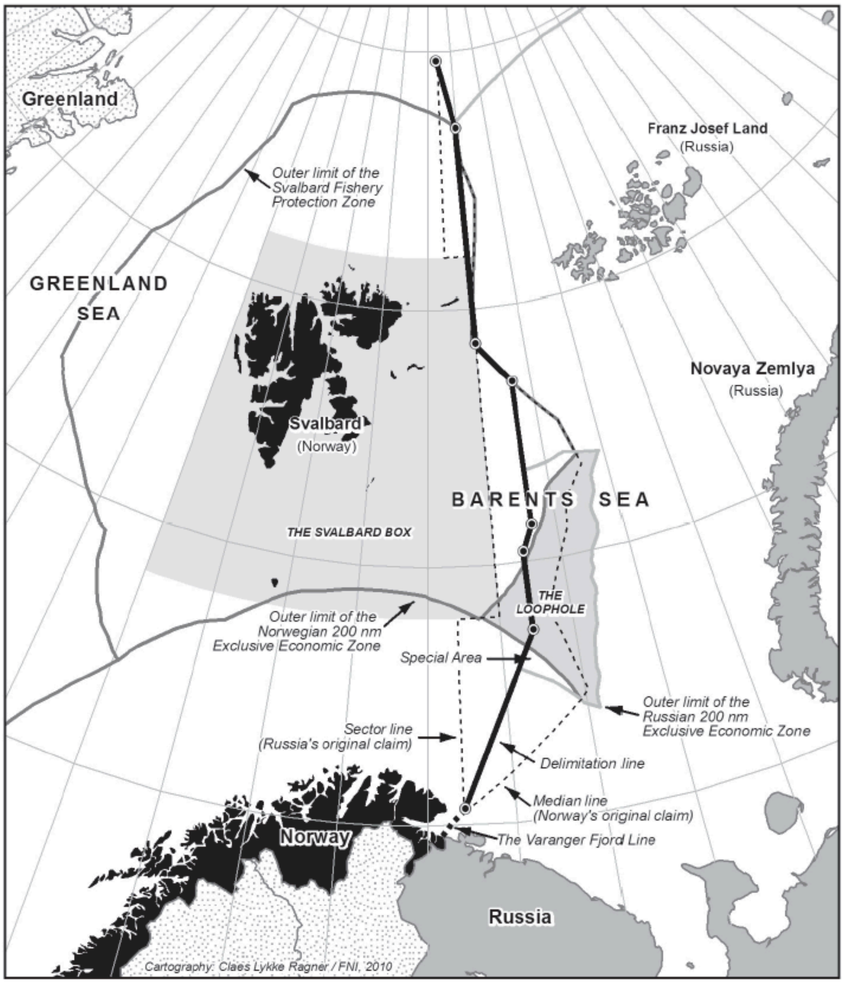

Figure 1.2 Economic zones and the delimitation line of the Barents Sea (from Jensen, 2011). The original claims (stippled lines) are not of interest.

the biomass might increase and become commercially interesting in the Svalbard Fishery Protection Zone, so an account of management challenges in this zone is required.

Norwegian fishers have expressed an interest in joint management of snow crab in the Barents Sea, including access to Russian EEZ, as most of the commercial quantities are found there. For now, Norway and Russia have chosen to approach the Barents Sea snow crab separately with no common total allowable catch quota (Anon., 2014e). Norwegian fishers have also feared a repeat of the Icelandic scallop fishery in the 1980s (Anon., 2014f) [2]. Such a situation may be avoided by the decision to close the fishery (Anon., 2014d).

[2] The Icelandic scallop fishery was seen as a commercial opportunity in the Barents Sea, with an instant increase in fishing effort under an absence of regulations. The stocks outside Svalbard, Bjørnøya and Jan Mayen were depleted in three fishing seasons between 1985-1987 (Garcia, 2006).

At present, Norwegian authorities have not decided upon a management goal for snow crab in the Barents Sea, thus it is unsettled if it will be perceived an invading threat or a potential goldmine. It is expected that Norwegian authorities will initiate the work with a white paper on snow crab within 2015.

1.4 Research subject and limitations

If Norway is to manage the species according to socioeconomic needs, the status of the Barents Sea snow crab must be clarified. The objective of this thesis is to provide general as well as specific information on some of the most urgent issues relating to snow crab, which must be addressed before a more operationalized management goal and regime can be developed. The research subject of this thesis is therefore: *What ecosystem effects can we expect from the snow crab population in the Barents Sea, and which challenges does this species pose to management?* In practice the following research questions will be investigated:

- *What is the probable future geographical distribution of snow crab in the Barents Sea?*
- *What does Barents Sea snow crab feed on, and what role is the species likely to play in the Barents Sea food web?*
- *How does international law lay the ground for management of snow crab in the Barents Sea?*
- *How can the Barents Sea snow crab population be managed?*

To answer the research questions two approaches are used. First, a review of relevant literature introducing snow crab as a species provide a background for the discussion. The literature review has specific focus on habitat requirements and trophic relations, as well as international and Norwegian law of relevance, as this is directly related to the research questions. Secondly, a pilot study on snow crab diet is used to identify some main trends in the diet of Barents Sea snow crab. These approaches lay the foundation to further discuss the research subject and arrive at some conclusions.

2. Background

2.1 Taxonomy

The species got its first scientific name from Otto Fabricius in 1788. The taxonomy here follows the World Register of Marine Species (Anon., 2015c).

Kingdom: Animalia
  Phylum: Arthropoda
    Subphylum: Crustacea
      Class: Malacostraca
        Order: Decapoda
          Suborder: Pleocyemata
            Infraorder: Brachyura
              Superfamily: Majoidea
                Family: Oregoniidae
                  Genus: *Chionoecetes*
                    Species: *C. opilio*

2.2 Distribution

2.2.1 Geographical range in the Barents Sea

Theories on the spread of snow crab to the Barents Sea include human vectors such as ballast water, larval advection by ocean currents and migration by foot north of Siberia. The Barents Sea population seems to be genetically different from all other populations, although more similar to the Bering Sea and Canadian populations, than the Greenland population (Dahle et al., 2014). Recently snow crab was registered in the Kara Sea, neighboring the Barents Sea (Zimina, 2014).

In 2013 PINRO[3] estimated the commercial stock of the Barents Sea to be 370 million individuals, while total biomass was estimated to be 188,260 tons (Dvoretsky and Dvoretsky, 2015). As a non-indigenous species, there is no basis to assume any form of equilibrium for the stock, as the population dynamics seem to be very unstable and fluctuating. This resembles a pattern typical of invasive species, were the initial stage is characterized by a jump in abundance. In this stage there is a risk of high observation errors in abundance

[3] PINRO (Knipovich Polar Research Institute of Marine Fisheries and Oceanography) is a Russian equivalent of the Norwegian Institute of Marine Research.

estimates (Sokolov, 2014).

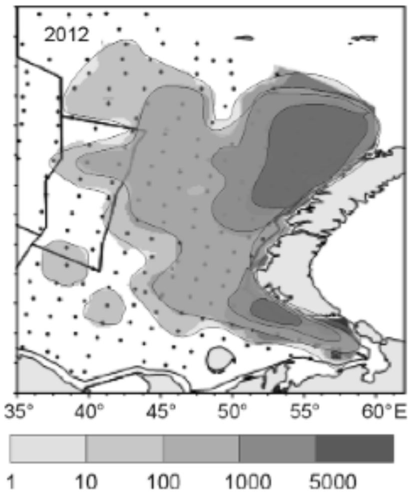

Figure 2.1 Individuals caught per 15 min of trawling in the Barents Sea in 2012. Novaya Zemlya to the right (PINRO data presented in Dvoretsky and Dvoretsky, 2015)

In the Barents Sea snow crab mainly occur in the east (fig. 2.1), but single animals have been recorded in western and northern parts of the Barents Sea. The known range of snow crab is between 69°N and 79°N and 27°E and 56°E, with the majority within the Russian economic zone (Dvoretsky and Dvoretsky, 2015). Fishers have supposedly also caught individuals closer to the Norwegian coast outside Berlevåg (Anon., 2015d). The Goose Bank has appeared as a main hatching and spawning ground in the Barents Sea, and survey data indicate that the main distribution is in waters with temperatures below 2°C (Alvsvåg et al., 2009; Agnalt et al., 2014). The largest proportion of large males (carapace width > 100 mm) occupy areas adjacent to the Goose Bank and the southern point of Novaya Zemlya (Dvoretsky and Dvoretsky, 2015).

2.2.2 Migratory behavior and population connectivity

When dealing with ecosystem dynamics and spreading of new species, it is of significant importance to understand spreading dynamics. Our knowledge on snow crab migratory behavior is limited, but some is known from snow crabs native areas, and we have some general knowledge on marine species. As most benthic marine species, snow crab possess dispersive larval stages, which may interconnect populations[4] through 'source' and 'sink' habitats, where reproduction either exceed or fall short of mortality (Lipcius et al., 1997; Cowen and Sponaugle, 2009).

A relatively long planktonic phase may facilitate long distance dispersal between widely-distributed populations (Hardy et al., 2011) and maintain demographic connectivity (gene flow) (Albrecht et al., 2014). Despite the long planktonic phase, genetically different populations may develop, as within the Labrador Sea (between Greenland and Atlantic Canada), where inhospitable "warm" bottom waters may favor genetic differentiation (Puebla et al., 2008; Albrecht et al., 2014). Adult male snow crabs can migrate several kilometers in a few days when disturbed, while berried females do not migrate over large distances (Conan et

[4] If there is population connectivity it can be argued that these are not separate population, rather subpopulations.

al., 1996). In the eastern Bering Sea the female population undertake ontogenetic migration (Ernst et al., 2005).

2.2.3 Spatial structure

Snow crabs tend to aggregate into mounds that are specific to biological categories such as sex, age and size (Conan et al., 1988). Immature males and females are found in the same aggregations, but sexes tend to separate when they get larger, only to congregate again at the time of mating. The geographical location of the concentrations seems to vary from year to year, only mature berried females tend to remain in similar locations (Conan et al., 1996). The shallow-water association between pubescent females and small adult males, and the deep-water association between multiparous females and large adult males are well documented for snow crab. By moving to shallow grounds to mate with pubescent females, small adult males probably maximize their chances of reproducing because there is little competition from large adult males (Sainte-Marie and Hazel, 1992).

2.3 Habitat requirements

All species have a limited geographic range. Shelford's law of tolerance is a conceptual tool for physiological ecology and can be stated as "the distribution of a species is controlled by the environmental factor for which the species has the narrowest tolerance" (Krebs, 2008). Limiting factors are a combination of physical and chemical conditions that need to be present for snow crab to establish. Various benthic life stages of *Chionoecetes opilio* have different depth, temperature and substrate preferences, but these also vary between populations.

2.3.1 Temperature

Snow crab is a stenothermic species, which mean it is only capable of living within a narrow temperature range. Early benthic stages have the narrowest temperature range (preferring 0.0-1.5°C), and may as such represent the weakest link in the snow crab life cycle (Dionne et al., 2003). Larger benthic stages of snow crab is typically found at bottom temperatures ranging between -1°C to 5°C (Anon., 2005a). Along the Scotian Shelf in Canada, snow crabs are predominantly found in areas where the bottom temperature does not exceed 7°C (Tremblay, 1997). In the Barents Sea snow crab is widely distributed in areas with bottom temperatures ranging from -0.7°C to 3.4°C (Alvsvåg et al., 2009). Temperature-dependent growth and reproduction of snow crab, and increasing temperatures in the Pacific-Arctic region are thought to be driving a northward displacement of the range of this species (Orensanz et al., 2004), as well as a latitudinal cline in adult body sizes observed in the Pacific and Atlantic

(Orensanz et al., 2007). Snow crab abundance has shown negative correlation with temperature with lags of 7 and 10 years (Boudreau et al., 2011).

Laboratory studies have shown that the confinement to cold water seems to be due to an energetical restriction. Slight temperature changes in the natural environment may therefore regulate growth and reproduction in this species (Foyle et al., 1989).

2.3.2 Depth range

In the Pacific individual snow crabs are found at depths ranging from 4 to 520 meters (Yosho and Hayashi, 1994), while in the northwestern Atlantic large males are found at depths down to 1400 meters (Lovrich et al., 1995). This can be explained by local environmental conditions. Snow crab are found at great depths in the Sea of Japan, this can be explained by warm mixed surface layers of water that extends much deeper than in the northwest Atlantic (Yosho and Hayashi, 1994; Lovrich et al., 1995). The upper depth limit for settlement is in many places determined by the position of the thermocline (Lovrich et al., 1995).

Depth range varies according to season and size. In Bonne Bay, Canada, individuals actively seek along the slopes of the fjord to optimal temperature and salinity for their current activity (Conan et al., 1996). In Canadian Gulf of Saint Lawrence crabs with carapace width (CW) less than 50 mm have occurred mostly on gravelly mud bottoms (>40% mud) at depths between 60 and 90 meters with temperatures lower than 3°C, while adults concentrated on deeper muddy bottoms (Brêthes et al., 1987). The majority of adult males with CW larger than 90 mm were in the same area found deeper than 80 meters, although migrated to shallower waters from March to May, probably to mate with multiparous females. Research from the Gulf of Saint Lawrence imply that snow crab move extensively during winter, not restricted by their summer habitat, to shallower coastal waters on sand or rock to shed their exoskeleton. Movement to shallow water is also linked to reproduction, as well as a mechanism to avoid predation and cannibalism (Lovrich et al., 1995). In the central region of Barents Sea a significant number of crabs have been found in deeper waters from 180 to 350 meters (Alvsvåg et al., 2009).

It has been postulated that males from deeper areas exert competitive exclusion in Bonne Bay. Cannibalism and competitive exclusion has been interpreted as the existence of a dominant class of snow crabs and one or more subordinate classes. Smaller crabs and those missing limbs (older) concentrate on shallower grounds. Larger adult males and multiparous females occur on deeper grounds. Adult crabs may have a greater temperature tolerance, as they no longer devote energy to somatic growth (Lovrich et al., 1995).

2.3.3 Sediment type

Crab distribution seems to be more related to substrate type than depth. Densities of male crabs with carapace width less than 50 mm and female crabs have been found to be greater on muddy than on sandy or gravelly bottoms (Robichaud et al., 1989 in Comeau et al., 1998). Snow crab may partially bury in bottom sediment. Early benthic stages settle anywhere that is best for protection from predation and cannibalism. Relationship to sediment is more opportunistic than actively directed (Conan et al., 1996)

2.4 Morphology

As with all Arthropoda snow crabs have an exoskeleton. The color can vary from sandy-brown to bright red according to the environment snow crab is found in. The main body (carapace) is flat with a circular shape, and five pair of flattened legs, including one pair of legs that work as claws (chelipeds) (see fig. 2.2).

Figure 2.2 Snow crab (*Chionoecetes opilio*) caught in the Barents Sea

The exoskeleton is shed to allow the crabs to grow, in a process known as molting. In contrast to most other crustaceans snow crabs undergo a terminal molt, during which the female develops a broad abdomen with long and curved setiferous pleopods and the male develops relatively more voluminous chelae and longer limbs (Sainte-Marie et al., 2008). The existence of a terminal molt has been disputed, as it is difficult to provide evidence for such an attribute (Dawe et al., 1991).

Adult snow crabs are characterized by a conspicuous sexual dimorphism (fig. 2.3). Most females become adult at a smaller size and a younger age than males; the mean carapace width (CW) and age at adulthood in any given population are easily 30–50 mm and 2–3 years less for females than for males (Sainte-Marie et al., 2008). In Canada adult males range from 60-165 mm in carapace width, while females reach 40-95 mm carapace width at maturity (Anon., 2005a). Juvenile males and small mature male can be of the same size, but juvenile males have smaller claws than morphometrically mature males of the same size (Comeau and Conan, 1992).

Figure 2.3 Adult female (top) and male (bottom) snow crab (*Chionoecetes opilio*) from Canada (Dfo, 2009)

2.5 Life history

2.5.1 Life-stages

The full natural life cycle of snow crabs is about 15 years, with the first months in planktonic stages. In Bonne Bay, Canada, hatching of eggs occurs in early May to early June. Zoea I larvae are released in the plankton where they metamorphose into zoea II and later into megalopae which settle on the seafloor by late August to early September. Larval development may last from two to eight months depending on temperature and planktonic food supply. At a carapace width (CW) of about 3 mm, the snow crabs settle to the ocean floor (Conan et al., 1996).

The majority of life is devoted to benthic life, and only a small fraction of individuals survive the planktonic and benthic phases and reach maturity (Conan et al., 1996). Once on the bottom, snow crabs go through a series of molts, with growth of roughly 20% between molts. While early benthic stages may molt several times a year, juvenile males molt mostly once a year during a short season in March to April (some juveniles may molt in the fall) (Comeau et al., 1998). It takes 5-10 years for male snow crab to reach legal size (95 mm CW) (Conan et al., 1996).

There are several definitions of snow crab maturation, both from a functional (able to mate), physiological (spermatophores present) and morphometric (possession of distinct morphometric characteristics) perspective. A male crab must become both functionally and physiologically mature before it can reproduce, while the ability to mate can depend on the attainment of morphometric maturity. Although physiological maturity is attained by male *Chionoecetes opilio* before they reach a CW of 60 mm, functional maturity is not attained until individuals have molted to become morphometrically mature and, even then, only by those animals that have attained a CW of 95 mm (Hall et al., 2006). Male snow crabs from the Gulf of St. Lawrence became physiologically mature at CW of only 28.5 mm (Sainte-Marie et al., 1995). Benthic stages are commonly divided into three life stages (Conan et al., 1996):

- Immature (gonads are not differentiated, external morphology of males and females is weakly differentiated)
- Juvenile/adolescent (gonads are differentiated, the external morphology of males and females is incompletely differentiated)
- Morphometrically mature (both the gonads and the morphometric secondary characters are fully differentiated, males and females are fully functionally reproductive)

Preceding the terminal molt the crabs are white and soft-shelled, a period that may last several months. During this period the crabs have little meat and experience increased susceptibility to predation and cannibalism (Anon., 2005a). At the point of terminal molt the individuals reach their maximal size. This is achieved over a wide range of ages (minimum five years) and sizes. Females stop growing after the molt in which the abdomen widens substantially for carrying eggs. Males stop growing after the molt in which the claws enlarge appreciably for mating. Age and size of terminal molt depends upon environmental and genetic conditions (Conan et al., 1996). After the last molt the crabs loose the ability to regenerate limbs, thus older individuals often have abraded decalcified carapaces and numerous missing legs, autotomized during fights between males at time of mating. Most individuals die from senility 4 to 5 years after achieving terminal molt (Conan et al., 1996).

2.5.2 Reproduction

A primary component in population biomass is fecundity (mean number of offspring $female^{-1}yr^{-1}$), related to number of spawning events as well as number of eggs and egg size (Dorit et al., 1991). Snow crab exhibit a complex reproductive biology that includes the possibility of either immediate fertilization at copulation or storage of sperm for subsequent autonomous fertilization (Elner and Beninger, 1995). Female snow crabs mate for the first time shortly after terminal molt (usually between December and April). Each brood is incubated under the abdomen of the female for up to two years. The second and later matings take place immediately after hatching of the previous brood of eggs in late May to early June (Anon., 2005a). At insemination, each of the males first pair of gonopeds (snow crab equivalent of penis) are inserted into the female crab's vagina; seminal fluid and spermatophores are pumped from the penes through the ejaculatory canal of the first gonopeds, by piston-like movements of the second gonopeds. Fertilized eggs are extruded onto the females pleopods within 24 hours of copulation As mentioned, females have a much broader abdominal flap than males; which is used to hold as many fertilized eggs as possible. Under the abdominal flap they have two spermathecae, where males deposit spermatophores (capsules of sperm). The sperm in the spermathecea are viable for up to three years[5]. Females produce broods of tens of thousands of larvae that are released from April to June and carried by currents (Elner and Beninger, 1995).

Primiparous (first-time spawners) females and small male adults have a shallow-water association. In primiparous mating, the male retains the female in a mating embrace (abdomen-to-abdomen) and drive away intruding males for a week prior to her puberty molt. During this span, the female will undergo her final molt, in which the male will assist. The copulation lasts for about 45 minutes, after which the pair remains embraced for about eight following hours. Multiparous (repeat spawners) females and large adult males have a deep-water association. During multiparous mating, pairing lasts up to two months. Copulation occurs shortly after the female releases larvae from her previous clutch. Morphometrically mature males usually retain the female until new eggs are extruded, 6 to 24 hours after copulation. Virtually all mature females have grasping marks as a result of mating (Elner and Beninger, 1995). It is believed that primiparous are less productive than multiparous spawners (Anon., 2005a).

Male chela size is a secondary sexual character justified by males holding the pereipods of females, as well as competing with other males (Comeau and Conan, 1992). A sexual dominance hierarchy exists among males: adolescents and adults with a new shell are usually

[5] This sperm can be considered back-up sperm to be used in the following years if the number of available males is small (Elner and Beninger, 1995).

excluded from mating by adults with an old shell, and within this last group, larger adults are relatively more successful than smaller adults (Sainte-Marie et al., 2002).

The spawning period in the Barents Sea is estimated to be between April and June, except for first time spawners, which spawn between December and April. Females produce two, maximally three cohorts. Egg production varies from 12 000 to 160 000 eggs and normally primiparous produce fewer eggs than multiparous females (Agnalt et al., 2014).

2.5.3 Population fluctuations

Population size of snow crabs in Canada (Conan et al., 1996) and Alaska (Zheng et al., 2001) have shown a cyclical nature. In Bonne Bay, Canada, series of three to four years of good recruitment has been followed by series of five to six years of poor recruitment. Swings in year-class strength, is attributed to intrinsic (egg production and cannibalism) and physical controls (egg and larval survival). Most of the recruitment variability in the Bonne Bay stock in the 1990's results from intrinsic effects involving selective cannibalism by older males on early benthic recruits and molting individuals. These "missing cohort dynamics" appear to exist all over the northwest Atlantic with the fluctuations being more or less synchronous in all known locations (Conan et al., 1996). In the eastern Bering Sea (Alaska) the core years of pseudocohort strength are approximately seven years apart, the average time elapsed in the life of an average individual female snow crab between egg extrusion by her mother and terminal molt. This correspondence suggests dynamic linkage between the pulses, where each pulse becomes the parental stock for the next (Parada et al., 2010).

2.6 Epibionts and pathogens

Hydrozoans, bryozoans, polychaets, and acorn barnacles are commonly found on large crustaceans as epibionts (Savoie et al., 2007). The parasitic dinoflagellate *Hematodinium* sp is the main pathogen found on snow crab. The commercial and ecological significance of these parasites are based upon their ability to impact the size and structure of important host, but mortalities are centered on juveniles and females (Stentiford and Shields, 2005). *Hematodinium* live in the hemolymph (blood) and causes a condition known as bitter crab disease (BCD) known from species such as snow crab (*Chionoecetes opilio*), tanner crab (*C. bairdi*) and Norway lobster (*Nephrops norvegicus*). This disease can kill the crab but also causes the crabmeat to have a bitter flavor, hence the name bitter crab disease. Infected crabs can be identified from their opaque white shell (not to be confused with white/molting crabs) and general poor condition (Anon., 2005a; Shields et al., 2005). Diseased crabs display signs of acute morbidity, such as dropping limbs and mouthparts and the hemolymph is milky white in color (Taylor and Khan, 1995).

Since 1985 BCD has been an increasing problem in Alaskan tanner and snow crab populations. The prevalence of BCD showed an alarming increase in Newfoundland from the 1990s until 2003 (Pestal et al., 2003). Prevalence and distribution of the parasite and its controlling factors are poorly understood, although it seems to be density regulated. The effect of BCD on catchability is poorly understood, however it has been speculated that increased nutritional demands increase the catchability of infected crabs in baited traps (Mullowney et al., 2011). Outbreaks of *Hematodinium* species often occur in constricted areas or areas with entrained water masses such as lagoons, embayments or fjords with shallow sills. Research has shown a higher prevalence of BCD at depths >200 meters, with the highest prevalence at >250 meters (Shields et al., 2005).

2.7 Trophic role and feeding

Feeding habits as well as their role as a prey, are important factor in determining the snow crabs role in and effect on the ecosystem. Snow crab interacts with habitat and its inhabitants in a variety of ways, including providing habitat for smaller invertebrates, and competing for food and shelter. There is a tradeoff balancing the ratio of energy content consumed and energetic cost of handling prey, and an interest in choosing optimal prey (Elner and Hughes, 1978).

2.7.1 Diet

Snow crabs have two distinct methods of feeding. One involves capturing their prey with their chelipeds (front claws), then grasping and tearing it apart, and finally transferring the food item to the mouth. The other method consists of sieving organisms using third maxillipeds following the scooping-up of sediments by the lesser chela. Cuticle creates a set of hard teeth in the head region of the crab, which allows for efficient chewing and grinding of materials to increase the surface area and absorb as many nutrients as possible. The mouth of the snow crab has three sets of jaws, one for holding the food while the other two grind the materials. *Chionoecetes opilio* possess a double stomach, an intestinal tract and an anus. The first stomach is used to pulverize and break down the food source. The second stomach possesses digestive enzymes and juices that help with breaking down the food. As snow crabs are primarily carnivorous, and consume food sources with high nutritional value the intestinal system is fairly short and is lined with finger-like projections called villi, which create greater surface area for optimal nutrient uptake. Indigestible materials are then passed through the anus and out of the crab's body (Dorit et al., 1991).

Decapods are successful and versatile predators, preying at more than one trophic level, mostly on benthic invertebrates, but occasionally consuming algae or detritus. Some species, have demonstrated large effects on benthic community structure, either as keystone species or by inducing trophic cascades (Boudreau and Worm, 2012). Little information is available on snow crab's selection of habitat and food resources, as most studies of feeding is limited to stomach contents (Wieczorek and Hooper, 1995). They find the majority of prey on the substrate they live on and burrow into the substrate for protection from predators. Snow crabs are known to feed on algae, mollusks, crustaceans, polychaets, echinoderms and fishes (Lovvorn, 2010). Normally one food group is dominant, varying across regions. Stomach contents from the northeast Newfoundland Shelf reflected a broad spectrum of prey types, with about three-seven prey types commonly occurring in most stomachs, with a large contribution from shrimp and fish. More than 80% of consumed prey items consist of taxa with calcareous shells, including mollusks and echinoderms (Squires and Dawe, 2003). Feeding on taxa with calcareous shells may have a role in achieving calcium carbonate needed for molting (Zanotto and Wheatly, 2002).

There are some differences in diet between sexes and size-classes of snow crab, which can be attributed to larger and stronger legs and chela (claws) of large males, which result in greater mobility and strength. Larger crabs consume larger preys that require greater handling ability such as harder-shelled bivalves and gastropods, larger polychaetes, fish and other snow crabs. Smaller crabs consume softer, more easily manipulated prey, such as small bivalves with thin or incompletely calcified shells (Lovrich and Sainte-Marie, 1997; Squires and Dawe, 2003; Kolts et al., 2013).

In the Barents Sea, a negative correlation has been found between biomass of snow crabs and shrimp, which can be explained by predator-prey interactions. Still, shrimp are not a dominant food item, and in comparison to fish species, the snow crab has a negligible effect on shrimp (Dvoretsky and Dvoretsky, 2015). In the northeast Newfoundland shelf the predominant fish prey species was capelin (*Mallotus villosus*), as well as Atlantic spiny lumpsucker (*Eumicrotremus spinosus*) and redfishes (*Sebastes*). Observations of capelin remains indicated that at least some of the capelin likely resulted from predation on live fish rather than scavenging of dead individuals. It is not possible to determine the relative importance of these prey types in the snow crab diet based on the stomach contents data (Squires and Dawe, 2003). Consumption of capelin eggs by red king crab in the Barents Sea is considered too low to significantly regulate the capelin population (Anisimova et al., 2005; Mikkelsen, 2013).

Dvoretsky and Dvoretsky (2015) investigated if red king crab and snow crab has had an effect on commercial fish and shrimp in the Barents Sea. They documented no negative impact on commercial fish populations, and all correlations were positive. They concluded that both the red king crab and snow crab has not adversely affected major fish stocks, while resulting in positive economic benefit. They did, however, not rule out negative effects on other parts of the ecosystem, and recognize that the snow crab is too new to see long-term effects.

2.7.2 Cannibalism

Cannibalism of early benthic stages by larger snow crabs may represent an intrinsic density-dependent mechanism for maintaining regular recruitment periodicity (Squires and Dawe, 2003), explaining the observed cyclical fluctuations. Conspecifics as prey in this way benefits as a source of energy, and as a mechanism to reduce the number of mating competitors. Cannibalism in snow crab may occur only occasionally because small crabs and large crabs are not found in the same locations. There is a marked segregation by size in the distribution except late winter and early spring migrations. Habitat segregation might rather be a result of either large crabs forcing smaller crabs in marginal habitats or eliminating smaller crabs through cannibalism (Dutil et al., 1997). Lovrich and Sainte-Marie (1997) suggest that large pre-recruits are not subject to intraspecific predation (cannibalism), even during their vulnerable molting period. This is consistent with the fact that premolt adolescent males migrate to remote shallow grounds where the density of large, hard-shelled adult males and predatory fish may be very low, presumably to escape intra- and interspecific predation at molting. In stomach content analyzed by Lovrich and Sainte-Marie (1997) conspecifics other than exuviae[6] occurred in stomachs of 7.2% of wild caught *C. opilio* and were probably derived through predation rather than scavenged (necrophagy). Studies suggest that the importance of scavenging has been overstated and marine carnivores derive their food mostly through predation (Britton and Morton, 1994).

[6] Exuviae is the remains of exoskeleton and related structures from molting.

2.7.3 Snow crab as prey for cod

The decline and collapse of the Atlantic cod (*Gadus morhua*) in the northwest Atlantic Ocean over a period of years coincided with an increase of the snow crab population, which resulted in a changed ecosystem (Frank et al., 2005). Cod predation is primarily directed towards small, immature snow crabs. In eastern Canada the range of snow crab sizes found in cod stomachs ranged from 6 to 70 mm CW. Periods of high consumption of snow crab by cod appear to occur when there are large peaks in abundance of young instars on the bottom, thus predation by cod may stifle increases in abundance of adult crabs resulting from recruitment waves (Chabot et al., 2008). A negative correlation between the abundance of commercially sized snow crab and the abundance of cod three to six years previously have been registered (Bailey, 1982 in Orensanz et al., 2004). Snow crab abundance appears to be largely influenced by temperature during the early post-settlement years and becomes increasingly regulated by top-down mechanisms, such as cod predation, during the years approaching fishery recruitment (Boudreau et al., 2011).

2.8 Snow crab fisheries and management

Snow crab fisheries have been economically important in the Alaskan Bering Sea and eastern Canada, but all substantial fisheries are rather recent, starting with the Canadian in the 1960s (Anon., 2005a). The Canadian and the Alaskan Bering Sea fisheries for snow crab will be described after some general comments on specific management challenges for snow crab and an account of ecosystem based management, a dominating paradigm within fisheries management. As mentioned, snow crab populations in native areas have fluctuated in size more or less systematically. In the northwest Gulf of Saint Lawrence, strong year classes recur approximately every eight years. Each year class impacts the spring fishery there about ten years after the benthic settlement (Sainte-Marie et al., 1996). Three management strategies are traditionally considered when managing fluctuating resources (Anon., 2005a):

- Stabilize the exploitation rate (proportion of removed commercial biomass)
- Stabilize catch
- Stabilize escapement – allow a constant residual biomass to remain after the fishery

A second specific challenge is that only a small fraction of snow crab populations are commercially interesting, that is large crabs of good quality, which in practice means morphometrically mature males. The first year after terminal molt the crabs are white and of low commercial quality, while they generally have premium quality the second year after molting. Thereafter the quality degrades by loss of nonregenerating legs and fouling of carapace. Thus the commercially interesting part of the population is rather narrow. Non-targeted crabs, such as undersized males, female and molting crab are discarded. As the market price is higher for snow crab greater than 102 mm carapace width (CW), also legal sized crab smaller than 102 mm CW are often discarded, this is known as high grading. Discarding live crabs involves a substantial amount of "discard mortality". Discard mortality can be decreased by decreasing air exposure time and drop height. Soft-shelled snow crab, or white crab as they are also known, is the future recruitment to sustain the commercial fishery and to mate with the available females, thus it is especially important to conserve them (Anon., 2005a). As snow crab has been affected by disease in several areas, it is of interest to note that the common practice of releasing females is not advantageous when a fishery is affected by a parasite, rather it is advisable to retain females in the catch in most cases (Kuris and Lafferty, 1992).

Fishing can change a population as it is acting in conjunction with, or in opposition to natural factors, modifying the context for sexual competition, mate choice, and sexual conflict. A male-focused size-selective fishery includes the potential to reduce average size of the males in the population, the density of males in the population, and/or raise the ratio of females to males. All of these effects may change the mating dynamics of the population by reducing the amount of sperm that males provide to females and decreasing the number of males available for copulation (Carver et al., 2005; Fenberg and Roy, 2008; Sainte-Marie et al., 2008).

It is generally accepted that the structuring and functioning of marine ecosystems change through time, altering the foundations of fish stock productivity (Vert-Pre et al., 2013). In this lays the recognition that social, legal and economic aspects of resource management must be coupled with an understanding of ecology and resilience; that is, the extent which ecosystems can absorb natural and human disturbances and continue to regenerate without slowly degrading or unexpectedly flipping into alternate states. Ecosystem based management includes effect of targeted species and fishing activities on other components of the ecosystem (Hughes et al., 2005). Taking the ecosystem into account in fisheries management has been promoted and agreed upon in several international treaties, intergovernmental organizations and codes of conduct for the last 25 years or so, but operationalizing such an approach has proven difficult (Tudela and Short, 2005). The FAO Committee on Fisheries (COFI) has adopted a framework called the Ecosystem Approach to Fisheries (EAF) (Anon., 2003). One way is to include ecosystem drivers of stock productivity either in stock assessment models or in harvest control rules. Before setting a quota for the Barents Sea fishing for capelin, Russia and Norway sets aside the estimated food requirement for cod to ensure a healthy and productive cod stock (Skern-Mauritzen et al., 2015). For snow crab shifts in productivity can be addressed by incorporating an algorithm, such as Rodionov's sequential t-test analysis for regime shifts (STARS; Rodionov and Overland, 2005), into harvest control rules (Szuwalski and Punt, 2013).

The evolution of a fishery is usually described in six phases: Predevelopment, growth, full exploitation, overexploitation, collapse and recovery (Csirke and Sharp, 1984). Developing fisheries will almost always experience declining catch rates, non-sustainable levels of catch and the need to reduce fishing mortality after the initial growth in catch and fishing effort. The equilibrium-oriented view of the gradual increase to an optimum level of catch is rarely if ever achieved in real fisheries. Flexibility in fishing pressure is essential for good management of fisheries (Hilborn and Sibert, 1988).

2.8.1 Profile: Canadian Northwest Atlantic

During the last 30 years the Canadian coastal snow crab fishery has grown to be an important income for the country and fishers. It has been fished commercially in eastern Canada since the late 1960s, and constitutes one of the most commercially valuable Canadian fisheries. Total value of all Canadian snow crab landings was CAD $623.3 million in 2004. The snow crab fishery in Newfoundland and Labrador in 2012 landed 50 514 tons worth CAD $217 million (Winger et al., 2015).

Catches began to drop throughout the Atlantic region during the mid 1980s. Total Atlantic landings fell sharply from 48 300 tons in 1982 to 22 400 tons in 1989. By 1991-92 the landings had recovered to early 1980s levels, and a period of unprecedented growth started, as the cod fishery collapsed. Expansion was lead by a snow crab biomass increase and an expansion of fishing effort in boats and areas. From 1992 to 2002 snow crab landings almost tripled from 36 500 tons to 106 000 tons. The entrance of thousands of new licenses in coastal areas pushed the larger inshore vessels to concentrate fishing efforts on grounds further offshore (Anon., 2005a). With over 3400 licensed fishing enterprises in Newfoundland and Labrador in 2009, the number of individuals participating is estimated to be 10 000, with 1.2 million active traps fished each year (Anon., 2009a).

Medium-sized inshore fishing vessels (shorter than 65 feet) characterize the Canadian snow crab fishery. The fishing is primarily conducted with baited conical shaped pots, smaller and lighter than the ones used in the Alaskan fishery. Most vessels operate in the bays and coastal regions and return to port daily, but some vessels fishing up to and beyond 200 nautical miles conduct trips up to five days. The snow crab is to be landed live, thus duration of fishing trips is limited (Anon., 2005a). It is a male-only fishery, subject to a minimum legal size of 95 mm CW (the females do in general not grow this large), to allow all males to reach reproductive age. As such the fishery prosecutes the sexually most competitive segment of the male breeding population. Less than 100% of snow crabs with carapace width (CW) above 95 mm are harvested, allowing some mature males to mate with available females (Anon., 2005a).

Fishing commences in early spring and continues to late summer and early fall. The fishing seasons are established each year as part of the annual harvesting plans for each fishing area, and varies significantly depending on area. In the Canadian Gulf of St. Lawrence the fishery is conducted in spring, April to early summer and has the advantage that it avoids harvesting during the mating season of primiparous spawners and molting snow crab. The Fisheries Resource Conservation Council (FRCC) recommends a snow crab season opening as close as possible to April 1st and close as close as possible to July 15 (Anon., 2005a).

The causes of the decline in catches in the 1980s remain uncertain, but the industry was generally undisciplined with a “race for fish” and high incidence of soft-shelled crab. Thus, fishing practices may have been a factor. Following an increased effort was focused on snow crab fishery management, and individual boat quotas began to be introduced. Early in the development of the fishery, Fisheries and Oceans Canada (DFO) banned the use of trawls to harvest snow crab and limited the number of traps per vessel. A minimum size limit was introduced at CW 95 mm, making it illegal to land smaller-sized crabs. In addition regulations set the trap mesh-size large enough to allow the female snow crab to escape. Excluding females from the harvest became a fundamental principle of harvesting (Anon., 2005a).

Harvesters are input regulated with a license scheme and a restriction on number of traps per vessel and restraints on fishing periods. Harvest is output regulated with restrictions against harvesting molting crabs and an area-based total allowable catch (TAC), in compliance with a constant exploitation rate strategy (Anon., 2005a). From 2009 snow crab in the

Newfoundland and Labrador Region is managed through an Integrated Fisheries Management Plan. Individual quotas were implemented in 1995, and currently all fleets are fishing under this management regime (Anon., 2009a).

The FRCC has concluded that the main threat to snow crab conservation in Atlantic Canada and Québec is the catch and discarding of immature male snow crab and molting crab. A goal is to allow males to mate once and be harvested as valuable commercial size snow crab. This can be achieved through (Anon., 2005a):

- Better matching the fishing season with the molt cycle of snow crab
- Closing areas where molting snow crab represents a high percentage of the catch
- Careful handling of snow crab that will be discarded to reduce post-harvest mortality
- Improved selectivity of fishing gear such that immature and female snow crab are left on the bottom
- Development of protected areas to enhance the long-term sustainability of snow crab.

Ecological, economic and social sustainability is a goal in the Canadian fishery. As with all fisheries, both selectivity and ghost fishing is a challenge for the Canadian snow crab fishery. A particular type of biodegradable twine to avoid ghost fishing is now a mandatory condition of license for all fishing enterprises targeting snow crab in the Canadian province of Newfoundland and Labrador (Winger et al., 2015).

2.8.2 Profile: Alaskan Bering Sea

Historically the eastern Bering Sea crab fishery has been the largest and most valuable crab fishery in the USA, with snow crab as a component (Hardy et al., 2011). The snow crab fishery began in 1977, where landings increased from about 20,000 tons in the early 1980s to 150,000 tons annually by 1991. In the 1990s catches declined to 12,000 tons and in 1999 the stock was declared overfished, but poor recruitment and shifting environmental conditions may have contributed to the collapse (Anon., 2005a). A rebuilding harvest strategy was developed and adopted in 2000. The stock was declared rebuilt in 2011 with an estimated biomass of 447,400 tons. Retained catch in 2013/2014 fishery was 24,480 tons, with a total catch estimated at 28,200 tons (estimated discard mortality included). The estimated number of males with CW larger than 101 mm was 138.5 million in 2014. The average size of retained crabs has remained fairly constant over time ranging between 105 mm and 118 mm (Turnock and Rugolo, 2014).

The Bering Sea crab fishing fleet is comprised of larger vessels than the Canadian, averaging about 115 feet in length, typically with a crew of five. The gear used is steel-framed pots measuring about 2 meters square by 75 centimeters high, weighing about 350 kilograms. Until 2005 the fishery was largely an open access fishery, heavily overcapitalized by both harvesting and processing capacities. The management was based on a TAC, a season start date and closing the season at a date of projected quota achievement. It developed into a "derby style" fishery operation, where vessels operated at maximum capacity for the whole season opening in an attempt to harvest as much as possible in competition with every other vessel in the fleet. During the 2004-2005 season the fishery lasted for only four days. Working in the Bering Sea crab fisheries have been known as the most dangerous occupation in the United States. From 1991-2005 26 vessels sank and 77 deaths occurred in these fisheries. The nature of this fishery has changed after the implementation of an individual transferable quota regime (Hughes and Woodley, 2007).

Currently the Eastern Bering Sea and Aleutian Islands king- and snow crab fisheries are managed through a joint fishery management plan. The management plan consists of output control in the form of harvest control rules such as an overfishing level, acceptable biological catch and a minimum stock size threshold. The primary output control is in the form of TAC, with minimum size and sex restrictions. This is combined with input controls through seasonal as well as area closures and a license and permit regime. In addition fishers are required to install escape panels and rings on their pots to prevent ghost fishing and reduce bycatch. Minimum legal CW is 78 mm, however the market only accepts animals with CW greater than 101 mm (Turnock and Rugolo, 2014). Fishing seasons are used to protect crabs during molting and mating portions of their life cycle (Anon., 2011). The 2014-2015 season opened October 15^{th} and lasts through May 15^{th} in the eastern part of the district and May 31^{st} in the western part (Anon., 2014g).

2.9 Non-native species in marine ecosystems

2.9.1 Terminology and ecology

The terminology used to describe non-native species is inconsistent and inaccurate in the literature, but is important, as it plays an important role in the understanding and perception of the Barents Sea snow crab. Several terms are used to describe species that have not previously been found in a habitat. To avoid misunderstandings this thesis uses terminology described by Falk-Petersen et al. (2006). Non-native species are defined as species whose change in distribution has been caused by humans (directly or indirectly). Alien is often used as a synonym to non-native, but as this word has several connotations, its use is discouraged. However, the definition of alien has legal implications (section 2.9.2). Immigrant species denote organisms that become established in new areas independent of human introductions, that is through their own migratory abilities. Whether a species is a non-native or an immigrant does not necessarily have any ecological implications (Falk-Petersen et al., 2006).

Other terms are used to describe the impact of organisms. Invasive species are non-native organisms expanding their range on their own. Pests are invasive species that reduce the availability, quality or value of some human resource, and can be considered a socioeconomic term (Falk-Petersen et al., 2006). A more ecologically based term is transformers. Transformers change the character, condition, form or nature of ecosystems over a substantial area relative to the extent of that ecosystem (Wells et al., 1986; Falk-Petersen et al., 2006).

The establishment of a non-native species can be seen as a disturbance adding stress to the ecosystem. Trends expected in stressed ecosystems include changes in energetics, nutrient cycling, and community structure and function (Odum, 1985; Molnar et al., 2008; Lehtiniemi et al., 2015). Non-native species is considered the second most important cause of biodiversity loss globally, second to direct habitat destruction (Barnosky et al., 2011). As native organisms have not evolved together with the non-native organism, they may lack evolutionary responses to predation, and be more vulnerable to predation than similar species in the native ecosystem of the non-native species. This can be called an evolutionary trap (Schlaepfer et al., 2005). In addition, effects of predation by non-native species may cascade down the food web[7], and molluscivore predators have shown to alter pore-water biogeochemistry and affect the toxicity of the environment (Van Gils et al., 2012). Crustaceans are among the most successful marine invasive species, sometimes reaching extremely high population densities. This subphylum often causes a substantial impact due to their omnivorous role leading to shifts in energy fluxes, nutrient cycles and thus, affect critical ecosystem services, biodiversity and fisheries (Hänfling et al., 2011).

[7] Trophic cascades are indirect effects of changes in the abundance of individuals in one trophic level on other trophic levels (Pace et al., 1999).

2.9.2 Obligations to deal with non-native species

Several international treaties deal with the spread of non-native species. Only the most important treaties and laws to consider for Barents Sea snow crab will be dealt with here.

The United Nations Convention on Law of the Sea (UNCLOS) gives states an obligation to *prevent, reduce or control pollution of the marine environment resulting from … or the intentional or accidental introduction of species, alien or new, to a particular part of the marine environment, which may cause significant and harmful changes thereto* (part XII art. 196). States shall take, individually or jointly as appropriate, all measures consistent with UNCLOS that are necessary, *using for this purpose the best practical means at their disposal and in accordance with their capabilities, and they shall endeavor to harmonize their policies in this connection* (art. 194). Russia is also a contracting party to UNCLOS.

Norway and Russia are also contracting parties to the Convention on Biological Diversity of 1992 (CBD), which requires the states to as far as possible and as appropriate (article 8(h)) *control or eradicate those alien species which threaten ecosystems, habitats or species*, without giving a definition of *alien species*.

Norwegian law on non-native species is primarily founded in the Norwegian Nature Diversity Act of 2009, which states that no organisms may be imported no Norway without permission. It says nothing on how to deal with non-native species, but clearly states that the goal is to protect the functioning, structure and productivity of ecosystems, and to protect species (does not apply to non-native species) and their genetic diversity.

Norwegian management of living marine resources is primarily founded in the Marine Living Resources Act of 2008, which goal is to secure a sustainable and socioeconomically profitable management of the wild marine resources and its genetic material, and contribute to securing employment and settlement in the coastal communities. In this lays that Norway should follow a precautionary approach in line with international treaties and guidelines, and emphasize the ecosystem approach to management. The government should only take management measures necessary to secure a sustainable management.

2.9.3 Tools to manage pests

If a species is considered a pest, control strategies should be considered. In this section available management tools are reviewed. Management strategies is of course, dependent on the nature of the species, and there is a substantial difference in bringing a large, well established, broadly distributed population of a pest under control, versus a small less established and very concentrated population.

Marine ecosystems are complex adaptive systems with scales from individuals to the dynamics of whole system. In such systems, small changes can be magnified, facilitating regime shifts and collapses. Protection of the services these ecosystems provide must therefore maintain adaptive capacities of these systems by preserving a balance among heterogeneity, modularity, and redundancy; tightening feedback loops. The challenge for management is to strengthen the robustness and resilience of these systems and preserve their ability to provide ecosystem services (Levin and Lubchenco, 2008). Management of biological systems involves the application of ecological and evolutionary principles within a decision theory framework. All management options, including doing nothing, should be carefully considered (Shea et al., 2000). In cases where invasive species cannot be eradicated, management efforts should not pursue futile attempts to restore 'pristine' or 'ancestral' conditions (Schlaepfer et al., 2005).

Different control strategies include physical removal, biocide, biological control and genetic modification, and should be evaluated according to reversibility and risk of non-remediable collateral damage (Thresher and Kuris, 2004). Physical removal of each individual involves a significant cost, as the stock biomass (and density) decrease, more effort is needed to catch the next snow crab, and the cost per unit catch will increase (Smith, 1969). In addition for species such as snow crab, only a minor part of the population is thought to be commercially interesting, and the price is likely to decrease as supply goes up. Thus, it cannot be expected that the market will pay for such a measure. Biocides can be both pest-specific and non-specific toxins and are not considered suitable to large-scale operations (Thresher and Kuris, 2004). Often a variety of measures are combined, in what is known as integrated pest management (Eilenberg et al., 2001). Unless successful biological controls are developed, any management practice that relies upon perpetual intervention (e.g. application of biocides; physical removal) is likely to falter at some point in the future because of limitation of resources or changing priorities, essentially rendering all past efforts and investments moot

(Schlaepfer et al., 2005). Intensive management with intent to eradicate invaders is also likely to fail unless it precludes re-invasions by addressing the ecological conditions or vectors that made the invasion of the non-indigenous species possible in the first place (Byers, 2002).

Biological control

Non-native species commonly have fewer natural enemies than native species (Torchin et al., 2003). One management strategy that is commonly used in agriculture and aquaculture, and to some extent in larger terrestrial ecosystems, is biological control. Eilenberg et al. (2001) define biological control (biocontrol) as "the use of organisms to suppress the population density or impact of a specific pest organism, making it less abundant or less damaging than it would otherwise be". A major us of biocontrol agents is the control of terrestrial invertebrates using predators, parasitoids and pathogens (Eilenberg et al., 2001).

Some of the relevant natural enemies that can be used in marine biocontrol of crabs are parasitic castrators (Lafferty, 1993) and symbiotic egg predators (Goddard et al., 2005). Several strategies can be used, including inoculation, which control the pest for an extended period, but not permanently. It is very important that a biocontrol agent does not worsen the condition of the ecosystem; therefore a prerequisite should be that the biocontrol agent only targets the pest species, while other species are unaffected. The European green crab (*Carcinus maenas*) has spread from Europe to Australia, Japan, South Africa and both coasts of North America. It has been blamed for the collapse of bivalve fisheries on the North American east coast, and is feared to outcompete migratory bird populations on the west coast (Grosholz and Ruiz, 1996). It is thus considered a pest that should be eradicated or controlled. Several biocontrol agents have been proposed. This includes viruses, dinoflagellates, ciliates, nemerteans and rhizocephalans (Thresher et al., 2000). Many of them were concluded to be insufficiently host specific, virulent or too likely to evolve to exploit new hosts (Secord, 2003). While some have argued that nemerteans are insufficiently host specific, Kuris et al. (2005) argues that there is strong circumstantial evidence for host specificity of nemertean symbiotic egg predators. The European parasitic castrator (*Sacculina carcini*), a rhizocephala, has been mentioned as the most seriously considered biocontrol agent. It parasites both male and female crabs, castrating them and behaviorally feminize the males (Thresher et al., 2000). It reduces the fertility rate substantially, as well as reducing crab size and population biomass. The host range has in laboratory experiments shown that it settles also on native crabs in Australian and Californian waters (Kuris et al., 2005). Secord (2003) concludes that biocontrol with the parasitic castrator is a bad option, as biocontrol in marine habitats poses many more uncertainty and has a much sparser history than its counterparts on land. Kuris et al. (2005) are positive toward the potential of *Sacculina carcini*.

Evolutionary management

Native species, under the right circumstances, may either evolve or learn mechanisms to cope with the invaders (e.g. through chemical defenses, improved competitive abilities, predator-avoidance behavior) and ultimately persist on their own. This offers the possibility of manipulating native species to meet the conservation goal of long-term persistence, so-called 'evolutionary enlightened management'. A management plan of finite duration that subsidizes the survival of native species long enough to allow a transition to their novel selective regime is likely to be more cost-effective and successful in the long-term than attempts at eradication (Schlaepfer et al., 2005). This can be done by a mix of refugium and non-refugium habitat, where natural selection will favor the emergence within the prey population of traits that are likely to facilitate their long-term co-existence with the novel predator. Management efforts could focus on temporarily reducing the abundance, but not eradicating, an evolutionarily novel predator, as the goal is to maintain sufficient selective pressure to favor the emergence and spread within the prey population of traits that are likely to facilitate their long-term co-existence with the novel predator. Once this has been achieved, management efforts geared towards suppressing the abundance of the introduced predator would no longer be necessary (Schlaepfer et al., 2005). A second approach to counteract the evolutionary trap the native species experience with a novel predator is to actively manipulate the genetic composition of native populations to increase their rate of evolution. This could be carried out by inoculating 'naïve' populations with individuals from 'experienced' populations that contain morphological or behavioural traits that are potentially useful (Schlaepfer et al., 2005). The use of evolutionarily enlightened management represents a way to potentially ensure the co-existence and long-term survival of all native and non-native species (Schlaepfer et al., 2005).

2.9.4 The red king crab example

We have not seen many examples of non-native commercially interesting crustaceans entering northern waters. As the red king crab is the closest comparable example to snow crab it will be accounted for here. The red king crab (*Paralithodes camtschaticus*) is among the largest arthropods of the world. The red king crab has a maximum life span of about 20 years, can reach weights up to 10 kilograms, and has a pelagic larval stages that last for about two months (Jørgensen et al., 2005).

Soviet scientists introduced red king crab to the Barents Sea intentionally over from 1961 to 1969 to provide a new valuable fishery (Orlov and Ivanov, 1978). Prior to the introduction of the red king crab, no commercial crab species were found in the Barents Sea. Red king crab established and eventually spread into Norwegian Exclusive Economic Zone (EEZ). Initially Norwegian and Soviet (later Russian) authorities focused on building up a commercially viable population (Falk-Petersen, 2012). In the 1990s the crab population in Norwegian waters was growing to a substantial amount and starting to constitute a problem to other fisheries (Anon., 2007).

In addition it was discovered that biodiversity has been reduced in areas where red king crab has established and the benthic community has changed (Oug et al., 2011). This indicates, according to Falk-Petersen and Armstrong (2013) that ecosystem services are impacted. The red king crab preys upon the Icelandic scallop (*Chlamys islandica*) as well as the eggs of commercially important capelin (*Mallotus villosus*) and Arctic lumpsucker (*Cyclopteropsis macalpini*) (Anisimova et al., 2005; Mikkelsen and Pedersen, 2012; Mikkelsen and Pedersen, 2014). The capelin stock plays a key role in the Barents Sea ecosystem as an important prey species for other fish stocks, seals, whales and sea birds – in addition to supporting a fishery of catches up to three million tons (Falk-Petersen and Armstrong, 2013)

In the early 2000s the red king crab became an important economic resource for small fishing communities along the coast. Simultaneously there were growing concerns on the ecological impact of the new crab species establishing along the coast, and Norwegian obligations to protect biodiversity were stressed. Due to the sensitivity and complexity of red king crab, Norwegian authorities have released two white papers on the red king crab (Anon., 2007; Anon., 2015e). In 2004 Norway implemented a western limit of 26°E for king crab expansion in 2004; east of this limit the population is managed as a commercial fishery. The overarching objective for Norwegian management of red king crab is to “as far as possible limit a further spread of red king crab in Norwegian waters, and keep the population outside the commercial harvest area at the lowest possible numbers” (my translation) (Anon., 2007). The World Wide Fund for Nature (WWF) has demanded that the government remove all red king crabs. According to WWF, Norwegian authorities management of red king crab is in violation with the Convention on Biodiversity (Anon., 2010). Norwegian authorities considere all obligations catered for within the current management regime (Anon., 2007).

For many years Norway and Russia had a common management of red king crab, but since 2007 the countries have managed the crab separately within their respective exclusive economic zones. In Russia the species has been seen exclusively as an economic resource and not as a threat to the ecosystem (Anon., 2007).

According to national statistics, the total landed value of red king crab in Norway was close to NOK 130 million in 2009, involving over 500 coastal fishers (Falk-Petersen and Armstrong, 2013). For many fishers this is the most economically important fishery, which supports many small local communities in northern Norway with income. Minister of Fisheries Elisabeth Aspaker stated at the opening of the 2014 king crab conference, that the management of the red king crab has been a success the last two years with a targeted fishing of king crabs west of North Cape. It is not considered possible by politicians, researchers or managers to eradicate such a marine species (Minister of Fisheries, 2014).

2.10 Rights to harvest and manage in the Barents Sea

The snow crab population is seen as an interesting economic resource, with many actors (fishers from several countries) interested in participating in a fishery. Thus, it is vital clarify who holds the right to fish and manage the Barents Sea snow crab. The right to exploit maritime resources is regulated by international law (Churchill and Lowe, 1999; Pedersen, 2008). Of relevance for snow crab in the Barents Sea is the concepts and implications of exclusive economic zones, the Barents Sea continental shelf, high seas and the Svalbard fishery protection zone. Which zones snow crab adheres to depend on the definition of snow crab as sedentary or not. The implications of both alternatives will be reviewed with here, while the likely outcome will be discussed in chapter 5.

States have a legal jurisdiction of both a personal and a territorial character, which means that it can regulate activities within its territory as well as its vessels. In that case Norwegian laws apply to Norwegian vessels anywhere in the world, and all vessels within Norwegian territory. The United Nations Convention on Law of the Sea of 1982 (UNCLOS) recognized the establishment exclusive economic zones (EEZ) 200 nautical miles (nm) outside coastal states, where the states have full sovereignty over resources. Both Norway and Russia are contracting parties to UNCLOS, and in 2010 the border between Norway and Russia was finalized through the Barents Sea Treaty (Henriksen and Ulfstein, 2011) as illustrated by the thick black line in figure 1.2. There is a section in the central Barents Sea that is not subject to EEZs, called the Loophole. The water column here is high seas (section 2.10.3), but the border is also drawn through this area, as the sea floor belongs to the continental shelf (section 2.10.2). In addition the Svalbard fishery protection zone is subject to a disputed legal regime (section 2.10.4).

Snow crab is found in all zones in the Barents Sea, with the largest fraction in Russian EEZ and the majority of fishing presently taking place in the Loophole. It is possible that commercially interesting snow crab concentrations will facilitate fishing in other areas in the future, such as Norwegian EEZ and the Svalbard fishery protection zone.

The Straddling Fish Stocks Agreement (Fish Stocks Agreement) is a multilateral treaty added as a supplement to UNCLOS in 1995 to *ensure the long-term conservation and sustainable use of straddling fish stocks and highly migratory fish stocks through effective implementation of the relevant provisions of the Convention*, and enhance the cooperative management of fisheries resources that span wide areas, and are of economic and environmental concern to a number of nations. Straddling stocks are fish stocks that migrate through, or occur in, more than one EEZ. What is defined by UNCLOS as sedentary species (section 2.10.1), are not subject to the Fish Stocks Agreement.

2.10.1 Continental shelves

For some resources, the rights of the coastal states go even further than the EEZ 200 nm. For living resources, this comprises what is called sedentary species. Although states' rights over the outer continental shelf (outside the 200 nm EEZ) are similar to the rights within the EEZ, there are several restrictions to the rights, as the water column above the continental shelf is regulated by the high seas regime. The continental shelves have been subject for several negotiations during the 1900s, and are now bound by UNCLOS part VI (Mossop, 2007).

Below the entire Barents Sea water column there is a continental shelf belonging to Russia and Norway, including in the Loophole. This was declared in 2009 when the Commission on the Limits of the Continental Shelf accepted Norway's continental shelf data (Anon., 2009b). The border Norway and Russia agreed upon in 2010, was not only a border for the EEZ, but also subject to the continental shelf. This implies that the Loophole, which is part of the continental shelf, is divided between Norway and Russia.

On the outer part of the continental shelf, the coastal state's rights become more ambiguous (Mossop, 2007). The coastal State exercises sovereign rights for the purpose of exploring and exploiting its natural resources on the continental shelf. The natural resources referred to in part VI of UNCLOS includes living organisms belonging to sedentary species, that is to say, *organisms which, at the harvestable stage, either are immobile on or under the seabed or are unable to move except in constant physical contact with the seabed or the subsoil*. Unlike the EEZ regime, if a coastal state does not exercise its rights to exploit the resources on the continental shelf, it is not required to share those resources with another state (UNCLOS article 77).

Long before the appearance of international law on this subject, there has been an opinion that sedentary fisheries were an exception to the rule that fishing in the high seas was free to all. Sedentary species have by many been considered as belonging to the soil or bed of the sea, rather than to the sea itself, and in this way being analogous to crops in a field (Young, 1961). In nature there is no simple line of demarcation between sedentary organisms and other, rather a long series of gradations from the unquestionably fixed to the sea floor at one extreme to the unquestionable free from the sea floor at the other. While some species, such as corals and clams, clearly fit into the category, there is a gray area surrounding organisms such as crabs, scallops and lobsters (Young, 1961; Mossop, 2007). This definition has been subject to several disputes, one such example was "the lobster war" between Brazil and France in the 1960s, where France contested that a lobster population did not constitute a part of the natural resources belonging to the continental shelf. Thus, France dispatched a warship "to protect French nationals and to ensure freedom of the seas". The countries never agreed, but Brazil gave French vessels permission to fish parts of the stock (Azzam, 1964). In the Japan-United States of America agreement on king crab fishing off Alaska (1965), Japan and the USA did not agree upon if king crab is a natural resource of the continental shelf over which the coastal state has exclusive jurisdiction, or a high seas resource. These parties agreed to disagree, but found a way of cooperating on the management of the stock. The UK position on sedentary species and crustaceans has been expressed as follows: lobsters swim and crabs do not; therefore crabs are within the definition of sedentary species in UNCLOS and lobsters are not (Ikirodah, 2005).

There does not seem to be any thorough legal assessments on whether snow crabs are legally sedentary or not, but according to a MSC fishery assessment for the Scotian shelf snow crab trap fishery, snow crab is a sedentary species (Garforth et al., 2012). In addition Fisheries and Oceans Canada states that the Northwest Atlantic Fisheries Organization (NAFO) does not cover snow crab because it is a sedentary species (Anon., 2015f). From this it seems as there may be a consensus, but as it for most cases is of no relevance, as most resources are harvested within EEZs, and the definition "sedentary" is of no importance, it is of greater importance to evaluate this for the Barents Sea snow crab as the primary fishing ground is in the Loophole. A single word decides if snow crab should be managed as a fish stock in international waters, or as a resource of the continental shelf, such as minerals and oil.

There is a clear impracticability in managing mobile fish and sedentary species in the same waters under different regimes. Interference and conflict seem inevitable (Young, 1961). In addition there is a challenge for coastal states to monitor and enforce rules on the outer continental shelf. Although UNCLOS explicitly provides for jurisdiction of coastal state to board vessels in the EEZ to ensure compliance with its fisheries regulations (UNCLOS article 73), there is no corresponding authorization regarding fisheries on the outer continental shelf. Article 92 of UNCLOS provides for the exclusive jurisdiction of the flag state on the high seas. State practice on this subject, however, indicates that states may not regard this absence of an explicit authorization to board and inspect an insuperable obstacle. The Canada-US dispute on scallops centered on the legitimacy that scallops are sedentary, rather than the legality of the arrest of the vessel (Mossop, 2007).

2.10.2 The Loophole

If snow crab is not a sedentary species, the rules regarding living marine resources in the water column of the Loophole is of relevance. The Barents Sea Loophole is not covered by any EEZ and is thus by definition a high seas (international waters) pocket located between the exclusive economic zones of Norway and Russia. The Barents Sea Loophole spans some 62,400 square kilometers (Stokke, 2001a). The regulation of living marine resources in high seas is dealt with by UNCLOS article 118, which states that states that exploit the same living resource in the high seas shall enter into negotiations to take measures necessary for the conservation of the living resources concerned through regional fisheries organizations.

High seas fisheries in the Barents Sea Loophole are a rather recent phenomenon. The hub of the regional regime is the Joint Norwegian-Russian Fisheries Commission, which establishes total quotas and operational restrictions for the entire cod stock, based on scientific advice partly generated under the auspices of the International Council for the Exploration of the Sea (ICES) (Stokke, 2001b). In 1999 Iceland, Norway and Russia signed the *Loophole Agreement* designed to resolve a six-year dispute over unregulated fishing by Icelandic vessels for straddling stocks in the Loophole. The Agreement, gives Iceland fishing rights in the Norwegian and Russian EEZs in return for ceasing fishing in the Loophole (Churchill, 1999).

2.10.3 Svalbard waters

Through the Svalbard Treaty of 1920 (the Treaty) Norway gained sovereignty over Svalbard, but was deprived of certain rights. The Treaty gives foreign nationals (from signatory states) the same commercial rights as Norwegians (Molenaar, 2012). Norway holds that the Treaty stipulations do not apply to areas beyond the territorial sea of Svalbard, but there is not an international consensus on Norway's right to regulate fishing and exercise jurisdiction of the continental shelf in this area. The debates originate in the arguably weak references in the Treaty to its applicable maritime areas (territorial waters), made prior to the United Nations Law of the Sea (UNCLOS) and thus legal concepts such as the continental shelf and the 200 nautical miles Exclusive Economic Zone (Pedersen, 2008). Norway argues that it has the right under UNCLOS to establish a 200-mile economic zone around the archipelago and to exercise fisheries jurisdiction in the zone. Thus, in 1977 Norway established the Svalbard fishery protection zone (SFPZ) of 200 nautical miles around the Svalbard archipelago (fig. 1.2). One of the purposes of the zone was to ensure the protection and sound management of the living resources (Anon., 1977).

Other states have claimed that the Treaty and its provisions concerning the equal rights to engage in fishing also apply beyond the territorial waters of the archipelago, and that Norway may not impose restrictions or take necessary enforcement measures. It is indicated by Molenaar (2012) that the view of the other parties (not Norway) is more in line with the intentions of the negotiators of the Treaty in 1920. Norway is interpreting the wording of the Treaty more direct. It is against this background Norway chose to establish a fisheries protection zone rather than a full economic zone (Anon., 2005b).

Historically Norway has indicated that Svalbard has no separate continental shelf, in effect denoting that if the Svalbard Treaty is applicable to the SFPZ it would not necessarily be applicable to the shelf generated by the Norwegian mainland. Such a position could be used to secure Norway rights to sedentary species (and petroleum resources). Several scholars argue that this position is now abandoned (see e.g. Pedersen, 2008; Jakobsen, 2009).

Even though Norway maintains a legal right to reserve fishing in the zone exclusively for Norwegian fishermen, its management practices are non-discriminatory, and as such the Norwegian management measures in the SFPZ have generally been complied with in practice. Thus, even if many countries object to Norway's ability to establish an EEZ, these questions have not been further pursued (Anon., 2014h). This may change if new economic resources, such as snow crab or oil and gas can be exploited in the SFPZ. Even if the SFPZ is subject to the Treaty, it can be maintained that Norway is the legislative and managing authority (Jakobsen, 2009).

The non-discriminatory fisheries management is based on criteria of traditional fishing in the area, and as such vessels from Norway, Russia, the EU and the Faroe Islands are permitted to carry out traditional fishing activities in the area. Regulations on fisheries in the territorial sea is founded in the Svalbard law of 1925, while the fisheries management in the SFPZ is founded in the law on Norwegian EEZ of 1976 (Anon., 2014h).

Portugal, Spain and the Russian Federation have frequently challenged Norway's enforcement in the SFPZ. Russia did so in 2011 in response to the arrest of the Russian trawler *Sapphire* II by the Norwegian coast guard (Molenaar, 2012). Several challenge that Norway has this right in the SFPZ. Still, the Treaty does not provide other States Parties with the right to be involved in decision-making or enforcement in the SFPZ, as such the Supreme Court of Norway has upheld Norway's right establish the SFPZ and enforce regulations (see e.g. HR-2006-1997A case 2006/871).

2.10.4 The North East Atlantic Fisheries Commission

The North East Atlantic Fisheries Commission (NEAFC) is a regional fisheries management organizations (RFMOs) including the Barents Sea (Anon., 1980). Contracting parties are Denmark (in respect of the Faroe Islands and Greenland), the European Union, Iceland, Norway and Russia (Anon., 2015g).

During a NEAFC meeting in November 2014 the EU proposed that snow crab and northern shrimp should be subject to NEAFC management (Anon., 2014i). The Norwegian Fishing Vessel Owners Association has argued that NEAFC should temporarily manage snow crab until it is decided whether it is a sedentary species, as it is not suitable to only regulate Norwegian vessels in the fishery, while other nationals are fishing freely (Fiskebåt, 2015i).

2.10.5 Norwegian-Russian cooperation

Since the mid 1970s, Norway and Russia have developed a joint management regime for major commercial fisheries harvested by both countries in the Joint Norwegian Russian Fisheries Commission (JNRFC). This included cooperation both at research and management level. The cooperation has worked well, as both parties have had an interest in a successful management of the common stocks (Hoel, 2008). The Mutual Access Agreement secures parties' access to the EEZ of the other in certain fisheries (Stokke, 2001a).

The bilateral cooperation between Norway and Russia aim to achieve an ecosystem-based management of the entire Barents Sea on the basis of common knowledge and principles. Norway has developed a holistic management plan for the Barents Sea and Lofoten area. Russia is also developing such a management plan (Anon., 2015h).

3. Material and methods

3.1 Study area: The Barents Sea

As the Barents Sea is the new habitat of snow crab, it is important to understand species composition and other factors important to snow crab distribution and ecosystem impact. For this purpose a general description of the Barents Sea will follow with special focus on conditions of relevance for handling the research subject, that is ecosystem characteristics and factors limiting distribution (climatic conditions, bathymetry, sediments and the benthic community).

Physical features

The Barents Sea is an open arcto-boreal shallow shelf sea bordering the Arctic Ocean in the north and the mainland of Norway and Russia in the South, stretching from Novaya Zemlya in the east to the Norwegian Sea in the west. It covers about 1,4 million km^2 and is rather shallow, with an average depth of 230 meters and a maximum depth of 500 meters as shown in figure 3.1. Extensive shallow areas are found, especially west and southwest of Novaya Zemlya and around Svalbard as well as large isolated banks such as the Central Bank, the Great Bank and the Svalbard Bank (Wassmann et al., 2006).

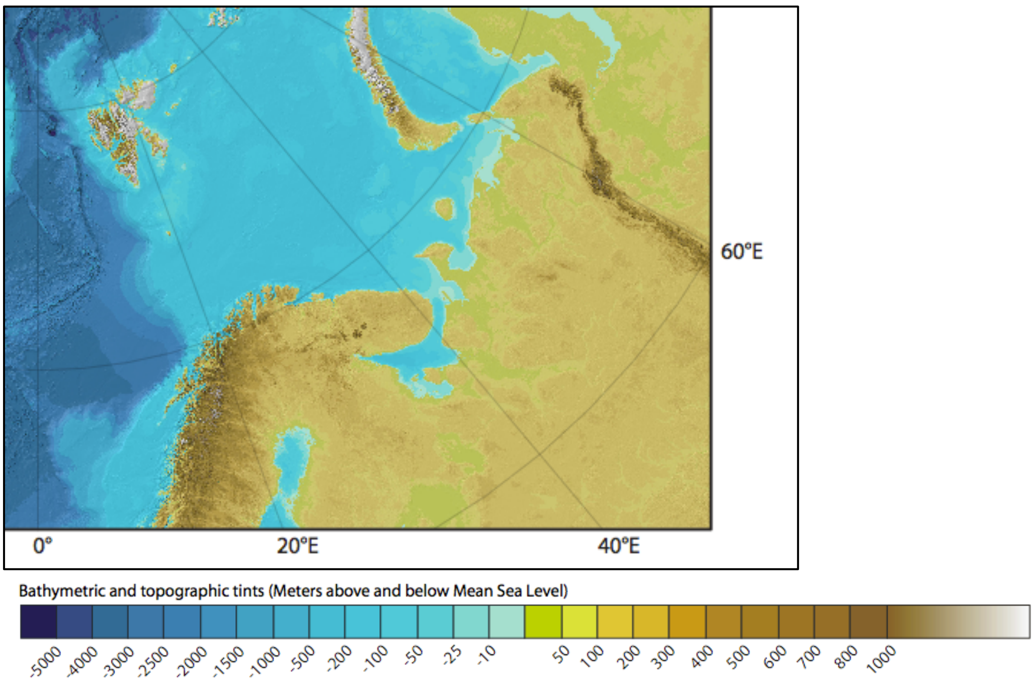

Figure 3.1 Bathymetry of the Barents Sea (from Jakobsson et al., 2012).

Water depth and sediment type are determining the composition of the benthic fauna (Kendall, 1996). The sediments are strongly influenced by the depth and slope of the sea bottom, with finer muds predominating in deeper areas with slow water movement, and sandy to stony sediments common in shallower banks and slope areas with rapid water movement (Eldholm and Talwani, 1977).

The Barents Sea is characterized by ice-cover and extreme seasonality of solar radiation; it is a one-way flow-through ecosystem with complex bathymetry and hydrography. Sea ice can cover up to 90% of the Barents Sea surface in winter. Surface layers in southwestern Barents Sea is strongly influenced by warm water from the Atlantic Ocean, while less saline and less dense Arctic water occupies the northern part. The boundary between these two main water masses is known as the Polar Front. The inflowing Atlantic water controls the nutrient concentrations in the southern and central Barents Sea (Loeng et al., 1997; Wassmann et al., 2006). There is a general decrease in temperature from west to east and from south to north (fig. 3.2) (Ozhigin et al., 2011). October is the month with the highest mean water temperature (Matishov et al., 1998).

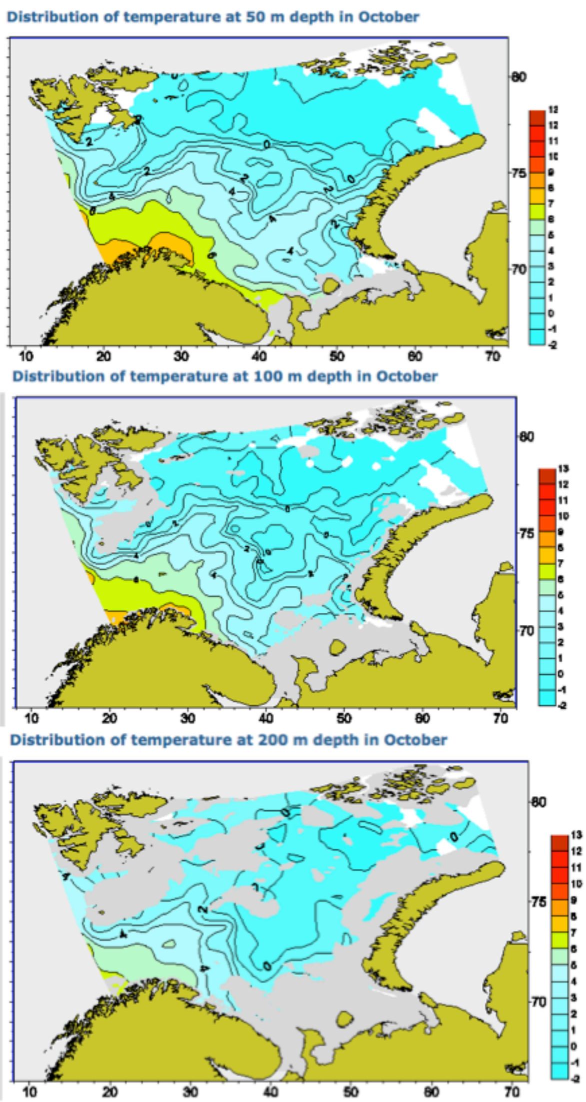

Figure 3.2 Mean (1898-1993) October water temperature recorded at different depths (50, 100 and 200 m) in the Barents Sea from the Climatic Atlas of the Barents Sea (from Matishov et al., 1998)

No ecosystem is static, and currently several factors imply that the Barents Sea is in change. Preliminary forecasts indicate a 20% reduction of the polar ice pack during winter, and 80% during summer, by the end of this century due to climate change (Johannessen et al., 2004). A changing climate can lead to a mismatch between phytoplankton blooms and the grazer community, and can as such give rise to high vertical export of biogenic matter to the benthos (Sakshaug, 2004) and a northward shift of biogeographic boundaries (Wassmann et al., 2006). Cod (*Gadus morhua*) has recently been recorded as far north as 82°N, on the edge of the Barents Sea shelf to the Arctic Ocean (Johansen et al., 2013). Climate variability and climate change will result in food web change (Wassmann et al., 2006), which will act simultaneously as snow crab finding its role. In addition fishing activities is moving northwards, while ocean acidification and invasive species may affect biodiversity and the functioning of benthic systems (Jørgensen et al., 2014). In the entire Arctic the temperatures has raised two to three times as quick as the global average, and the sea-ice has receded. In the southern Barents Sea the temperature of the inflowing Atlantic water has had an increases of about 1,5°C from 1977 to 2013 (Van Der Meeren et al., 2014).

Production and species interactions

The most important factor determining interannual differences in primary production and its spatial variability is the position of the ice edge in spring and late summer. The interannual variability in primary production is more than 200%. Primary production increases rapidly in the spring with the productive period from May to early September. Generally, water column productivity is inversely related to ice cover. This annual variability causes a large variability in nutrition available to the present species, and a migratory behavior among some species. The primary production mainly happens in the open water masses by phytoplankton, which is then consumed by zooplankton (Wassmann et al., 2006).

The Barents Sea is characterized by a high degree of species interactions (Wassmann et al., 2006). The food web is simple, and the food chain is short. It primarily consists of only a few robust species adapted to the cold climate. The simplicity and short food chains makes such an ecosystem extra vulnerable and less resilient. The vulnerability of ecosystems to environmental perturbations and disturbances depends on their sensitivity and adaptability to maintain functions under changing conditions. Functional diversity accounts for diversity of biological attributes and has been suggested as an indicator of ecosystem resource dynamics, productivity and stability, and is widely accepted as a key driver of ecosystem functioning. High functional diversity in fish species composition has been observed in central areas of the Barents Sea as well as off the Norwegian coast and the southwestern Barents Sea and appears to maintain high levels of adaptability. High functional diversity in the central-western area is likely to be associated with mixed water just south of the polar front. The functional diversity has been very low in southeastern areas far from the Norwegian Sea. Further to the north and east, the community vulnerability appears to be higher due to lower functional diversity (Wiedmann et al., 2014).

The pelagic-benthic coupling in the Barents Sea is strong. In total 80% of the harvestable production is channeled through the deep-water communities and benthos, which thus play an important role for energy flow and trophodynamics (e.g. Piepenburg and Schmid, 1996). The abundance and biomass of the benthic community in polar marine systems is directly influenced by food supply from the overlying water column (Wassmann et al., 1996). As the benthic-pelagic coupling is so strong, other species can be affected by changes in the benthic community (Jørgensen et al., 2014). The benthic biomass is correlated with the flow of phytodetritus to the bottom and to chlorophyll content of the bottom sediments (Anisimova et al., 2011). Often dominant echinoderms on Arctic shelves play an important role in the redistribution and remineralizition of organic carbon reaching the seabed (Bluhm et al., 2009 in Jørgensen et al., 2014). The annual variability in primary production causes variation in available energy to the benthic community and benthic organisms have to adapt to this.

In total 3245 invertebrate species have been recorded in the Barents Sea (Sirenko, 2001). Compared to other Arctic seas, the diversity is relatively high in the Barents Sea. Dominant contributors to the Barents Sea biomass weighs toward molluscs (35%), polychaetes (17%), echinoderms (19%) and crustaceans 15%). Polychaetes are regarded as a dominant component of the benthic ecosystem in terms of numbers (35%), similar to molluscs. There is a great spatial variation in biomass across the Barents Sea, with the highest biomass occurring in the shallows of the Spitsbergen and Central Banks (Wassmann et al., 2006). Large populations of fish, sea birds and marine mammals migrate northwards into the Barents during summer to feed on the lipid-rich zooplankton that can occur in large swarms. The copepods *Calanus finmarchius* and *C. glacialis* together with capelin (*Mallotus villosus*) and herring (*Clupea harengus*) are key stone species in the Barents creating the basis for rich assemblages of higher trophic level organisms, facilitating one of the worlds largest fisheries (capelin, cod, shrimp, seals and whales). Northeast Arctic cod (*Gadus morhua*), seals, whales, birds and man compete for harvestable energy with similar shares (Wassmann et al., 2006).

A correlation between the distribution of northern shrimp and sedentary polychaeta in the Barents Sea has 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). Foraminifera are known to form part of a key link in marine food chains, assimilating energy available from minute autotrophs and also retrieving energy available during the final stages of degradation of organic debris. They support a variety of larger organisms and thus contribute to the diversity and secondary productivity of ecosystems (Lipps and Valentine, 1970). Foraminifera represent an important link between lower and higher levels of marine food webs, and play a potentially significant role in deep-sea carbon cycling (Gooday et al., 1992).

The red king crab is found on coarse and mixed sediments down to 200 meters in the coastal shoal of the southern Barents Sea, not extending into the habitat of snow crab. No commercially interesting crabs have been present in the Barents Sea, but one large crab in addition to red king and snow crab, the northern stone crab (*Lithodes maja*), is found in the southwest Barents Sea (Jørgensen et al., 2014).

The main flow patterns and transformations of the Atlantic waters determine large-scale biogeographic patterns where the Barents Sea changes form a boreal region in southwest to mostly Arctic conditions in the northeastern area. Jørgensen et al. (2014) suggests four bioregions:

- Southwestern region (SW) consisting of the coast of northwestern Svalbard and the shallow Spitsbergen Bank
- Banks and slopes in the southeast and west (SEW)
- Northwestern region (NW)
- Northeastern region (NE)

The SW region is characterized by the inflow of warm Atlantic water associated with relatively high primary production, strong water currents that resuspend food material, and the presence of hard substrate. Dominated by filter feeders (sponges) in the inflow area of warm Atlantic water, and detrivorous fauna (echinoderms) in the deeper trenches (Jørgensen et al., 2014).

The SEW region has strong seasonal and shorter-term temperature variations. The SEW region stretches almost uninterrupted from the northwestern coast of Svalbard, across the Barents Sea and into the southeastern area as a “benthic Polar Front”. This boundary between the northern and southern regions separates the boreal and the Arctic biogeographical regions.

Predators such as snow crab, sea stars and anemones dominate the SEW (Jørgensen et al., 2014).

The NW region lies close to, or to the north of the Polar Front in the western part of the Barents Sea. The cold NW region had the highest number of benthic taxa. Southern parts of the NW regions include the Hopen Deep, Storfjord Trench and banks south of the Central Bank. Dominated by plankton feeding brittlestars (Jørgensen et al., 2014).

The NE region is separated from the NW region by the elevation of the Skolten Bank in the south, Central Bank, and the Great Bank in the north. The northern part of this region had almost year-round ice coverage (293 d $year^{-1}$) and had the highest mean biomass and abundances recorded in this region. The NE had an increasing snow crab population (Jørgensen et al., 2014).

3.2 Data collection

Currently little data exists on the snow crab population in the Barents Sea. In cooperation with the Directorate of Fisheries, the Norwegian College of Fisheries Science (NCFS) and others, the Institute of Marine Research (IMR) has collected specimens for analysis.

The crabs were collected in several cruises by different vessels from 2011 to 2014 and only stations with catch are presented (fig. 3.3). The distribution of stations with catch autumn (August and September) and winter (January and February) is quite different, and covers large parts of the Barents Sea.

As it is difficult to distinguish between juvenile and mature crab, the crabs are for the purpose of this thesis divided into two size groups: Small crabs width carapace width below 40 mm and large crabs with carapace width above 40 mm. The small crabs in the data set were primarily sampled during winter.

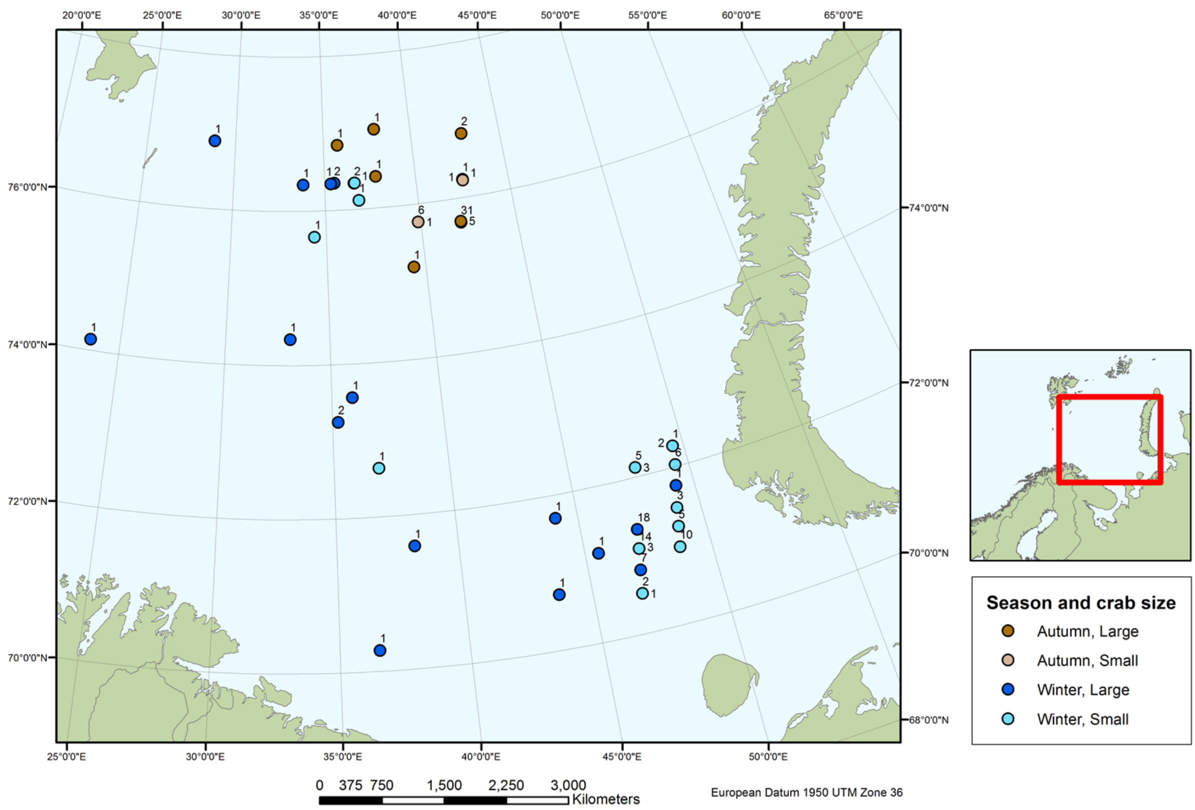

Figure 3.3 Stations of sampled male snow crab (*Chionoecetes opilio*). Each point represents a sampling station, numbers reflect number of crabs per station.

The data set consists of 171 individuals in total, of which 17 are female and 154 male. 62 crabs were collected in the autumn and 109 during winter. All crabs were collected by the use of trawl. The sampled crabs came from several depths in both autumn and winter, and thus represent a diverse composition of the population (table 3.1). The autumn crabs were collected at fewer stations than winter crabs, with larger catches per haul (fig. 3.3).

The winter crab came not only from a large geographic area, but also from a huge depth range (85-407 m) compared to the autumn crab were more than 50% came from one station, and the other stations were quite close in both area and depth (fig. 3.3; appendix table A1). Seasonal (autumn/winter) differences in sampling area and depth, but also differences in carapace width (see fig. 3.3) may have consequences for availability of food as well as size-classes sampled. Therefore it is important to take this into consideration when presenting the diet data.

Table 3.1 Sampled snow crab *Chionoecetes opilio* for stomach analysis from the Barents Sea. More details in Appendix table A1.

Season	Sex	Size	Number	Mean depth (m)	No of stomachs analyzed (empty)	Number weighted	No w/ chela measures
Autumn	F	Small	0	-	0	0	0
	M	Small	2	297,5	2	0	0
Autumn	F	Large	10	288,1	9 (1)	1	5
	M	Large	50	279,4	50	14	34
Winter	F	Small	0	-	0	0	0
	M	Small	37	149,8	37	37	31
Winter	F	Large	7	196,1	7	7	7
	M	Large	65	187,8	64 (1)	65	65

All crabs were frozen whole at sea. Some of the crabs were width measured and weighed onboard the vessels before freezing, others onshore in laboratory. The stomach content was extracted in laboratory; some stomach content samples were analyzed immediately, while others were stored on ethanol before analysis.

The “standard length measurement” used for snow crabs is the caprapace width (CW; mm). In addition measurements of chela height, length and width are of interest for male maturation. Crabs were measured and registered following procedures from Jadamec et al. (1999). Size is of relevance to diet, but as this is some of the first available material for snow crab in the Barents Sea, also weight-width relations and morphology will be presented, even though the data set may not represent the population in total.

3.3 Lab work – identification of stomach content

Stomach analysis was performed in cooperation with skilled personnel at the Institute of Marine Research (IMR). Coat and gloves were used to avoid contamination of the samples.

As the crabs were frozen upon arrival at the lab, they were thawed for a few hours. Thereafter the carapace was divided from the abdomen from behind using a scalpel. The stomach was removed using forceps (figure 3.4) and rinsed easily on the outside to avoid particles to blend with the stomach content. Following the stomach was placed on a petri dish and then cut open with a pair of scissors. The stomach content was flushed out inside a 500 µm filter.

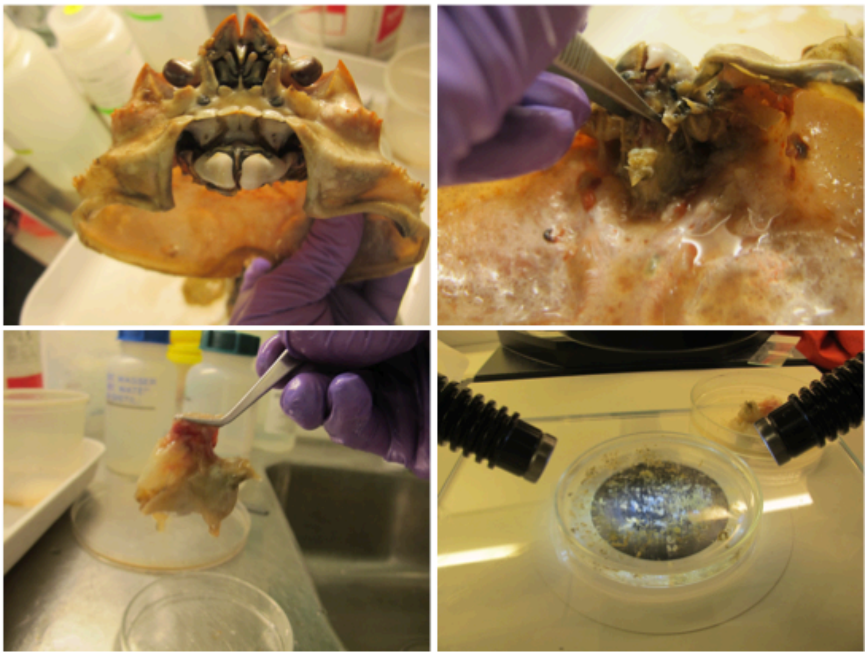

Figure 3.4 Removing the stomach from the carapace of a snow crab (*Chionoecetes opilio*) from the Barents Sea for diet analysis

The stomach content was then exported to a clean petri dish that was placed under a magnifier for analysis. An adaptation of the criteria laid out by Squires and Dawe (2003) helps to explain how prey items were identified and grouped (table 3.2).

Table 3.2 Grouping of prey items by code used, criteria used for identification and examples of prey items identified

Code	Prey item	ID criteria
Ind	Indetermined	Highly digested matter; unidentifiable matter
Biv	Bivalvia	Fragments of shell with growth lines; ligament
Pol	Polychaeta	Chaetae; pieces of sand tubes; jaws
Cru	Crustacea	Fragments of chitinous shells; pieces of antennae; rostrum; mouthparts; legs
Ech	Echinodermata	Hard items with structure resembling glass pearls; spines
For	Foraminifera	Small, circular structures, with concentric whorls of crystalline material
Gas	Gastropoda	Fragments of thin opalescent shell of helical shape; operculum
Pla	Plastic	Non-organic strings of plastic
Alg	Algae	Plant cells; pieces of algae
Ost	Osteichtyes	Pieces of bones from ribs/vertebrae; scales; otoliths
Cep	Cephalopoda	Beaks
Por	Porifera	Spicules
Egg	Eggs	Eggs
Hyd	Hydrozoa	Branching plant-like structures
Mol	Mollusca	Miniature ivory; small calcified spicules; other hard structures
Bry	Bryozoa	
Tun	Tunicata	
Nem	Nematoda	

Visual identification of prey items is challenging (see examples in fig. 3.5), this is especially challenging for an untrained eye. A large amount of the stomach content is highly digested and with no clues that can facilitate clear evidence for identification. This calls the need for the category "indetermined".

Scaphopoda or Alpacophora were grouped together as Mollusca, as there were very few items. In the group Mollusca are also some other items that was not of further identified from phylum level.

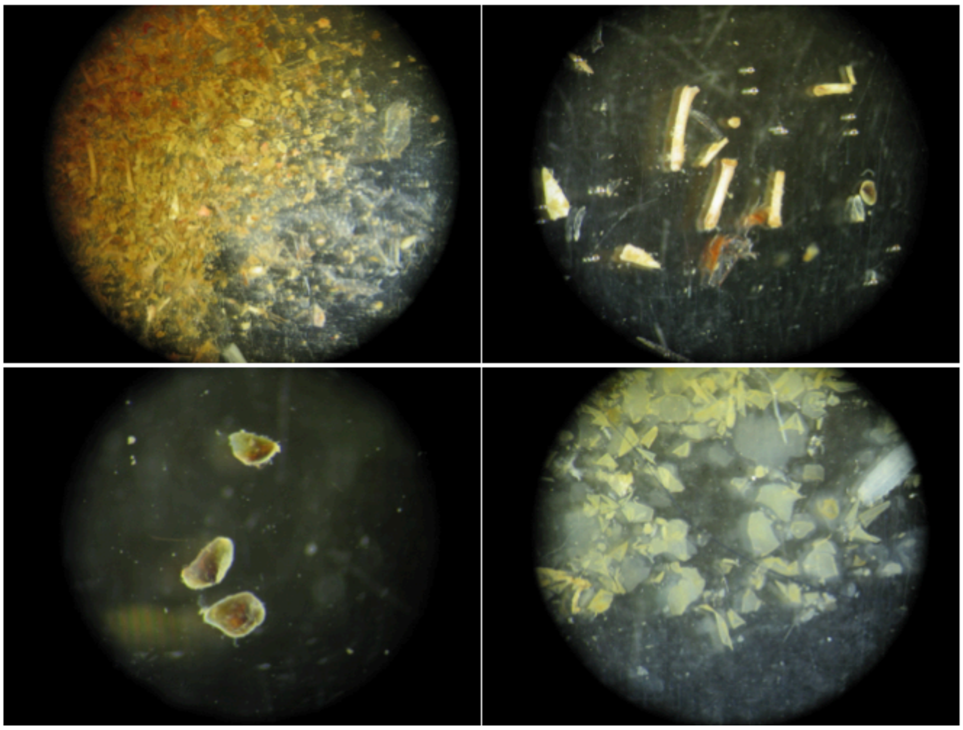

Figure 3.5 Examples of analyzed stomach content. In the lower right picture there is a blue string of plastic, in the lower left picture there are traces of what was identified as cephalopod beaks. In both upper pictures Crustacea dominates.

3.4 Statistical analysis

Biological characteristics of the sampled snow crab

Size- and sex distribution

Size and sex distribution was graphed, as all other statistical analysis performed, by the use of the software SYSTAT. From this it is possible to get an overview of the sampled crabs, and identify potential size-groups.

Weight-width relationship

The weight-width relationship tells us something about growth pattern of the species, and can be used to compare conditions and feeding status. Easily graphed using carapace width (CW) as the independent variable (x) and wet weight in grams as the dependent variable (y) and log scales to visualize a linear relationship. This gives us an indication about the relation and differing trends among groups. As the size distribution of females and males are different (chapter 2.4) it is logical to analyze the sexes separately.

The relationship between weight and width can best be described by $W = a\ CW^b$, which in linear form translates to $\ln W = \ln a + b \ln CW$, where a is the intercept and b is the slope. To analyze and compare weight-width relationship for multiple groups, regression analysis and analysis of covariance (ANCOVA) was used.

(1) Slope of regression lines

The ln weight - ln width regression model for winter (W) and autumn (A) crabs we estimated:

H_0: $Slope_A = Slope_W$

H_1: $Slope_A \neq Slope_W$

Model:

$\ln W = constant + \ln CW + Season + \ln CW * Season$

Where ln CW*Season expresses the slope of the regression line. Using $\alpha=0.05$ H_0 is accepted if $p > 0.05$ and the ln CW*Season (slope) is not statistically significant different for winter and autumn crabs, and this term should be removed from the model.

(2) Height of regression lines

It is of interest to see if the height of the regression lines is equal, that is if there is no difference in weight according to the same carapace width, provided that the slope is equal, i.e. if the crabs are heavier in one of the season, which might say something about the condition of the crabs:

H_0: $Height_A = Height_W$

H_1: $Height_A \neq Height_W$

Model:

$\ln W = constant + \ln CW + Season$

Using $\alpha=0.05$ H_0 is accepted if $p > 0.05$, thus there is no statistically significant difference in weight of crabs of the same size between autumn and winter.

Morphology

The relationship between the right chela and CW of males is of interest to the maturation process and differentiation of life-stages as accounted for in chapter 2.4. The chela-length/height/thickness was thus graphed against CW to shed light on development stages of the sampled crabs.

Diet study

For the diet study a present/absent methodology has been used. Two issues were of interest: Number of food items consumed and which prey items had the highest occurrence, tested against variables "size-group" and "season".

Number of prey items in snow crab diet

The number of prey groups consumed gives information on the diversity in feeding habits. It is of interest to investigate if the crabs consume a similar variety of prey items during autumn and winter, and if large and small crabs consume a similar number of prey items.

(1) Seasonal differences in number of prey groups consumed

It is of interest to test whether the mean number prey items consumed during autumn (A) is statistically significant different from mean number of prey items consumed during winter (W). In case of differences between size groups, these should be treated separately. As small crabs only appear for winter, seasons are only compared based on large crabs. Stated as hypotheses:

H_0: Mean number of prey items_A = Mean number of prey items_W

$\mu_A - \mu_B = 0$

H_1: Mean number of prey $\text{items}_A \neq$ Mean number of prey items_W

$\mu_A - \mu_B \neq 0$

Where "A" is large male crabs caught during autumn and "W" is large male crabs caught during winter. Using $\alpha=0.05$ H_0 is accepted if $p > 0.05$, thus there is no statistically significant difference in mean number of consumed prey items.

(2) Differences in number of prey groups consumed for large and small crabs

It is of interest to test whether the mean number prey items consumed by large crabs is the same as for small crabs. As small crabs only appear during winter in this case, winter crabs should be the only crabs analyzed in this case. Stated as hypotheses:

H_0: Mean number of prey items$_{Large}$ = Mean number of prey items$_{Small}$

$\mu_{Large} - \mu_{Small} = 0$

H_1: Mean number of prey items$_{Large}$ ≠ Mean number of prey items$_{Small}$

$\mu_{Large} - \mu_{Small} \neq 0$

Where “large” means large male crabs caught during winter and “small” is small male crabs caught during winter. Using α=0.05 H_0 is accepted if $p > 0.05$, thus there is no statistically significant difference in mean number of consumed prey items.

Identified prey items in snow crab diet

The prey items consumed are what primary is of interest to assess the ecological importance of snow crab in the Barents Sea, which is one of the main research questions for this thesis. It is not only of relevance to investigate what snow crab as a whole consume, but also if there are differences within the population, with respect to size and season.

Effect on prey items from season and size class was tested with Fisher’s exact test, as it is categorical data of a present/absent nature in a cross tabulation, and with a small sample size (see e.g. Routledge, 2005).

Relationship among prey items

It is also of interest to see whether any prey groups appear together, and thus if there is any relationship with respect to species interactions. To test if they co-occur in any pattern gives us information to reveal bias in the stomach analysis as well as assessing feeding habits of the different size classes and among seasons. A cluster analysis was performed to illustrate the relationship between prey items.

4. Results

4.1 Biological characteristics of snow crab

Size- and sex distribution

Almost all size groups of snow crab are present in the available material, from crabs smaller than 15 mm, up to large crabs of 134 mm carapace width (CW) (fig. 4.1). It seems as if there are two size groups within the winter sampled crabs, one with CW below 40 mm and a peak CW around 20 mm; the other with CW larger than 40 mm and a peak occurrence around 100 mm. Small crabs (<40 mm CW) are represented by only two individuals in the autumn, thus when comparing large and small crabs, only winter crabs will be used. In addition very few females are registered. Thus, as a deviating feeding and size pattern may be expected from females, and the numbers of females are too small to give any significant information, the females will be excluded from the further analysis.

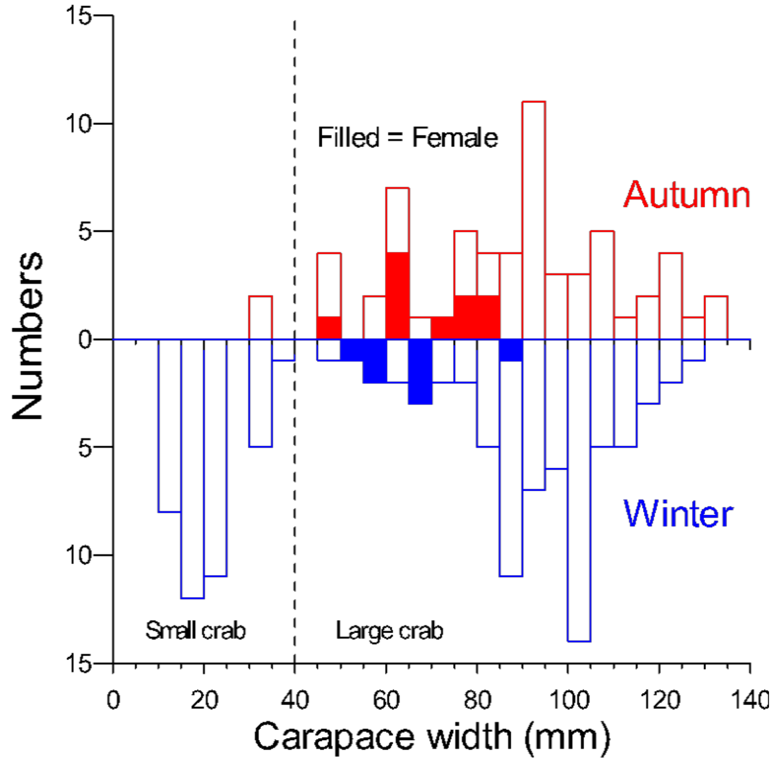

Figure 4.1 Carapace width (5 mm groups) and sex distribution of male and female snow crab (*Chionoecetes opilio*) from the Barents Sea caught in autumn and winter. The dotted line marks the chosen border between small and large crab.

Weight-width relationship

The weight-width relationship is presented in figure 4.2 with regression lines inserted for all crabs in autumn and winter. All regression lines are highly significant (table 4.1a). The slope of the regression lines for the ln weight-ln width relationship for autumn and winter crabs are not equal ($p<0.05$), implying a significant difference in the slope. But the winter sample consists of many small crabs, compared to the autumn crabs. The small crabs significantly affect the slope of the regression line for the ln weight-ln width relationship of winter crabs (fig 4.2a). In addition most individuals were weighed on a vessel in motion, the uncertainty of the registered weight is within a few grams. Thus the discrepancy is relatively larger for the smallest individuals, and the "0 g-crabs" should be ruled out. It is more correct to compare individuals within the same size range, male crabs larger than 40 mm CW (see fig. 4.2b and table 4.1b). As seen from the plot (fig 4.2b) and from the slope (b-values) (table 4.1b) no differences in slope (ANCOVA: $F_{1,75}=0.14$; $p=0.71$) but differences in height registered (ANCOVA: $F_{1,76}=12.1$; $p<0.05$) meaning that the winter crabs have statistically significant higher weight than autumn crabs of the same size.

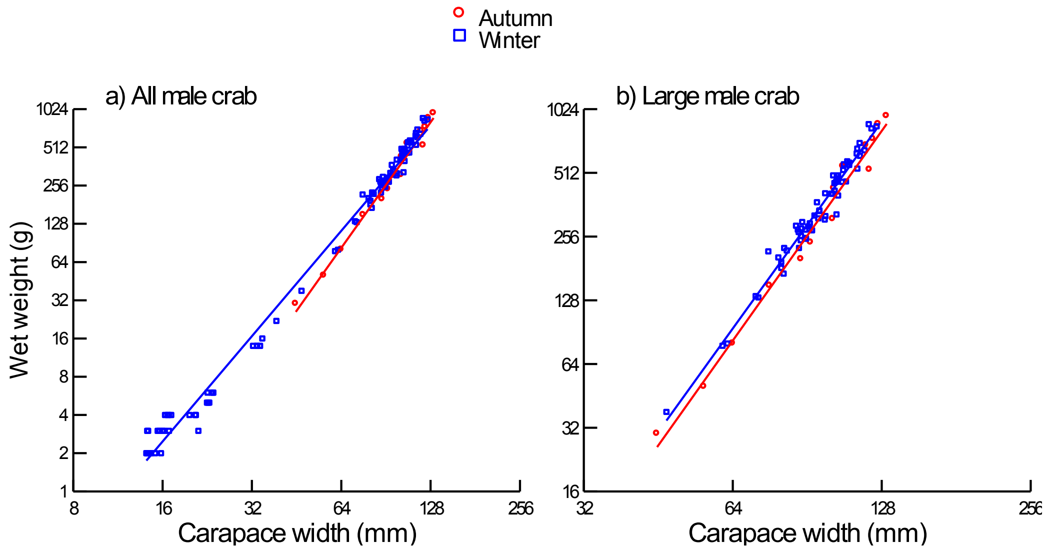

Figure 4.2 Weight-width relationship for (a) all male snow crabs (*Chionoecetes opilio*) and (b) only large (CW>40 mm) from the Barents Sea, caught during autumn and winter. Note log scales.

The results from the regression analysis on the weight-width relationship provide us with the numbers for the relationship, as shown in table 4.1. When comparing male autumn and winter crab, the difference in slope and height of the weight-width relationship seems significant when the small winter crabs are included, as shown in figure 4.2 and table 4.1a. But as illustrated in figure 4.3 and table 4.1b the difference in slope and height seem less apparent when only including large crabs.

Table 4.1 Results from ln weight-ln width regression analysis of snow crab (*Chionoecetes opilio*) in the Barents Sea.

a) All male crabs

Season	N	ln a	b	se b	r^2	F	P
Autumn	14	-9,266	3,289	0,122	0,982	723,1	<0,001
Winter	102	-6,729	2,754	0,025	0,992	12533,3	<0,001

b) Male crabs with carapace width larger than 40 mm

Season	N	ln a	b	se b	r^2	F	P
Autumn	14	-9,266	3,289	0,122	0,982	723,1	<0,001
Winter	65	-8,945	3,244	0,075	0,967	1887,1	<0,001

Morphology

There is a clear relationship between carapace width and the right chela of male crabs, which indicates a division of male crabs into two groups in the area between 80 and 120 mm CW, implying that the crabs that are in the upper right are morphometric mature (fig. 4.3).

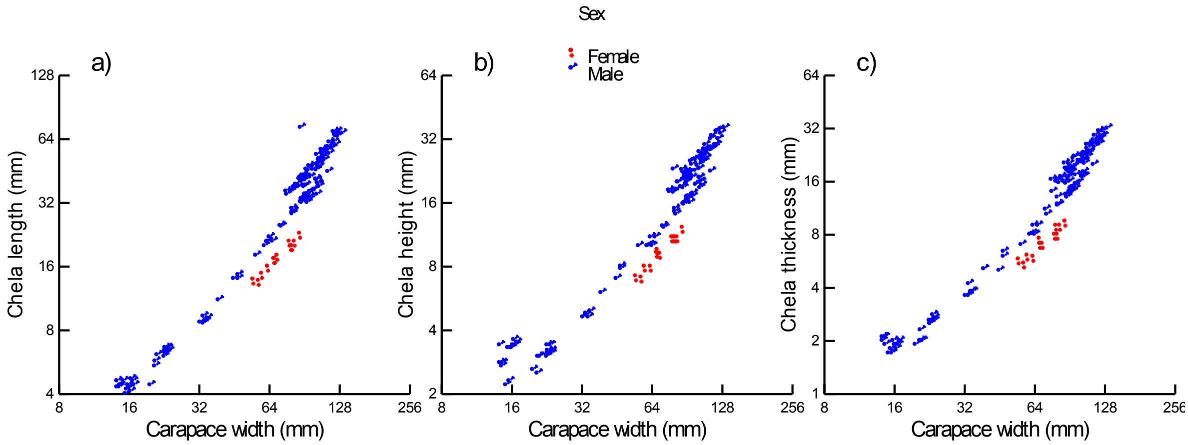

Figure 4.3 Chela size according to carapace width for snow crab (*Chionoecetes opilio*) from the Barents Sea. a) chela length-CW relationship b) chela height-CW relationship c) chela thickness-CW relationship. Note log scales.

4.2 Diet study

Number of prey items in snow crab diet

The number of prey groups identified per large male crab stomach is illustrated in figure 4.4. There were two crab stomachs with no content (see appendix figure A3), included in the ≤2 bin in this figure. The number of sampled crabs is larger for winter than autumn, which must be taken into account when interpreting the figure, as it is the pattern of each season, not the height that is interesting to compare. The mean/median number of food items are 5.5/6 and 4.4/4 for autumn and winter, respectively, and testing the central tendency with a Mann-Whitney test (p=0.006) tells us that large autumn and winter crab consume a statistically significant different mean number of prey groups. Thus, we can from this conclude that autumn crab consumes a larger diversity of prey groups than large winter crab. While the distribution pattern is tested with a chi-square test (x^2=12.0;df=6;p=0.06) that shows no statistical significant difference in distribution of food items.

Differences in number of prey groups consumed for large and small crabs. As visible in figure 4.6 it seems as if small crab consume a larger diversity of prey items during winter, than large crabs do and the mean/median number of food items are 5.4/5 and 4.4/4 for small and large crabs respectively, and testing the central tendency with a Mann-Whitney test (p=0.005) tells us that large crabs consume fewer food items than small crabs, also the distribution pattern is tested with a chi-square test (x^2=13.8;df=6;p=0.032) that shows a statistical significant difference in distribution of food items.

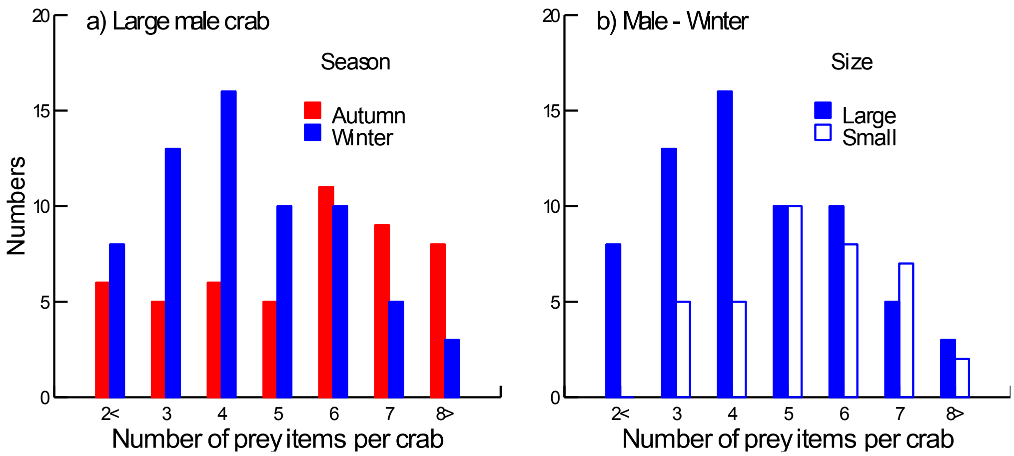

Figure 4.4 Number of prey groups per a) large male snow crab (*Chionoecetes opilio*) from the Barents Sea in autumn and winter and b) large and small snow crab from the Barents Sea in winter. Small crab are defined as ≤40 mm CW, large crabs are defined as >40 mm.

Identified prey items in snow crab diet

All prey groups identified in analyzed male crab stomachs are presented in figure 4.5 in accordance with descending occurrence. The taxon with the highest relative occurrence in both winter and autumn is Bivalvia, which taxonomically belongs in phylum Mollusca together with Gastropoda and Cephalopoda that were also common. The second highest occurring prey group is Polychaeta, followed by Crustacea, which in many cases belonged to order Decapoda. Uncertainty on many of the identified items lead to the use of subphylum level Crustacea.

From the figures, it seems to be a substantial difference in relative occurrence in autumn versus winter for the following three taxa: Echinodermata, Foraminifera, Gastropoda, as well as algae, Osteichthyes and Cephalopoda. When only comparing large crabs from autumn and winter (fig. 4.5b), Bivalvia points out as a taxa with a large difference among autumn and winter crabs. When excluding small winter crabs it does no longer show a difference between autumn and winter crabs for echinoderms and bony fish, but the difference in relative occurrence of Foraminifera seems to increase. The difference in relative occurrence in Gastropoda does not seem to change when small winter crabs are excluded.

When comparing small and large winter crab (fig. 4.5c) there is also a large difference in relative occurrence of Bivalvia. Thus it seems as if large winter crabs in this data sets consume less Bivalvia than both small winter crabs and large autumn crabs. From figure 4.5c it is also apparent that there is a large difference in the relative occurrence of Echinoderms between small and large winter crabs, at the same time as there is no difference between large winter and autumn crabs, so here it seems as if small winter crabs have a different diet. Whether this is due to other prey availability or preferences is not known. Small winter crabs consume more algae and Foraminifera than large winter crabs.

The effect on diet from season and size class was tested by the use of Fisher's exact test (results found in appendix table A2). For the lower part of appendix table A2 the results of the significance test are suspect, as the expected values were so low. The results show that feeding on Foraminifera is statistically significant different between both seasons and size classes. The same is the case for Bivalvia, but the difference between seasons is not significant if small crabs are included. For Gastropoda the difference in occurrence is statistically significant for seasons when small winter males are excluded and included. The same is the case for Cephalopoda and algae. Echinodermata has a statistically significant difference in occurring by size classes in winter. Small male snow crabs have a higher occurrence of Crustacea in their stomachs.

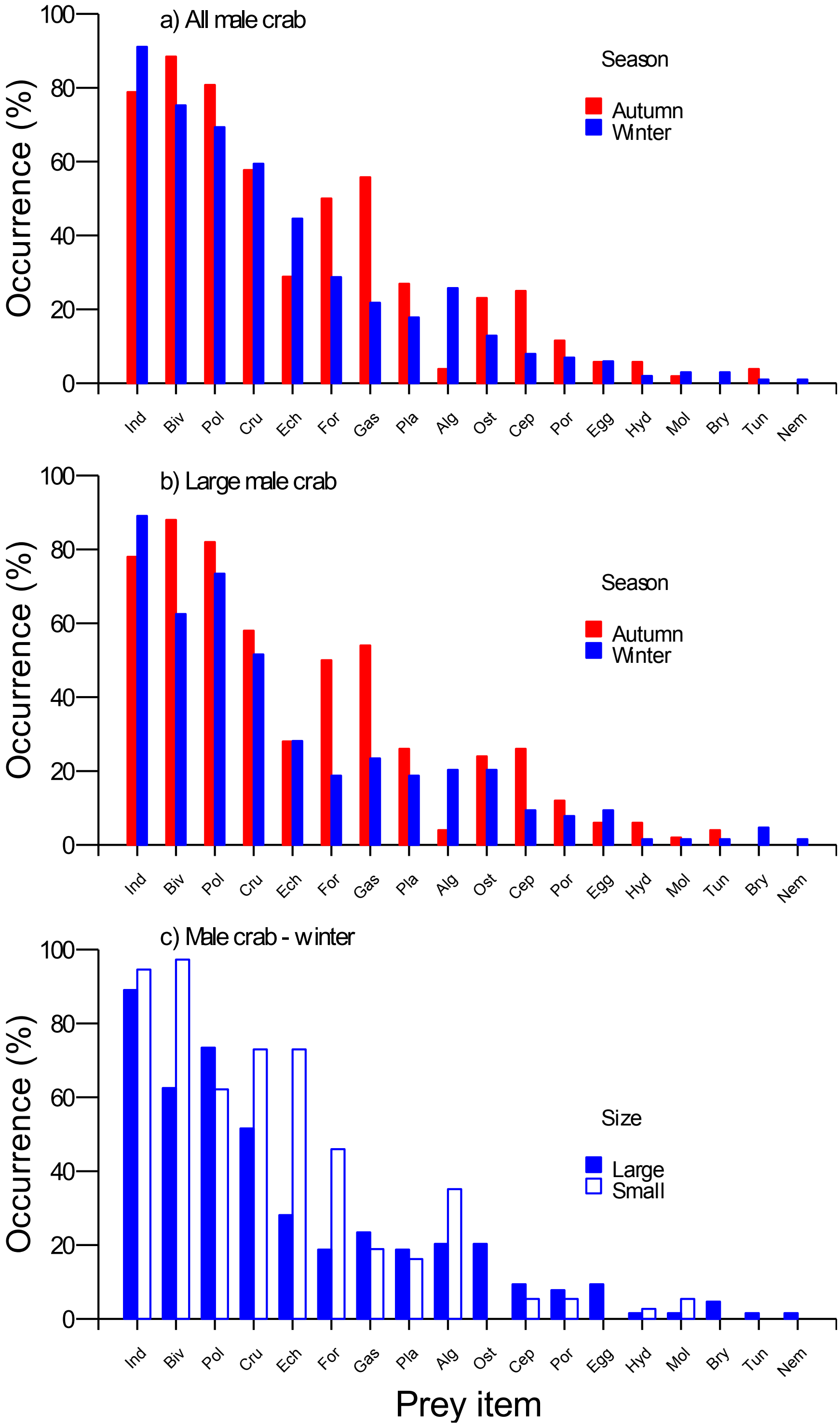

Figure 4.5 Occurrence of prey items in snow crab (*Chionoecetes* opilio) stomachs from the Barents Sea for a) all male b) large (>40 mm CW) c) winter crab.

Relationship among prey items

A cluster analysis on Jaccard similarity index was performed on the most commonly occurring taxa (see appendix table A2). This index measures the similarity between food items based on the presence of prey items in the crab stomachs. The lower the distance to the intersection of two prey items on the x-axis in the cluster trees (fig. 4.6, 4.7 and 4.8), the more commonly the prey items co-occurr. For large crabs caught during autumn, it seems to be a similarity between the occurrence of Bivalvia and Polychaeta, but also a similarity with these items and indetermined food items, and to some extent Crustacea. Together these prey items has a connection to Foraminifera and Gastropoda, that commonly occurs together. The other prey items are less commonly found in crab stomachs and show a small degree of patterns in co-occurrence (fig. 4.6).

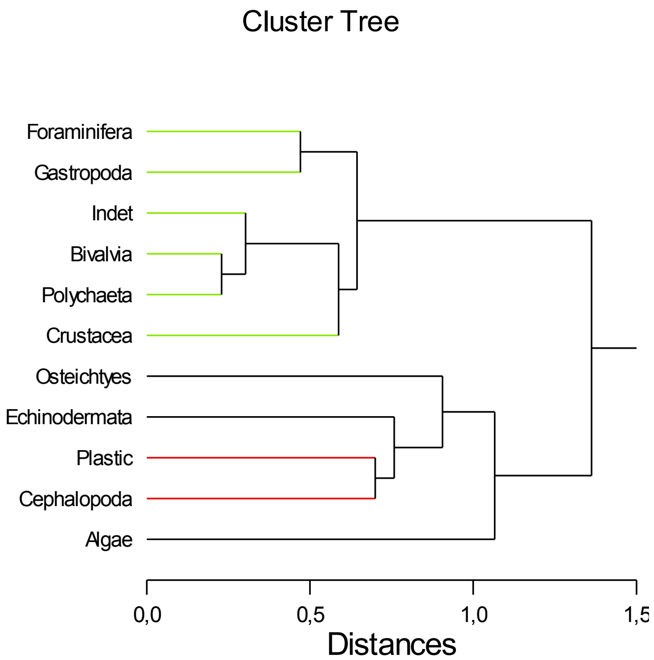

Figure 4.6 Cluster analysis of prey groups among **large male autumn caught** snow crabs (*Chionoecetes opilio*) from the Barents Sea.

For large male crabs caught during winter indetermined food items and Polychaeta commonly co-occur, also often together with Bivalvia, and to some instance Crustacea. These are the most common prey items. The other prey items have a more distant relationship, with no clear trends (fig. 4.7).

For small crabs caught during winter the relations seem somewhat different. The most commonly co-occurring prey items are indetermined food items and Bivalvia that very commonly co-occur, often together with Crustacea. These also occur together with other common prey items such as Foraminifera and Echinodermata (fig. 4.8).

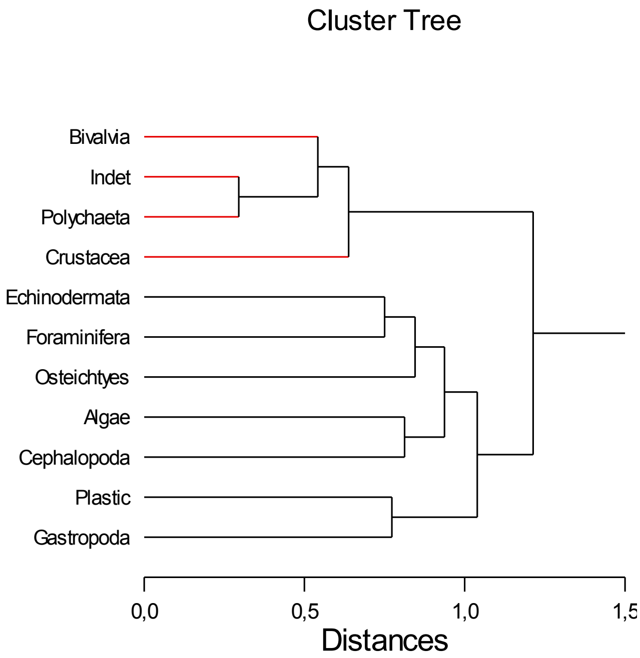

Figure 4.7 Cluster analysis of prey groups among **large male winter caught** snow crabs (*Chionoecetes opilio*) from the Barents Sea.

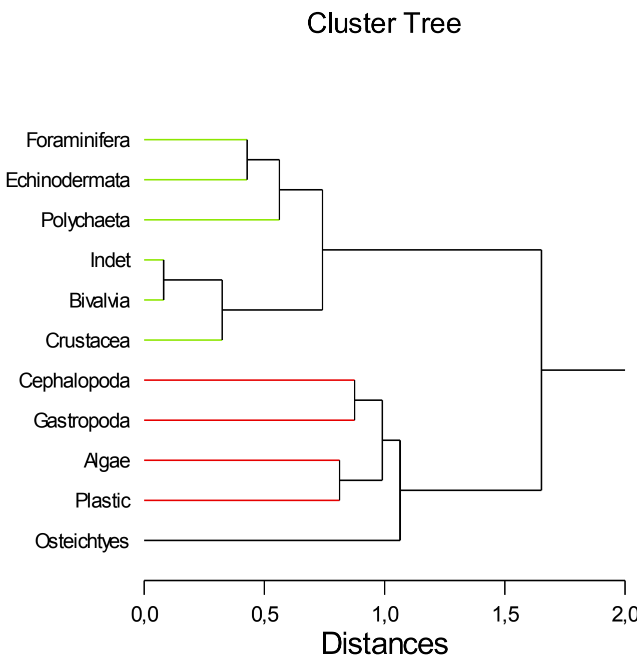

Figure 4.8 Cluster analysis of prey groups among **small male winter caught** snow crabs (*Chionoecetes opilio*) from the Barents Sea.

5. Discussion

5.1 Probable future geographical distribution

For the purpose of this thesis the widest tolerance ranges for the limiting factors are used, to understand the maximum distribution potential of the Barents Sea snow crab. Some factors, such as chemical conditions will not be dealt with due to limitations in the work with this thesis.

5.1.1 Migratory behavior

The long-distance dispersal of snow crabs primarily happen in larval stages, which is controlled by advection (Conan et al., 1996). As the Goose Bank is the primary spawning and hatching ground (Alvsvåg et al., 2009), larval advection will primarily spread from here. These larvae will later settle in other areas, and benthic stages can spread from there. While large male crabs can move several miles over a few days (Conan et al., 1996), it may be the migratory behavior of females that limits the distribution of a self-reproducing population, as it takes females to reproduce. Multiparous females can even reproduce without male presence if they carry spermatophores. Adult females are not known to move over large distances, even if this cannot be ruled out.

5.1.2 Temperature

As a stenothermic species temperature is a significant limiting factor. For the establishment of self-reproducing populations early benthic stages is the weakest link limiting distribution. These stages prefer temperatures between 0.0°C and 1.5°C (Dionne et al., 2003), although they are found outside this range.

There are several temperature ranges described for larger snow crab in the literature. As there are not enough history or documentation for the Barents Sea population, one of the broadest temperature ranges described in the literature will be used for the purpose of this discussion, which is -1°C to 5°C (Anon., 2005a). Alvsvåg et al. (2009) has described an narrower range in the Barents Sea, -0.7°C to 3.4°C, but this is based on limited data in early stages of the population development, so there is not sufficient evidence to conclude that the Barents Sea snow crab have such a narrow temperature tolerance. Provided that snow crab can establish permanently with significant abundance in areas where the bottom temperature does not deviate from the range -1°C to 5°C, the following question is: Which parts of the Barents Sea falls within this range?

The Barents Sea experiences extreme seasonality and has a rather clear temperature shift over the Polar Front. North of this the temperature is low (but bottom temperature will not fall below -1°C), while the southern part of the Barents Sea, and especially the southwestern part is heavily influenced by warm Atlantic water. In the deeper regions (200 m), only a small part of the southwestern Barents Sea had a mean temperatures of 5°C (fig. 3.2) in the warmest month in the 20th century. In the same period (October) a 4°C thermocline has created a barrier toward the Norwegian coast in the warmest part of the year if the climatic patterns are similar to the preceding century (Matishov et al., 1998). For shallower waters that situations is slightly more limited, especially as early benthic stages prefer shallow grounds and are the most sensitive to temperatures. If the climate warms even more the entire southwestern part of the Barents Sea will be uninhabitable for snow crab, while the southeastern Barents Sea and the northern Barents Sea including Svalbard, seem to be within the temperature range of snow crab even in the warmest periods (fig 3.2). It is expected that climate change will significantly affect the biogeographic boundaries of the Barents Sea (Jørgensen et al., 2014). This entails significant uncertainty, and will not be further pursued in this thesis.

5.1.3 Depth

Snow crab is in native habitats found at depths between 4-1400 meters (Yosho and Hayashi, 1994; Lovrich et al., 1995), and it is known that depth distribution varies across different geographic areas. It is also a clear difference in depth distribution among life stages and size classes, where larger crabs are found at larger depths. Mating happens at shallower waters. It is my hypothesis that the distribution is not limited by depth in it self in the Barents Sea. Distribution is therefore primarily a function of temperature and bottom substrate, which are partly functions of depth.

In the Barents Sea the depth is rather similar over the whole, with a mean depth of 230 meters, and a maximum depth of 500 meter (Wassmann et al., 2006), that cannot be considered a barrier as snow crab is found at greater depths elsewhere. There are thus no large depths limiting the migration of adult snow crab within the Barents Sea and the upper depth limit is likely more determined by the position of a thermocline as well as bottom substrate.

5.1.4 Bottom substrate

It seems as snow crab primarily settles on muddy bottom. This is likely due to feeding behavior, as well as a possibility to bury within the sediment for protection. Muddy bottoms are where we can expect most of the population to settle, but research has also shown that the relationship to sediment is rather opportunistic, and that early benthic stages settle anywhere predation and cannibalism can be avoided (Conan et al., 1996).

In the Barents Sea finer muds predominate in deeper area with slow water movement in northern and eastern areas, while the southwestern region with shallower water and more energy has more of a hard bottom substrate.

5.1.5 Food

The feeding of snow crab is not only a component in deciding the ecosystem effect, but also a factor limiting the species distribution. Snow crab has an omnivorous diet, and thus not likely to be limited by specific prey taxa. However, it can be argued that benthic stages have a large demand for calcareous prey items, but it seems both bivalves, crustaceans and gastropods are common all over the Barents Sea.

5.1.6 Conclusion

With only a limited assessment, it is possible to draw some conclusion on potential habitat for snow crab in the Barents Sea. There are no major barriers limiting the distribution of benthic stages in the Barents Sea. Due to temperature restraints, it is not likely that the snow crab will colonize the coast of Norway or the southwestern Barents Sea during the current climate regime. Thus it will likely not overlap with the red king crab in distribution. In general, bottom temperatures are low throughout the year. The sediments are primarily suitable in all other regions than the southwestern. We can conclude that snow crab may spread across most of the Barents Sea and colonize southeastern parts, as well as the north including the Svalbard Fishery Protection Zone.

Provided that it is possible to get access to updated data on annual maximum and minimum seafloor temperatures from the Barents Sea, as well as detailed data on sediments, and draw some assumptions on the Barents Sea snow crab, it is possible to perform a more thorough GIS-analysis[8] of the potential distribution area of benthic stages of snow crab. Looking at ocean currents, it is also possible to estimate where the main larval distribution will go.

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[8] Geographical information systems (GIS) are computer software tools designed to capture, store, analyze and present all types of spatial data (Wikipedia).

5.2 Ecosystem effects

As mentioned, ecosystem effects are a combination of distribution, population size and trophic interactions. In this chapter trophic interactions and the role of snow crab as a novel species in the Barents Sea will be discussed, as well as the international legal framework to deal with non-native species.

5.2.1 Snow crab diet in the Barents Sea

From the nature of method of analysis of the sampled crab stomachs, the results present no quantitative information on how much food is consumed by snow crab in the Barents Sea. A present/absent investigation neither reveals how prey items are consumed, (what comes through e.g. scavenging and what is the result of direct predation) or gives us information on when items were consumed (it is difficult to tell how long items stay in the stomach before they are decomposed). In addition a lack of experience of the investigator reveals clear weaknesses within the results. Combined with a low number of snow crab stomachs in the sampled material, the lack of females and small crabs, and the lacking overlap of winter and autumn stations, the results of this study are of limited value to reach any conclusions on the Barents Sea snow crab population. However, the results help to shed light on the population and reveal new questions and hypotheses.

The results from the stomach analysis show, in accordance with results from other areas, that the Barents Sea snow crab is a highly omnivorous benthic feeder. The highest occurring prey item independent of seasonality and size classes is Bivalvia, this can perhaps partially be attributed to a need for calcium carbonate for molting, in addition to other nutrients. Bivalvia is a class of animals that filter water and thus is suspected to have an important role in the remineralization and redistribution of organic carbon reaching the seabed, thus an impact on Bivalvia can potentially have an impact on the ecosystem as a whole. This is dependent, however, on the quantities consumed.

Polychaeta is the second highest occurring group of animals, and it is not unlikely that a significant portion of the indetermined part of the stomach content is polychaetes, so its significance might be even higher. Northern shrimp (*Pandalus borealis*), which is also subject to a fishery, has been known to correlate with polychaetes. If snow crab highly affect the polychata community, and northern shrimp depends on this class of animals, this can have an effect on the commercial shrimp stock.

Crustacea is the third highest occurring group of prey animals. From observed stomach content it is likely that shrimp constitute a major part of the Crustacean stomach content, thus it is possible that the snow crab population may directly affect the population of various shrimp, among them northern shrimp. It has been found a negative correlation between biomass of snow crab and shrimp in the Barents Sea, but for now the predation by snow crab is said to have negligible effects (Dvoretsky and Dvoretsky, 2015). What the future will bring, however, is unknown.

Echinoderms are also among the most common prey items; a phylum known to play an important role in redistribution and remineralization of organic carbon on Arctic shelves (Bluhm et al., 2009). A change in abundance and composition of echinoderms may as such lead to large structural changes in the ecosystem. Also as Foraminifera is highly occurring in the Barents Sea snow crab diet and represent an important link between lower and higher levels of the food web (Gooday et al., 1992), this can potentially have an effect on the ecosystem as a whole.

Bony fish is also a prey item in the Barents Sea, but not one of the main prey items according to the diet analysis. From other areas, such as Newfoundland, it has been shown that capelin, the Atlantic spiny lumpsucker and species of redfish has been the primary fish prey species (Squires and Dawe, 2003). These are both ecologically and commercially important fish in the Barents Sea, so an effect on these can have substantial ripple effects. It has to be noted, however, that is not certain if the occurrence of fish in the diet analysis are primarily the result of scavenging or predation. The abundance of eggs was very low in the sampled material, and as described, the consumption of capelin eggs by red king crab does currently not pose a threat to the capelin population (Anisimova et al., 2005; Mikkelsen, 2013). From this we can conclude that it is unlikely, although not impossible, that snow crab will have an effect on commercially important fish species in the Barents Sea. Snow crab might have a larger effect on fish stocks as competitor for food than as a predator.

There are significant differences in feeding behavior between size-classes of snow crab and between seasons (remember: the data must be considered preliminary and cannot be considered fully comparable). Especially the difference in occurrence of Foraminifera depending on size-class and seasons is apparent. Foraminifera are highly occurring in large snow crabs caught in autumn and small crabs during winter, but not in large crabs caught during winter. It is of relevance to note that there was an absence of small autumn caught snow crabs in the data set. The same is the case for Bivalvia that is close to occurring in 100% of small crabs during winter and common in large autumn caught crabs, although less common in large winter caught crabs. For small snow crabs, this can be attributed to the mentioned need for prey with calcareous shells, providing calcium carbonate needed for molting, which naturally should be more prevalent for small snow crab. This may also explain that small male snow crabs caught during winter consume significantly more crustacean than large snow crab caught both during winter and autumn. The presences of crustaceans could also imply cannibalism, due to the fact that smaller size-classes to a larger degree overlap and perhaps a higher density. Autumn caught large snow crab consumes significantly more Gastropoda than both large and small snow crab caught during winter, while winter snow crab of both size-classes consume significantly more algae than during autumn. Autumn snow crabs consume more Cephalopoda than winter snow crab of both size classes. It must be noted that there was a significant uncertainty on the identification of the items registered as Cephalopoda, as it could be spikes from Chondrichtyes instead of beaks from Cephalopoda.

These findings confirm and enhance the assumption that snow crab population in the Barents Sea is as omnivorous as in other places. It is a heterotrophic organism, and seems to be mainly carnivorous, while scavenging cannot be ruled out by these results. As omnivorous organisms finding the majority of their prey on the substrate they live on, we can expect snow crab to eat most of what they come across. It has not been identified if there is certain specific groups of potential prey items in the Barents Sea that snow crab avoid. Feeding cannot alone account for the ecosystem impact of snow crab, but is part of a puzzle that together comprises the ecosystem effect. While many prey items in the native areas of snow crab are similar to the ones in the Barents Sea, the difference is that in the native areas prey and predator have co-evolved. In the Barents Sea there has been no similar species in this scale, thus the prey species lack adaptation to the predator’s behavior, and may be heavily affected. If the overall production or biomass in the Barents Sea does not increase while the biomass of snow crab increases, this must implicate that the snow crab biomass is obtained at the cost of other species, and must influence total biomass and composition of prey items. The magnitude of this effect is determined by the impact on certain prey items and competitors, but we see from the results that the Bivalve community is a major prey item and might be impacted. Snow crabs feed on more than one trophic level, this might paradoxically reduce the ecosystem impact, as it can be considered a more "balanced harvesting", but could also cause major shifts. As snow crab is probably predated by several fish species, and itself feeds on benthic organism, it can be speculated if snow crab makes benthic biomass formerly not available to the water column available, and as such increases the harvestable production in the Barents Sea.

We know that the benthic communities are of key importance in the Barents Sea ecosystem with a high degree of benthic-pelagic coupling. If we expect the snow crab population to grow even larger and spreading across even larger areas, in an ecosystem lacking a similar highly abundant omnivorous predator, snow crab will most likely have an impact on the ecosystem and can be expected to cause changes. Dvoretsky and Dvoretsky (2015) found no negative impact on commercial fish and shrimp from neither red king crab or snow crab in the Barents Sea. It is however regarded as questionable to conclude on the effects of snow crab just yet, as the population is increasing and spreading, but we cannot know exactly what effects snow crab will have. While Dvoretsky and Dvoretsky (2015) only considered commercially important species, it is important to note that snow crab may affect other species that have not yet been investigated, which can be argued to have a value in itself, but may also hold important ecological roles or potential for future commercial benefits.

5.2.2 Snow crabs role in the Barents Sea ecosystem

It is difficult to assess how snow crab spread to and colonized the Barents Sea. There are currently no indications that snow crab was, as red king crab, intentionally introduced to the Barents Sea. One possibility is that snow crab was unintentionally introduced to the Barents Sea through human activities; it is, however, the leading perception that snow crab has migrated to the Barents Sea on its own, perhaps because of changed environmental conditions. If this is the case snow crab is an immigrant and not a non-native species according to the definitions by Falk-Petersen et al. (2006). This however, has no ecological consequences, and for all practical matters snow crab regarding the role of snow crab in the Barents Sea, it can be considered a non-native species, except for the legal debate.

If it snow crab is considered a non-native species it is also an invasive species. It is not so that all invasive species have significant effects on the receiving ecosystem. Considering the diet of Barents Sea snow crab, no major effects have been identified. It seems as if snow crab has found a niche previously not occupied, but it still may compete with other species. An interesting aspect is that snow crab may strengthen the pelagic-benthic coupling in one way by making benthic biomass (such as infauna) available to other actors in the ecosystem. Without doubt snow crab affects the benthic community through predation and foraging behavior, but it is currently difficult to assess the magnitude of this influence. As snow crab is omnivorous it may not heavily affect single species, but Bivalvia is one group that could be impacted. If the number and density of snow crab continue to increase, the effect of the species will most likely increase and get more visible. This could heavily affect the pelagic-benthic coupling, subsequently nutrient cycling and ecosystem services. Trophic cascades are difficult to predict, but should be monitored. If the pelagic benthic coupling and species composition in the Barents Sea go through changes due to snow crab, it could be considered as a transformer species.

Socioeconomic processes are different from the ecological ones, because they consider economic values based on goals set by society. While from an ecosystem point of view changes do not have “positive” or “negative” effects, society can consider changes as either positive or negative. For now snow crab establishing in the Barents Sea seem to be of positive value to society as the species may support a fishery of considerable future revenue, and no substantial negative effects have been uncovered. However, there is a considerable risk adherent to the establishment, and cost may be uncovered at a later stage. As such snow crab may prove to be(come) a pest.

5.2.3 Legal framework on management of non-native species

As snow crab is to our best available knowledge not an intentional or accidental introduction by human vectors, this leaves no obligations to reduce or control snow crab in the Barents Sea, as an alien species. However, UNCLOS also states that it is the sovereign right of the coastal state to exploit natural resources in accordance with their duty to protect and preserve the marine environment (art 193). To reduce or control pollution should happen in cooperation with the best practical means at their disposal and in accordance with their capabilities, and they shall endeavor to harmonize their policies in this connection (art. 194).

CBD requires the states to as far as possible control or eradicate alien species that threaten ecosystems. The lack of a definition of alien species keeps this open to interpretation, but as all definitions of alien species in invasion biology literature only include species introduced directly or indirectly by human actions, snow crab can be excluded from this definition and this part of the CBD is not of relevance to snow crab.

The government of Norway writes in a recent white paper that “alien species in the Barents Sea are mostly associated with coastal, inshore areas” (my translation) (Anon., 2015h), this can be argued to say that Norway presently does not consider snow crab an alien species. Norway is thus not obliged by international law to consider snow crab a pest species, control or eradicate it. Still, Norway has sovereignty over considerable resources, and is bound by UNCLOS to protect the environment in these areas. Norway adheres to follow management principles for sustainable fisheries from soft laws such as the FAO Code of Conduct for Responsible Fisheries (1995) and the “Ecosystem approach to fisheries” (EAF). Norway has adhered to the EAF and the precautionary approach through the Marine Living Resources Act. So from the international scene, there is no hard law on sustainable management, but Norwegian law requires the ecosystem to be taken into account, which should imply a cautionary approach to a novel organism in the ecosystem.

5.3 Rights to harvest and manage snow crab in the Barents Sea

The competence to manage snow crab within EEZs lies to the coastal states that have full rights to all living marine resources, including sedentary species. Of most interest is if snow crab is a sedentary species and can be managed as a part of the continental shelf, in resemblance with e.g. oil and gas, or not. This will be discussed together with management challenges in the Svalbard Fishery Protection Zone.

5.3.1 Sedentary or not, that is the question

It is the authorities of Norway and Russia responsibility to define whether the species is sedentary or not. This definition is of importance for the rights to harvest and manage snow crab in the Barents Sea, as the magnitude of the fishery is carried out outside EEZs but inside continental shelves. If it is a sedentary species, it is managed according to the continental shelf (UNCLOS part VI), if not is subject to high seas regulation (UNCLOS part VII). If snow crab is not a sedentary species it should be considered a straddling stock, which implicates that the coastal states are obliged to cooperate on management of the population.

The definition of sedentary organisms in UNCLOS covers organisms, which at the harvestable stage are unable to move except in constant physical contact with the seabed or subsoil. The commercially harvestable stage of snow crab at present, are large males, which together with the other benthic stages live on the seabed and bury in the sediments. According to Warrenchuk and Shirley (2002) snow crab movement could be described as lifting the walking legs, pushing and sliding the body across the substrate. If we follow this, snow crab is sedentary. If anyone wishes to challenge the classification of snow crab as sedentary, it can be questioned whether snow crabs are *unable* to move except in constant physical contact with the seabed.

The definition of "sedentary" has dramatic consequences, as it can be used to close most of the Loophole for snow crab fishers from all other countries than Russia. Otherwise this can be a significant resource for both Norwegians and other nationals as the population looks today. Either way it is potential for larger aggregations also in the Norwegian part of the Loophole and other areas of Norwegian EEZ and the SFPZ in the future. If Norway upheld the claim that Svalbard has no separate continental shelf, and thus the continental shelf around Svalbard is under full Norwegian sovereignty independent of the SFPZ, the question on sedentarity would be of relevance also to the discussion on the snow crab resource in Svalbard waters. It is argued by some (e.g. Pedersen, 2008) that this is no longer the position of Norway, and as this is a matter of politics and technicalities in law, it will not be dealt with here.

It seems as if it can be concluded that snow crab is sedentary. However, a management regime enforcing a different set of rules for vessels fishing in the water column and on sedentary species can prove challenging. Currently there are other fisheries happening in the Loophole, as this is a productive fishing ground, and it is expected an increase in conflict between fishing gear used for cod and shrimp (trawl) and snow crab (pots/traps). Such conflicts can increase if the fishing activities intensify. It could be expected that fishers might harvest snow crab with trawl to bypass a ban on snow crab fishing. Enforcing a different set of rules would imply close monitoring and controlling.

5.3.2 Svalbard and management cooperation

There is a general conflict regarding the resource rights outside the territorial waters of Svalbard. Based on the Norwegian stand there is a non-discriminatory management of resources, practiced through criteria of traditional fishing. There is no precedence for distribution of rights of new resources. The implications of the Svalbard Treaty for the SFPZ and the discussion whether Svalbard has a separate continental shelf are sensitive matters subject to both international law and politics. If snow crab becomes a commercially interesting species within the SFPZ, as is likely, this can, if it is a sedentary species, be the dress rehearsal for what will happen if petroleum resources are found in the area and are to be exploited. Snow crab in the SFPZ can also be a large enough economic resource in itself that other parties to the Treaty may challenge the Norwegian management regime. This may be avoided if Norway finds a way to wisely distribute fishing rights among interested signatory states.

The potential fishery within the SFPZ can be an argument for Norway and Russia to seek common management of the Barents Sea snow crab. This might open the Loophole and Russian EEZ to Norwegian fishers. If it is a sedentary species the arena for management can be the JNRFC, as it is solely a Russian and Norwegian resource. If it is not a sedentary species, or for the sake of practical matters in the Looophole, snow crab can be subject to management under NEAFC. Whether Norway and Russia decides to manage snow crab jointly or not depends on political will, more than international obligation to do so. It could be argued that both countries get a benefit from cooperation if management can increase yield and open larger areas for fishers from both countries. Another point is that there is no point for one of the countries to manage Barents Sea snow crab as a pest, if the other manages with a goal of highest possible production; sink effects would likely lead to continued invasions.

5.4 Mitigation or adaptation – possible management strategies

A magnitude of approaches should be considered before deciding upon a management goal for the Barents Sea snow crab, including doing nothing. Doing nothing, however, would in my opinion only be a good option if it turns out that (1) the snow crab has virtually no impact on ecosystem services in the Barents Sea or (2) there is no way of controlling population biomass (either as a pest or an economic resource). As an ecosystem effect is expected, and as experience from native snow crab areas indicate that population biomass can be affected by fishing, these prerequisites are not present. Thus a management goal and strategy should be implemented.

Eradication or control of the Barents Sea snow crab may be considered an unreachable goal, but it is likely that environmental non-governmental organizations (NGOs) will advocate for a removal of snow crab from the ecosystems, as they have with red king crab. Thus even if there is no evidence suggesting that snow crab is currently a pest, or international treaties forcing action, it is of interest to discuss two management strategies[9], “the pest control strategy” and “the ecosystem based fishery strategy”.

5.4.1 Pest control strategy

If the species is considered a pest and the countries want to eradicate or control the species there are several possible management measures. The cost of physical removal increases as the population density decreases, so this strategy to totally eradicate the species is considered impossible, as the cost would sky rocket. In addition, if there is a possible connection to other populations that act as sources, we can expect continued sink-effects and continuous establishment as long as the environmental conditions facilitate it. Physical removal can however be a strategy to keep a population within certain limits, and can be combined with a harvest regime. If such an approach is chosen, it should consider physical removal of smaller crabs in addition to commercially sized males.

Another approach is to implement biocontrol measures, which might be considered a radical step, as biocontrol has to a negligible degree been practiced in open marine ecosystems. Such a step could pose threats to other species, especially similar decapods such as *Lithodes maja*, in the ecosystem. If not bullet proof in terms of collateral damage and host-specificity, biocontrol would likely not be supported by most environmental NGOs either. A parasitic castrator might be the best option of biological control, but this could be achieved by other means as well, such as biotechnology. As it is highly unlikely that there exists an organism that solely targets and efficiently controls snow crab in the Barents Sea, it can be concluded from the risk and cost of such a measure that biocontrol is not an appropriate pest control measure in this case.

Evolutionary management is another possibility. If certain native species are heavily affected, they could theoretically be functionally or evolutionary trained to withstand effects from snow crab. But, in large ecosystems like the Barents Sea this cannot be done for the whole array of potentially impacted species.

The last option would be biocides. To find a biocide solely targeting snow crab would not be possible, thus other species would be impacted. This is a solution for smaller aquatic ecosystems, such as rivers and lakes, and used to combat parasites such as *Gyrodactylus*

[9] These strategies do not include maximum fishery profitability.

salaris (see e.g. Johnsen and Jenser, 1991), but would not be compatible for a whole sea. Biocides are not considered a palatable solution politically for a large area.

As described, there are several theoretically possible management options for a pest in an open marine, but most of them have severe side effects with the potential to cause significant ecosystems effect, even worse than snow crab. As snow crab has not yet shown any signs of detrimental effects unbearable to the ecosystem or unbearable to stakeholders, the costs of controlling or eradicating the species are too high.

5.4.2 Ecosystem based fishery strategy

If the Barents Sea snow crab is viewed as a commercial resource, it presumably will be managed under the current Norwegian-Russian goal on an ecosystem based management. Implicitly, the sole purpose of the fishery is not maximum economic yield. This could give weight to a potential impact on native species. Some fishers even argue that the unknown effects on the ecosystem is an argument for a liberal management regime (Anon., 2014j).

Several issues need to be addressed when designing a management regime. At first a goal needs to be put in place. The three management strategies for fluctuating resources is as mentioned (chapter 2.8) to either stabilize the exploitation rate, catch or escapement. A fourth option could be introduced when dealing with a non-native species that should be controlled: Stabilize population size. Taking the risks of a non-native species into account, it can be of interest to set a limit for a maximal desired biomass, and adapt the effort to this. This would be in line with the precautionary approach. Thus, a management goal for Barents Sea snow crab could be "keep the population within a level that reduce the risk of impairing ecosystem services and sustains a commercially viable fishery".

Taking the goal into account, a main management measure should be chosen to reach a desirable population level. Initiating a fishery on a stock that is evolving poses challenges, as it makes it even harder to understand if population levels are fluctuating due to fishing activity or environmental factors such as ecosystem responses to the new species. In the early phases a total allowable catch quota may not be advisable, as it is of interest to get information about how the population evolves under fishing activity. In addition it is of interest to gather as much information from the fishers as possible, and if they have no legal limits, they have no incentives to lie in their reports. When more information on the population is available relevant measures to reach the defined goal could be harvest control rules (HCR) or a total allowable catch (TAC), or a combination of the two. For a cyclic resource it is common to conserve the reproductive potential by sex, size and season.

A major difficulty when managing snow crab populations is understanding fluctuations in the population size. If the Barents Sea population reveals patterns similar to the cyclical nature seen in Canada and Alaska, one may ask if fluctuations can be dampened, or if biomass levels can be predicted several years in advance.

In addition to biomass levels, several issues need to be addressed when deciding on fisheries regulation. As only large males are commercially interesting, it should be decided if a minimum size limit should be implemented as in other snow crab fisheries. For other crustaceans, such as the European lobster (*Homarus gammarus*), preserving larger individuals is a good thing as they continue growing throughout their life and increase fertility. This is not the case for snow crab, which has a terminal molt and suffer from decreasing quality. A male-focused size-selective fishery has the potential to reduce the average size of the males in the population, reduce the density of males in the population, and/or raise the ratio of females to males. All of these effects may change the mating dynamics of the population by reducing the amount of sperm that males provide to females and decreasing the number of males available for copulation (Carver et al., 2005; Fenberg and Roy, 2008). Thus some sort of a balanced harvesting regime should be considered (see e.g. Zhou et al., 2010), this could increase harvested biomass, and if alternative uses for small crabs are found, for example within bioprospecting, balanced harvesting could even increase profitability of the fishery.

It should be decided if it should be a particular fishing season, and this should be considered according to both mating seasons, proportion of soft-shell as well as if there are any seasons the condition, and thus quality and value, of crabs are better. The results of this thesis show a higher weight for large male crabs of the same size during winter than autumn, which could be used as an argument for a winter fishery. This should, however, be weighed up against weather conditions as well as soft-shell and mating interference.

Bycatch of non-targeted snow crab as well as other species should be avoided to the extent possible, thus selectivity in fishing is important. In addition soft-shell (molting) crabs should be avoided, to let these reach commercial quality. This can be achieved by closing the entire fishery in seasons with high occurrence of soft-shell, or close specific areas when the proportion of soft-shell is high are possible solutions. If there is bycatch, measures to lower handling mortality are important. Such measures include reducing time of air exposure and height of release. In addition technical regulation to avoid ghost fishing, such as biodegradable twine should be considered to ensure sustainability.

6. Final remarks

Several disturbances are acting simultaneously in the Barents Sea; a materialization of human influence is the occurrence of plastic in 20% of the snow crab stomachs. What effect the plastic has on snow crab (if any) is unknown. In addition the ecosystem is under stress from a changing climate and shifting biogeographic boundaries. The establishment of snow crab in the Barents Sea can be seen as either a natural expansion of distribution with prospect of substantial new commercial benefits, or as an alien invasion of a dangerous pest. The unavoidable matter of fact is that snow crab has established in the Barents Sea and is likely to spread throughout most of the eastern, central and northern Barents Sea. Snow crab may occupy a niche in the ecosystem with little competition and potential for severe impacts on the ecosystem. If the population grows large enough it may impact pelagic-benthic coupling and can eventually lead to a trophic cascade. The extreme outcome would be a total collapse of the ecosystem and the Barents Sea fisheries. With a simple and short food chain the Barents Sea is rather vulnerable, but a collapse is still highly unlikely, as ecosystems generally are resilient and dynamic.

Ecosystem effect is a rather vague term, although it represents the essence of what we need to understand about the snow crab colonization of the Barents Sea. It is difficult to obtain sufficient information on ecosystem effects, but there are indicators, pieces of the puzzle, that helps us understand. Information on the diet is one such piece. Currently, what is primarily needed for the snow crab resource is more research. The available data is very limited, as Norway is not running any stock assessments. A condition for acquiring a license for fishing snow crab could thus be to collect population data such as size, weight, numbers and so on. The need for more research is urgent, and as a potential for substantial future profit, the government could be anticipated to have an interest in investing in such research. Present knowledge weighs towards describing snow crab more of a disturbance than a disaster to the Barents Sea ecosystem as it is likely to influence the pelagic-benthic coupling, but not impair it. By making benthic biomass available to the water masses the Barents Sea snow crab might in fact strengthen the pelagic-benthic coupling.

From a biological point of view the debate on whether snow crab is sedentary or not is rather intriguing, as the understanding of sedentary in biology and law are two different things. Following from an online dictionary sedentary species is either (a) not migratory or (b) permanently attached to something (Anon., 2015j). Snow crab is not attached to the seafloor and migrates throughout life. It may even have migrated to the Barents Sea. In addition the snow crab life cycle consists of several planktonic stages. Following from this few biologists would conclude that snow crab is sedentary. Still, following a strict interpretation of the wording in UNCLOS, snow crab is at the harvestable stage (for the most) in constant physical contact with the sea floor, and can be argued to be sedentary. This implies that most of the commercial stock is Russian, but as the potential distribution range of snow crab in the Barents Sea is substantial; large commercially interesting densities of snow crab can be expected within Norwegian continental shelf within a few years. That is, if the spreading keeps the current speed. Thus a joint management regime of Norway and Russia with mutual access can be seen as beneficial for both countries. A joint management could in combination with management advice from ICES contribute to a greatly improved knowledge basis.

As snow crab proves to be of high commercial value, most stakeholders will consider the benefits of the novel organism much higher than the potential costs. If snow crab later show to have detrimental effects to the ecosystem, eradication or control strategies should be considered once again. At present there are no available tools to eradicate snow crab from the Barents Sea, but physical removal can be used to control the species, and as such be combined with an income-yielding fishery. A key question then is if the fishery's primary goal should be to control snow crab or to yield the highest possible economic revenue. As Norway adheres to the precautionary approach, and there is considerable uncertainty connected to the effect of snow crab, it could be argued that it is acceptable to implement a regime of high utilization, with the risk of overfishing. The worst-case scenario of such an approach would be a collapse of the snow crab population, which could be considered acceptable by some, as it might bring the ecosystem back to a more "native" state. It seems likely that a management regime will seek both biological and economic sustainability. As it is likely that neither geographical distribution nor population size have stabilized, a management regime will need some wiggle room.

Currently snow crab is closer to becoming a goldmine than a pest in the Barents Sea. No matter what the view of the species is, a profitable fishery proves to be a key component in the management strategy.

7. References

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Appendix

Figures

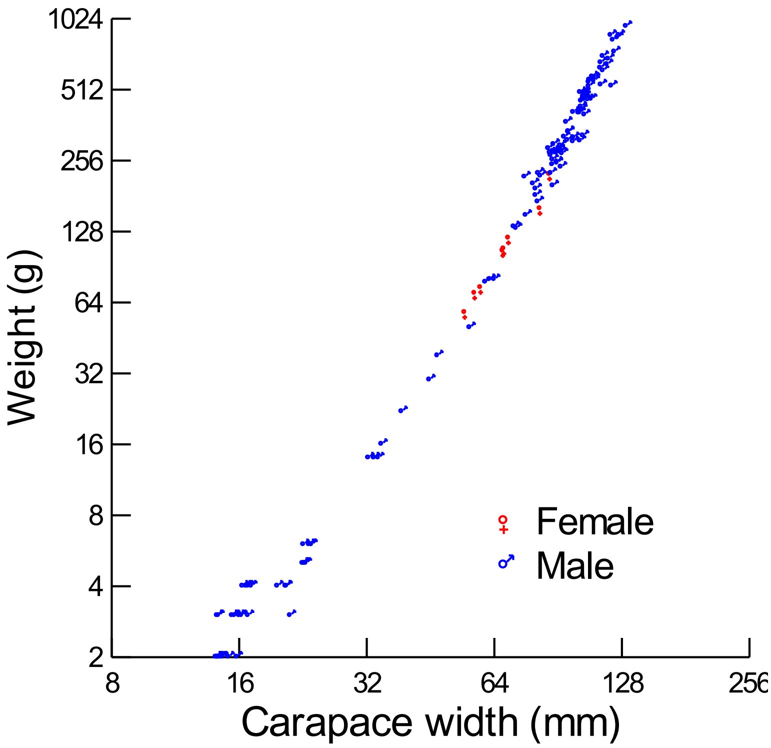

Figure A1 Weight-width relationship for male and female snow crabs (*Chionoecetes opilio*) caught in the Barents Sea. Note log scales.

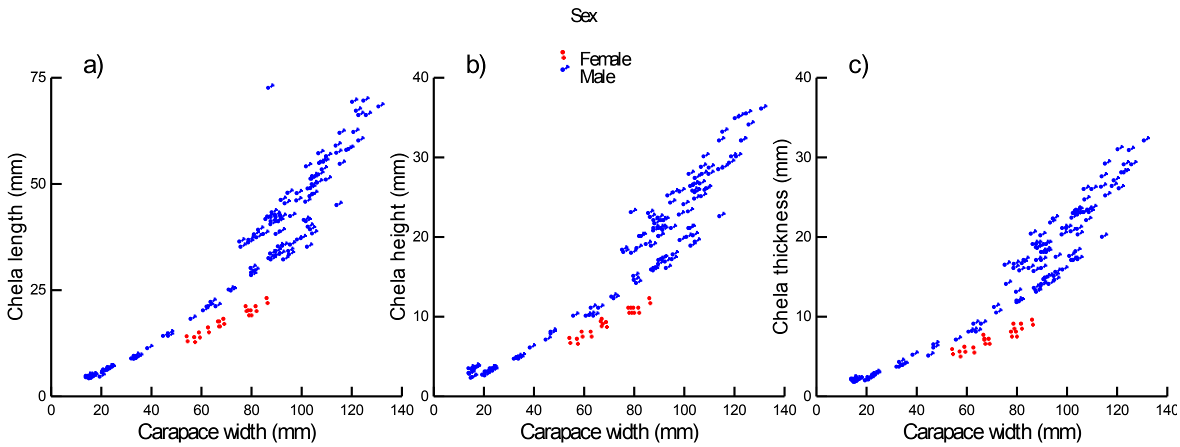

Figure A2 Chela-carapace width relationship for snow crab (*Chionoecetes opilio*) caught in the Barents Sea without log scales.

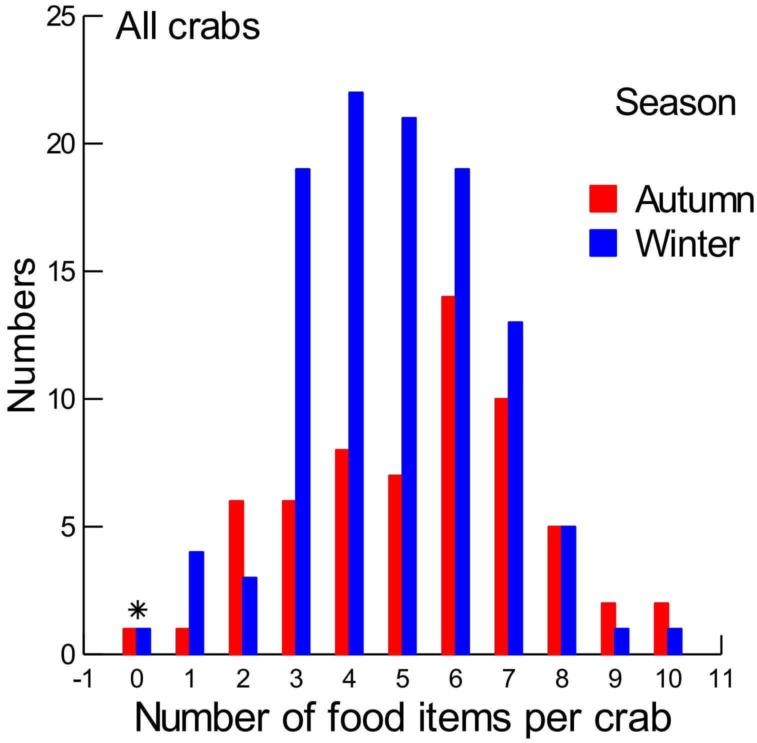

Figure A3 Number of food items for autumn and winter caught snow crabs (*Chionoecetes opilio*) from the Barents Sea. * marks number of empty stomachs.

Tables

Table A1 Stations with collected snow crab (*Chionoecetes opilio*) from the Barents Sea used for diet analysis, with information on position, depth (m), season, sex (1=female; 2=male) and size class (small<40 mm CW; large>40 mm CW).

St	Latitude	Longitude	Depth	Season	Sex	Size class	Number
38	76,8417	35,7900	159	Autumn	2	Large	1
2347	75,1933	39,3900	202	Autumn	2	Large	1
2383	75,7650	39,8683	287	Autumn	2	Large	6
2385	75,6867	42,1017	288	Autumn	2	Large	31
2387	76,2350	42,5350	287	Autumn	2	Large	1
2397	76,4100	37,8350	241	Autumn	2	Large	1
2414	75,7033	42,1067	306	Autumn	2	Large	5
2416	76,2233	42,5433	283	Autumn	2	Large	1
2419	76,8233	42,8783	213	Autumn	2	Large	2
2662	77,0195	37,9478	190	Autumn	2	Large	1
2383	75,7650	39,8683	287	Autumn	1	Large	2
2385	75,6867	42,1017	288	Autumn	1	Large	3
2387	76,2350	42,5350	287	Autumn	1	Large	1
2414	75,7033	42,1067	306	Autumn	1	Large	3
2419	76,8233	42,8783	213	Autumn	1	Large	1
2383	75,7650	39,8683	287	Autumn	2	Small	1
2416	76,2233	42,5433	283	Autumn	2	Small	1
70057	73,5657	35,9471	249	Winter	2	Large	1
70327	76,3533	35,5283	287	Winter	2	Large	2
70337	76,8817	28,8133	204	Winter	2	Large	1
70341	76,3400	33,8200	281	Winter	2	Large	1
70343	76,3450	35,3483	288	Winter	2	Large	1
70344	76,3400	36,6183	264	Winter	2	Large	2
70348	74,3383	33,0967	268	Winter	2	Large	1
70389	73,2533	35,2517	249	Winter	2	Large	2
70400	70,2717	36,5317	167	Winter	2	Large	1
70416	71,5917	38,2033	340	Winter	2	Large	1
70425	71,7000	44,0933	167	Winter	2	Large	1
70427	74,1400	23,5900	407	Winter	2	Large	1
70428	70,7183	43,6967	85	Winter	2	Large	1
70439	71,1483	45,5333	242	Winter	2	Large	1
70443	71,3400	47,2683	140	Winter	2	Large	18
70444	71,0917	47,1567	194	Winter	2	Large	14
70445	70,8200	47,0300	155	Winter	2	Large	7
70446	70,5183	46,8817	106	Winter	2	Large	2
70451	71,7650	49,2433	119	Winter	2	Large	1
70453	72,2700	49,5533	110	Winter	2	Large	1
70454	72,1233	47,7967	229	Winter	2	Large	5
70344	76,3400	36,6183	264	Winter	1	Large	1
70422	71,7850	40,7883	346	Winter	1	Large	1
70443	71,3400	47,2683	140	Winter	1	Large	1
70444	71,0917	47,1567	194	Winter	1	Large	1

70445	70,8200	47,0300	155	Winter	1	Large	2
70451	71,7650	49,2433	119	Winter	1	Large	1
70328	76,3417	36,6383	265	Winter	2	Small	1
70329	76,1150	36,8317	249	Winter	2	Small	1
70333	75,6633	34,3800	194	Winter	2	Small	1
70365	72,6317	36,9467	228	Winter	2	Small	1
70444	71,0917	47,1567	194	Winter	2	Small	3
70446	70,5183	46,8817	106	Winter	2	Small	1
70448	70,9867	48,7583	128	Winter	2	Small	10
70449	71,2467	48,9133	127	Winter	2	Small	5
70450	71,4867	49,0450	128	Winter	2	Small	3
70452	72,0283	49,4467	119	Winter	2	Small	6
70453	72,2700	49,5533	110	Winter	2	Small	2
70454	72,1233	47,7967	229	Winter	2	Small	3

Table A2 Seasonal and size effect on different prey items of snow crab (*Chionoecets opilio*) from the Barents Sea. Results from x^2-test (2x2 table) on present/absent of respective prey items. Since many of the tests have expected values less than 5, Fisher's exact test was used. Number of stars indicate grade of importance in discrimination over both season and size class. Line indicates a separation of “good date” (upper part) and “bad data” with very low expected values (lower part).

	All male	Large male	Winter male	
Prey item	Effect by season	Effect by season	Effect by size class	
Ind	0,043	0,126	0,480	*
Biv	0,059	0,003	< 0.001	***
Pol	0,177	0,369	0,268	
Cru	0,864	0,571	0,038	*
Ech	0,080	1,000	< 0.001	*
For	0,013	~ 0,001	0,006	****
Gas	< 0.001	~ 0,001	0,803	**
Pla	0,212	0,371	0,795	
Alg	~ 0,001	0,012	0,155	**
Ost	0,113	0,655	0,002	*
Cep	0,006	0,023	0,707	**
Por	0,367	0,531	1,000	
Egg	1,000	0,729	0,083	
Hyd	0,338	0,318	1,000	
Mol	1,000	1,000	0,552	
Bry	0,551	0,255	0,297	
Tun	0,267	0,581	1,000	
Nem	1,000	1,000	1,000	