UiT THE ARCTIC UNIVERSITY OF NORWAY

Faculty of Biosciences, Fisheries and Economics

Department of Arctic and Marine Biology

Reproductive ecology of female snow crab (*Chionoecetes opilio*) in the Barents Sea

Maturation, fecundity and brooding

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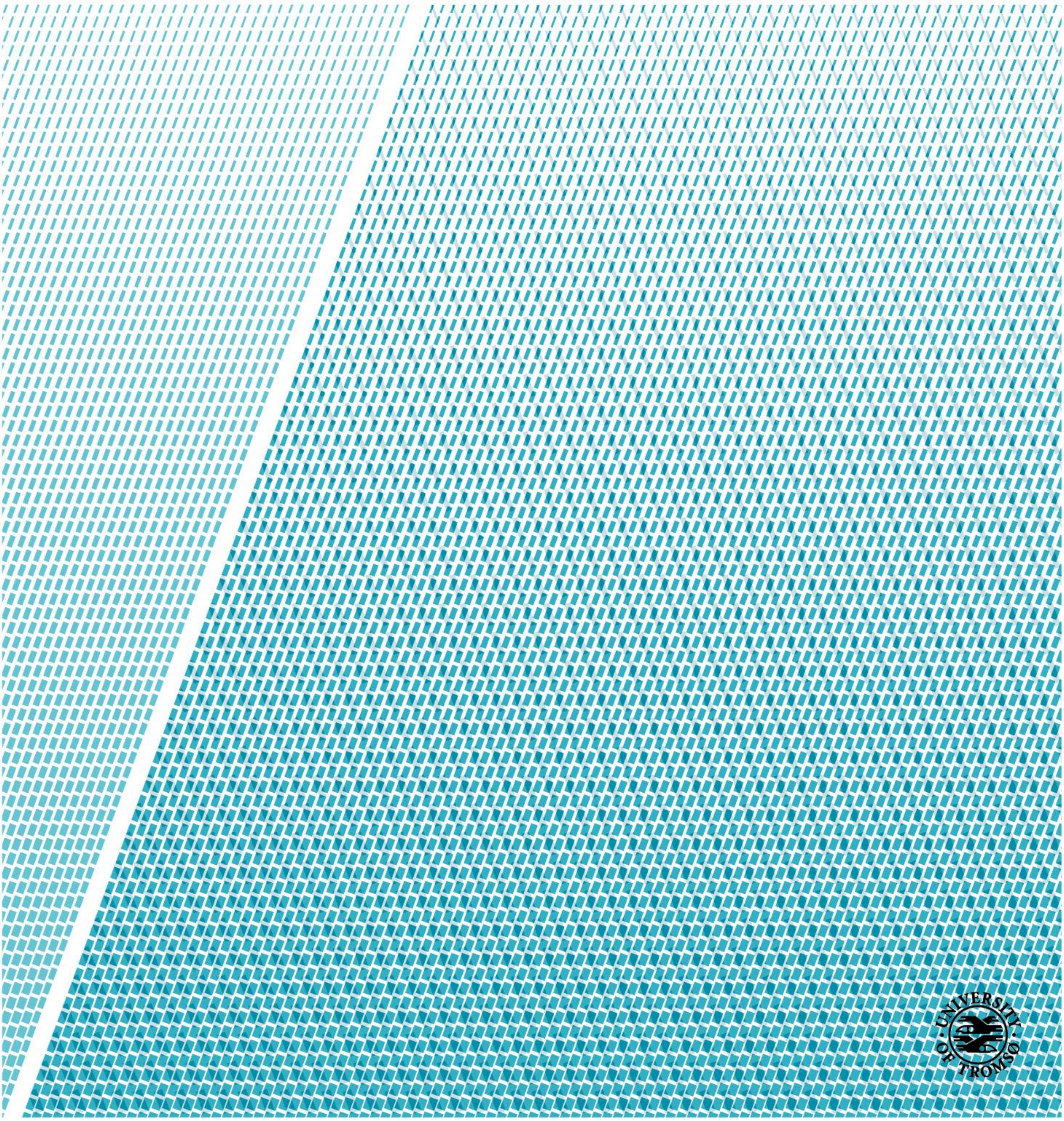
Hanna Ellerine Helle Danielsen

BIO-3950 Master's thesis in Biology, May 2018



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Supervisors:

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Abstract

The snow crab (*Chionoecetes opilio,* O. Fabricius 1788) relatively recently (first reports in 1996) established a population in the Barents Sea. Both the populations size and distribution area have drastically increased since then, and the species is now distributed over large parts of the northern and eastern Barents Sea, and further expansion northward and westward has been predicted. Despite an emerging fishery, the Barents Sea stock is poorly investigated with regards to basic biological properties important for fisheries management. The aim of this study was to describe several aspects of the reproductive ecology of female Barents Sea snow crab including estimates of fecundity, egg survival during brooding, size at maturity, and incubation cycle. In total, 4 133 female and male crabs were sampled between February 2006 and September 2017 from the central Barents Sea. Of these crabs, 1 803 were females with a size range of 10-100 mm carapace width (CW), and 2 330 were male crabs that ranged from 7-145 mm CW. About 54% (2 233) of all crabs (female and male) caught were between 15 and 20 mm CW. The size range of mature (and ovigerous) females was 48- 100 mm CW. Immature females ranged from 10 to 77 mm CW. The size of 50% maturity was estimated to be 62 mm CW. Most of the females (95%) had 100% clutch fullness. There was a significant positive relationship between fecundity (y) and carapace width (x) which can be described by the equation $y = 0.24 * x^{2.93}$. The modeled relationship gives an estimated fecundity of a 75 mm CW female (which was the mean size of mature females) of ~ 77 000 eggs in one reproductive cycle. From the observed fecundity and size frequency distribution it was deduced that more than 50% of the eggs in the Barents Sea population are produced by females between 65 and 79 mm CW. The categorization of primiparous and multiparous females based on exoskeleton condition was shown to be problematic. No evidence of egg mortality during brooding was found. Simultaneous occurrence of females with different developmental stages of the broods, and differences in ovary weight between these females at the same size suggest the existence of a biennial egg brooding cycle in the Barents Sea. Further research on the reproductive ecology and spatial dynamics of the Barents Sea snow crab population is advised.

Keywords: Snow crab, *Chionoecetes opilio,* reproduction, fecundity, Barents Sea, brooding, spawning, egg clutch, size-fecundity relationship, life history

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Glossary

- Abdomen/Abdominal flap – posterior part of the body, which is folded forward and in mature females covers the entire ventral side of the body and is used to hold fertilized eggs
- Brood - Used synonymously with “clutch” and “egg clutch”, see below
- Brooding – Keeping fertilized eggs under the abdominal flap from egg extrusion to larval release
- Carapace – the dorsal part of the shell covering the cephalothorax of the crab
- Clutch/ egg clutch – the body of eggs kept under the abdominal flap. Used synonymously with the noun brood
- Immature – male and female crabs that are morphologically immature, and for females that also means it is physiologically immature. Immature crabs include pubescent crabs
- Instar – a developmental stage, the period between molts
- Mature – Individual who is or has been physiologically capable of reproducing, for females this includes the two stages primiparous and multiparous, see below
- Molt – ecdysis, the event of shell changing
- Multiparous – female crab that has spawned two or more times
- Ovigerous female – female carrying eggs externally under the abdominal flap
- Primiparous – female crab that has only spawned once
- Pubescent – An immature individual, but with visible/clearly detectable ovaries

1 Introduction

1.1 Snow crab; a new species in the Barents Sea

The snow crab (*Chionoecetes opilio*, O. Fabricius 1788) is naturally distributed in the Bering, Chukchi and Beaufort Seas in the north Pacific and in Newfoundland and western Greenland in the northwest Atlantic (Figure 1). There are also reports of snow crabs found in the Laptev, East Siberian and southwestern Kara Seas (Zimina, 2014). It has relatively recently established a viable population in the Barents Sea; the first reports of snow crab in these waters came from Russian fishermen who found five grown specimens in the bank-areas in the southeast Barents Sea in 1996, and catch of snow crab in Norwegian waters was reported for the first time in 2003 (Alvsvåg et al., 2009). Both the populations size and distribution area have drastically increased, and the species is now distributed over large parts of the Russian exclusive economic zone (Russian EEZ), the entire Loophole (international waters in the central Barents Sea), and increasing parts of the Svalbard Fishery Protection Zone (Svalbard FPZ) (Bakketeig et al., 2016) (Figure 2). A further expansion north and west has been predicted (Sundet, 2015), and indeed in 2017 three observations of small snow crabs were made north of Spitsbergen (Berge et al., 2017, Ingvaldsen, 2017).

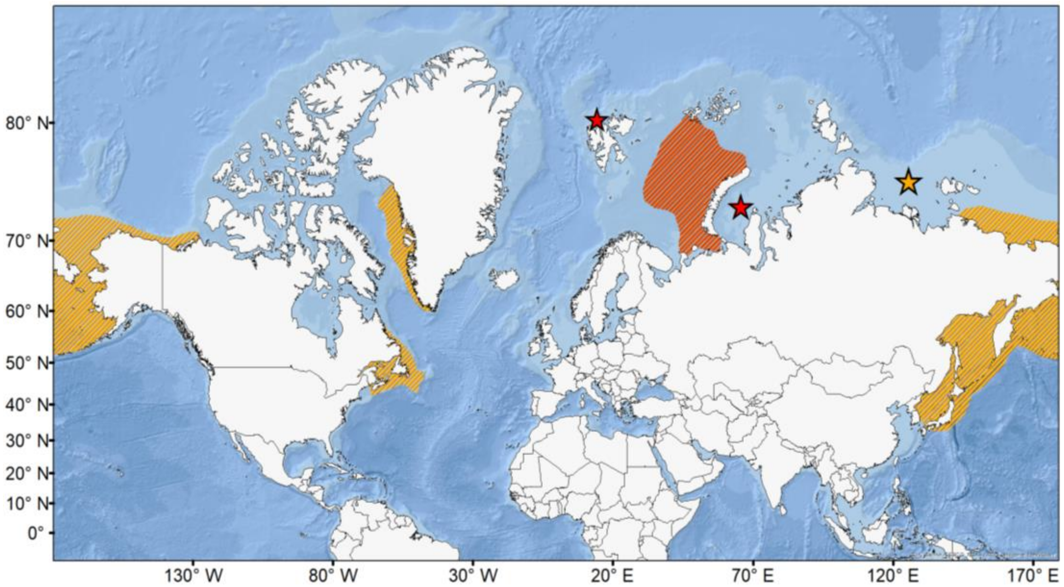

Figure 1: Map of the world-wide distribution areas of snow crab, Chionoecetes opilio. *The orange-shaded areas show the natural distribution area in the north Pacific and northwest Atlantic oceans, and the orange star represents the findings in the Laptev Sea. The red-shaded are shows the distribution of the newly established population in the Barents Sea, and the red stars indicate the recent findings northwest of Svalbard and in the southwestern Kara Sea. The map is modified from Alvsvåg et al. (2009) and Albrecht (2011).*

The introduction mechanism of the snow crab to the Barents Sea is not confirmed, but several theories have been put forward. Although the snow crab was not deliberately introduced to the Barents Sea, as was the case with the red king crab (*Paralithodes camtschaticus)* in the 1960's (Orlov and Ivanov, 1978), it has been suggested that it was unintentionally introduced together with the king crab (Zimina, 2014), presumably at the larval stage. Larval transport via ballast water in Russian fishing vessels while fishing on the Northwest Atlantic populations has also been suggested (Kuzmin, 2000, Agnalt et al., 2010, Zimina, 2014), along with the theory of natural migration from the north Pacific through the Russian Arctic Seas (Sundet, 2015). The latter is supported by findings of snow crab in both the Laptev and East Siberian Seas (Pavlov and Sundet, 2011), but contradicted by the fact that the crab was not found in the Kara Sea until 2012 (Zimina, 2014). Results from preliminary genetic analyses indicates that the Barents Sea snow crab does not originate from any of the Northeast Atlantic populations (Agnalt et al., 2011), contradicting the theory of introduction via crab-fishing vessels.

As the snow crab is a predator on the native benthic fauna (Kolts et al., 2013, Divine et al., 2017), and given the substantial size and expansion of the Barents Sea population, there is a valid concern about the effects on the Barents Sea ecosystem (Jørgensen and Spiridonov, 2013). It has been reported repeatedly, for example through the study of the effects of the invasive red king crab on Norwegian fjord systems, that alien invasive species can have negative effects on native ecosystems through predation on or competition with native species (Britayev et al., 2010, Falk-Petersen et al., 2011, Bhat et al., 2014). Due to the likely negative effect that the snow crab will cause on the native Barents Sea ecosystem, and the potential for further spreading, snow crab has been assigned the highest impact category "severe ecological risk" in the Norwegian black list (Gederaas et al., 2012).

In most of its native distribution range the snow crab stocks have for a long time supported commercial fisheries (Watson, 1970, Elner and Beninger, 1992, Burmeister and Sainte-Marie, 2010, Webb et al., 2016). The fishery in the eastern Bering Sea was one of the world's largest crab fisheries up until the end of the 1990s when it experienced a dramatic decline from which it has not recovered completely in spite of changes in management (Webb et al., 2016). Also in the Barents Sea a valuable fishery is emerging (Sundet, 2015, Lorentzen et al., 2018), and it has been predicted that the crab fishery in the Barents Sea may reach values close to the most important fish species traditionally caught in the area (Sundet, 2015).

The first Norwegian vessel started fishing for snow crab in the Barents Sea in 2012 and landed just over 2 tons of snow crab. The fishery quickly grew, and in 2015 about thirty Norwegian and foreign vessels participated, and landed just over 16 000 tons to Norwegian harbors (Norges råfisklag), most of which were fished in the Loophole (Hansen, 2016). Russian and Norwegian authorities have agreed to define the snow crab as a sedentary species (Bakketeig et al., 2016), which according the United Nations Convention on Law of the Sea (UNCLOS) gives the coastal states sovereign rights to exploit the resource on the continental shelf and relieves the two nations from cooperation on management (Hansen, 2016). This also has implications for management in the Svalbard FPZ where Norwegian authorities claim to have exclusive rights to resources on the continental shelf (including crab fisheries), but the European Union states disagree and have issued snow crab licenses to 16 vessels (Mehren, 2017). In 2017 and 2018, the Norwegian government has set the quota in the Norwegian management zone (including the Norwegian EEZ, the Norwegian part of the Loophole and the Svalbard FPZ) to 4 000 tons (Nærings- og fiskeridepartementet, 2017), following the recommendation from the Institute of Marine Research (Hvingel et al., 2017).

Given the importance of snow crab as a fisheries-resource, many aspects of the species biology are quite well studied in its native distribution areas (Elner and Beninger, 1992, Sainte-Marie, 1993). For instance, some of the earliest studies of female reproduction were carried out in Bonney Bay, Newfoundland, where the snow crab perform a spring breeding migration from deep to relatively shallow waters in April and May (Hooper, 1986). This permits close observation of mating behavior, which has been described by Watson (1972) and Hooper (1986). However, the Barents Sea stock is, despite the emerging fishery, poorly investigated with regards to basic biological properties important for fisheries management, which this study aims at describing.

1.2 Reproductive biology of female snow crab

Webb et al. (2016) argues that there is a need to move away from the use solely of mature male crab biomass as an index of reproductive potential and start considering including female reproductive capacity into the management. The following section presents some aspects of the reproductive ecology of the female snow crab, as reported from populations in the native distribution area.

1.2.1 Maturation

From the first larval stage to a full-grown adult the snow crab grows by molting (ecdysis); an event where the old shell is discarded, and a new, larger shell is formed. The development stages between the molting events are called instars and are often denoted with roman numbers. Counting from the first benthic instar, female snow crab in the Gulf of St. Lawrence have been reported to mature mostly at instar IX and X (~5.5 and 6.5 years post-larval age), and sometimes as early as instar VIII (4.5 years) (Alunno-Bruscia and Sainte-Marie, 1998). At the molt to maturity, the abdominal allometry shifts relative to the carapace; in the mature stage the abdominal flap covers most of the ventral side of the female, facilitating egg brooding (Elner and Beninger, 1992, Jadamec et al., 1999). The molt to maturity is believed to be a *terminal molt* and females go through this molt shortly before their first mating event, thus females spawning for the first time (primiparous females) do so in a soft shell condition (Watson, 1970). A female spawning for the second (or consecutive) time(s) is called multiparous. The presence of a terminal molt in female snow crab is widely recognized, however, there have been rare reports of multiparous females molting after larval release and prior to mating (Hooper, 1986). The two maturity stages are distinguished by the external appearance of the shell (color and physical marks), and absence (primiparous) or presence (multiparous) of grasping marks on the posterior pereiopods (walking legs) originating from the mating embrace (Elner and Beninger, 1992, Jadamec et al., 1999).

A life history parameter that is useful for management is the size at sexual maturation. Minimum, maximum, mean size, and size of 50% maturity (the size at which a crab has 50% chance of being mature) are commonly reported for the population, and these parameters and the relationships between them could be useful in management. It is useful to know the range and frequency of occurrence of sizes at maturity to estimate the total egg production of the population, and asses the importance of various size groups to the total reproductive potential of the stock. Parameters related to size of maturity within a population might change over time, and they are, therefore, important to monitor in exploited populations (Watters and Hobday, 1998, Hjelset et al., 2008). In snow crab, size at maturity seems to be temperature dependent ((Sainte-Marie et al., 2008, Burmeister and Sainte-Marie, 2010), see (Orensanz et al., 2007) for discussion) as crabs in cold waters mature at a smaller size than crabs residing in relatively warmer water (Burmeister and Sainte-Marie, 2010). Female snow crab start developing ovaries some time prior to the molt to maturity (e. g. at 21-29 mm CW in Atlantic Canada, reported by Alunno-Bruscia and Sainte-Marie (1998)).

1.2.2 Mating behavior

Both mature female crabs, still carrying their previous egg brood, and pubescent females, ready to molt, attract males presumably by the use of pheromones (Bouchard et al., 1996). The male, using his claws (chelae) picks up the female and carries her around by the walking legs. This behavior is called the precopulatory embrace and might last for several weeks (Watson, 1972, Elner and Beninger, 1992). During this time the male chases away other males and might feed the female. Prior to copulation, the male will facilitate either larval release (multiparous females) or molting (primiparous females) (Watson, 1972, Hooper, 1986). Multiparous females release the previous year's larvae shortly before mating again; Hooper (1986) reports that during larval release the male would hold the female up high and "*wave her back and forth*" as the female flapped her abdomen to release the larvae. This would go on for periods of several minutes at a time, and it might take several days for the female to release all the larvae (about 11 days was reported by Webb et al. (2007) for females in captivity). During copulation the male holds the female, abdomen facing up, by the backmost walking legs in the *copulatory embrace*. During copulation the male releases spermatophores into the females spermatheca, from where they will be used for fertilization. Like most brachyurans, the female snow crab has the ability to store sperm for later, autonomous fertilization (Watson, 1970, Watson, 1972). Thus, females can brood several viable clutches from one mating event, a trait that may help offset sperm limitation caused by the fishery typically focusing on the larger males (Watson, 1970, Watson, 1972, Elner and Beninger, 1995, Sainte-Marie and Sainte-Marie, 1999). Within ~24 hours after copulation, the females extrude eggs that she attaches to the pleopods. The females then brood the eggs under the abdominal flap until hatching (Watson, 1970, Elner and Beninger, 1995, Jadamec et al., 1999). The male may hold the female for some hours after copulation and egg laying, before abandoning her (Hooper, 1986, Elner and Beninger, 1992).

1.2.3 Incubation cycle

The duration of embryo development (i.e. egg brooding time) in snow crab is seemingly temperature dependent; Moriyasu and Lanteigne (1998) determined the embryo developmental time to be 24-27 months for females inhabiting the southern Gulf of St. Lawrence at water temperatures of +1 to -1°C. When females were held in captivity at 1.8-3.8 °C the embryo development was completed in 12-13.5 months, leading Moriyasu and Lanteigne (1998) to conclude that females inhabiting warmer waters would complete the brooding cycle in one year (annual cycle). Sainte-Marie (1993), who determined the embryo developmental time in the northwest Gulf of St. Lawrence to be ~27 for primiparous females, and ~24 months for multiparous females, pointed out the lack of convincing evidence for annual cycles to exist at all. The length of brooding has great implications for both the total lifetime productivity of every female, and the total yearly productivity of the stock. In an annual cycle, all the ovigerous females would release larvae every year, whereas in a biennial cycle (two-year cycle) the number of females releasing larvae could potentially be halved.

1.2.4 Fecundity

Fecundity varies with a number of parameters such as parental size and condition, resource availability and environmental factors (Lambert, 2008). These factors again, might vary over time both for the individual crab and for the population as a whole. To ensure a sustainable management, it is important to monitor fecundity over time to detect possible changes and adjust management regime if necessary.

For several snow crab populations across the species' distribution area, it has been shown that fecundity is positively related to body size (measured as carapace width, CW) (Jewett, 1981, Sainte-Marie, 1993, Comeau et al., 1999). For example in the Chukchi Sea mean fecundity of females increases from 12 900 eggs in females with 40-44 mm CW, to 37 100 eggs in females of 60-64 mm CW (Jewett, 1981). Reported values of the magnitude of fecundity increase with body size increase varies between areas (Jewett, 1981).

Female fecundity may also differ between primiparous and multiparous females. Sainte-Marie (1993) reports lower fecundity in primiparous females of about 77– 83% of the fecundity of a multiparous female of the same size and argues that this can be explained by the small body size of the primiparous female prior to maturity molt that would necessarily restrict ovary volume, and thus fecundity. Fecundity also seems to be more variable in females with old shell stage (measure of time passed since terminal molt and first mating) (Webb et al., 2016). Occasional occurrence of (presumably old) females with abnormally small broods has been reported (Sainte-Marie, 1993). Egg mortality over the incubation period is reported to range from virtually none (Sainte-Marie, 1993) to as much as 21%, being greater in larger females (Comeau et al., 1999).

Together with fecundity, size of the eggs as a proxy for quality might reveal aspects of the reproductive strategy of a species, or variations of this within the species (Ramirez Llodra, 2002). A quality-quantity trade-off might induce some individuals to invest more into each offspring; resulting in larger and/or more energy-rich eggs. Snow crab egg size increases as much as 20% during the brooding period as the embryo develops (Moriyasu and Lanteigne, 1998), Sainte-Marie (1993) reports a statistically significant difference in the egg diameter between primiparous and multiparous females, the former having slightly (1.4-2.7%) larger eggs.

1.3 Study area: The Barents Sea

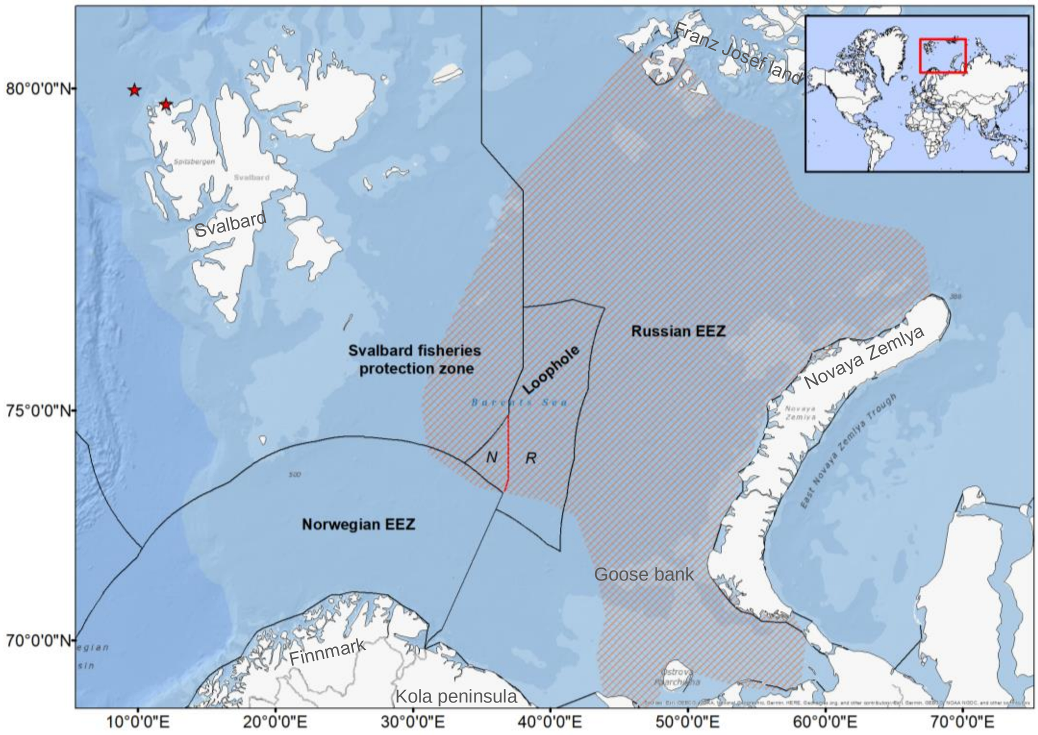

Figure 2: Map of the Barents Sea, with the marine borders marked with black lines. In the gap between the Norwegian and Russian exclusive economic zones (EEZs) and the Svalbard fisheries protection zone are the international waters, often called the Loophole. The sea floor underneath the Loophole is devided between Norway and Russia by the "Delimitation line" marked in red. The shaded area is the present confirmed distribution area of the snow crab, but observations outside this area have recently been made, such as the two observations northwest of Svalbard, illustrated by two red stars.

The Barents Sea reaches from the coast of Murmansk (Russia) and Finnmark (Norway) regions in the south to the shelf break north of Franz Josef Land and Svalbard where it meets the Arctic Ocean in the north. Novaya Zemlya defines the eastern border, and in the west the shelf break that runs from northern Norway to Svalbard marks the transition between the Barents- and the Norwegian Sea. The Barents Sea is connected to the Kara Sea north and south of Novaya Zemlya, and to the White Sea through a sound between the Kanin Peninsula and the Kola Peninsula (Ozhigin et al., 2011). Russian and Norwegian EEZs, and the Svalbard FPZ cover most of the Barents Sea, except the Loophole. The sea floor underneath the Loophole is divided into Norwegian and Russian territory (Hansen, 2016). The surface area of the Barents Sea is about 1 600 000 km^2. It is a relatively shallow shelf sea, and the bathymetry is characterized by several banks separated by deeper troughs and basins. The average depth is about 220 m, but depth ranges from 20 m at the Spitsbergen Bank to around 500 m in the Bear Island Trough. More than half of the sea is between 100 and 300 m deep (Ozhigin et al., 2011).

The Barents Sea connection to the Atlantic Ocean in the south west and the Arctic Ocean in the north is reflected in the properties of the water masses found in the different areas and depths throughout the sea. Warm saline water enters the Barents Sea by way of the North Atlantic Current between the coast of Finnmark and Bear Island, branching north- and eastwards. Cold, arctic water from the deep basins of the Arctic Ocean enters the Barents Sea from the north between Nordaustlandet in Svalbard and Franz Josef Land, and between Franz Josef Land and Novaya Zemlya. Where the two water-masses meet they form the “polar front”, which is characterized a distinct shift in hydrographical characteristics (Ingvaldsen and Loeng, 2009). The “Benthic polar front” differs somewhat in its geographical position from the surface polar front due to differences in water mass distribution (and hence temperature) through the water column (Jørgensen et al., 2015), for most of the Barents Sea the benthic polar front is situated further to the south than the oceanographic polar front. In the areas in the southwest that are dominated by Atlantic water, the temperature at the bottom is around ~5°C, as opposed to the Arctic influenced areas in the north and east where temperatures tend to be around 0°C and might reach temperatures below -1°C in deeper areas (Ozhigin et al., 2011).

The marked shift in environmental factors at the polar front is mirrored in the distribution and composition of the biological communities from zooplankton to fishes. At the seafloor, this has been illustrated by e.g. Jørgensen et al. (2015), who characterized four sub regions in the

Barents Sea based on similarity in composition of biomass of megabenthic taxa, and found that the division was explained by the hydrographic parameters depth, temperature, salinity and number of days/year with ice cover. Bottom temperature is an essential parameter for management of the snow crab, as it both affects the distribution (Comeau et al., 1998, Ernst et al., 2005) and the length of the female reproductive cycle (Moriyasu and Lanteigne, 1998, Webb et al., 2007).

1.4 Aim of the project

Recognizing the Barents Sea snow crab's ecological and economical importance as a new species in the Barents Sea, the overarching goal of the project is to contribute to the basic biological knowledge of this population. More specifically, the aim is to describe several aspects of the reproductive ecology of female Barents Sea snow crab including estimates of fecundity, egg survival during brooding, size at maturity, egg size and incubation cycle. The following hypotheses were tested and addressed by the respective objectives:

Hypothesis: The fecundity of Barents Sea female snow crab covary with body size (CW). Objective: Measure fecundity and test for correlation with carapace width, through fitting a linear regression on $\log_{10}$ transformed data.

Hypothesis: There is a significant egg loss during the brooding period, resulting in lower fecundity-at -size for females with late developmental stages for the brood, compared to females with early stage broods. Objective: test if there is a difference between the elevation of linear regressions fitted between the fecundity and carapace (as above) width of females with early and late stages of the brood.

Hypothesis: Size at 50% maturity (L50) in females does not differ from other studied populations. Objective: Determine size at 50% maturity and compare to findings from other populations.

Hypothesis: Egg size in the Barents Sea does not vary with CW. Objective: Measure egg size in the lab. Check for correlation between egg size and CW.

Hypothesis: The Barents Sea population of snow crab has a biennial egg incubation cycle. Objective: Collect females through several seasons and visually investigate the egg development stage. If the distribution of the embryo development stages is bimodal and there is no large portion of the mature females that is not bearing eggs, it is reasonable to believe that the population has a biennial egg incubation cycle (Comeau et al., 1999).

Alternative hypothesis: There is no synchronous mating season, and the disparity in egg development stage, if existing, is caused by differing time since extrusion, or; both annual and biennial occur at the same time. Objective: The investigation of female ovaries and egg mass development stages in the spring might reveal whether all mating occurs in spring.

2 Material and methods

2.1 Collaborations

The sample and data collection for this study was carried out through collaborations with Institute of Marine Research (IMR), the research group “Fisheries management, harvest technology and biology (BRIDGE)” at UiT-Arctic university of Norway, and two commercial fishing vessels; Kvitungen and Arctic Pioneer.

2.2 Data collection

2.2.1 Sampling and gear

The sampling took place in the central Barents Sea, mainly in the Svalbard FPZ, but also in the Loophole and in Norwegian and Russian EEZs. Snow crabs were collected during several research cruises and one commercial pot deployment between February 2006 and September 2017 (Table 1). During the research cruises different gears were used, mostly a Campelen 1800, but also an Alfredo cod trawl. In some of the trawl hauls a smaller “crab bag” was attached to the trawls ground gear, with the intention to catch crabs that were sitting low in the sediment and thus were missed by the main trawl. In one scientific cruise (BRIDGE 2017), a line of 30 small-meshed pots were deployed. An overview of the distribution of crabs collected by the different gear and between the different months is given in Table 2.

The Campelen 1800 trawl (described by e. g. Walsh and McCallum (1997)) is commonly used in scientific cruises and was used during all IMR and one of the BRIDGE cruises. It has a 44 mm mesh size cod end, with an inside cod end liner with mesh size 12.7 mm (mesh sizes are given as stretch measures from knot center to knot center). The fishing line of the trawl is 19.2 m and is usually equipped with a rock hopper footgear, however during half of the trawl hauls from the BRIDGE 2017 cruise a semi-circular footgear was used, as part of a research project comparing the two gears. At 3.0-3.2 knots trawling speed the distance between the doors was 48-52 m, and the height of the trawl opening was 6.0 – 6.5 m.

The Alfredo nr 3 trawl is a commercial sized trawl that is commonly used for ground fisheries, generally for cod and haddock. The trawl used had a fishing line of 18.9 m and was equipped with rockhopper ground gear. At the trawling speed of 3.2 – 3.6 knots, the distance between the trawl doors was 120-125 m, and the height of the trawl opening was 4.5-5.0 m.

A crab-bag (under sack), as described by Gjesteland (2017), was attached to the main trawl in many of the trawl hauls. The bag was 3.3 m wide, and the top of the crab bag was attached to the center of the main trawl's fishing line (bottom of the trawl opening). The mesh size of the bag was 135 mm, and the bag had a small-meshed cod end liner similar to the one used in the Campelen trawl. A custom ground gear made of 50 mm diameter rubber plates and a metal chain (ground gear and chain weighing ~20 kg in total) was attached to the fishing line of the crab bag to weigh it down. An opening in the bottom of the bag allowed heavy objects such as big rocks to fall out of the bag. Underneath the bag a "labbetuss" (a mat made of thick nylon) was attached to protect the bag from damage as it was dragged over the sea floor and the deck of the boat.

All the small meshed pots (traps) used in this study had a mesh size of ~12 mm. Four pots were rectangular with ~ 200 mm opening at each short end, and 26 were conical pots with either a diameter of ~70 cm, and a ~65 mm wide opening in the side (16 pots) or a bottom diameter of 130 cm and a ~500 mm wide opening on the top. The pots were baited with squid. The largest of the conical pots were similar to those used in the commercial industry, but with an extra cover of smaller meshing. These pots were deployed at one occasion for 6 days.

Commercial pots used on the boats that sampled for this study (and that are common in the Barents Sea snow crab fisheries) are conical in shape with a bottom diameter of ~130 cm and top diameter of ~70 cm, with a ~50 cm opening at the top with a plastic collar allowing the crabs to enter the pot but preventing them from escaping. These pots are usually baited with squid or herring. The pots are deployed in lines of up to several hundred that sit on the sea floor for approximately one week at a time.

Table 1: Overview of cruises by year where samples and data for this study were collected. For every cruise the year, the vessels used, the gears used and the sample size (male and female crabs combined) is given.

Cruise	***Year***	***Vessels used***	***Gear***	***Sample size (male and female)***
IMR	2006	Johan Hjort, G.O. Sars	Campelen trawl	84
IMR	2007	Johan Hjort, G.O. Sars	Campelen trawl	13
IMR	2008	Johan Hjort, G.O. Sars	Campelen trawl	30
IMR	2009	Johan Hjort	Campelen trawl	15
IMR	2010	Johan Hjort, Jan Mayen, G.O. Sars	Campelen trawl	25
IMR	2011	Johan Hjort, Christina E, Jan Mayen	Campelen trawl	112
IMR	2012	Johan Hjort, Helmer Hanssen	Campelen trawl	66
IMR	2013	Johan Hjort, G.O. Sars	Campelen trawl	127
IMR	2014	Helmer Hanssen	Campelen trawl	21
IMR	2015	Johan Hjort	Campelen trawl	285
IMR	2016	Johan Hjort	Campelen trawl	92
IMR	2017	G.O. Sars, Johan Hjort, Helmer Hanssen	Campelen trawl	759
BRIDGE	2016	Helmer Hanssen	Alfredo 3 trawl, small-meshed pot	155
BRIDGE	2017	Helmer Hanssen	Campelen trawl, small-meshed pots	2291
Commercial boat	2017	Arctic Pioneer, Kvitungen	Commercial pots	58
Sum: 15 cruises	**2006-2017**			**4133**

Table 2: Number of snow crab (females and males combined) caught according to gear used and month of sampling. The largest number of crabs was caught in March using a Campelen 1800# trawl.

		Month					
		January	***February***	***March***	***August***	***September***	***November***
Gear	***Campelen1800***	102	55	1 747	141	857	-
	Alfredo nr 3	-	-	-	-	-	113
	Crab bag	-	1	422	-	-	36
	Small-meshed pot	-	-	97	-	-	6
	Commercial pot	-	-	58	-	-	-

2.2.2 Stations with mature females

The main focus of this study was the female reproductive biology, and fecundity in particular. The stations where mature females were found are mapped in Figure 3, and an overview of these stations is given in appendix A. Female crabs were collected at a total of 52 different stations, of which 49 were trawl stations and three were pot stations. Most of the stations (47) were located in the south east part of the Svalbard FPZ, two were inside the Russian part of the Loophole, two were in the Russian EEZ, and one in the Norwegian EEZ (Figure 3). The pots used in the commercial deployment were spread over a larger area and since the crabs provided to this study were not individually marked by area the center of the area were the pots were deployed was used as the station location (dark green color in the maps in Figure 3). The depth of all stations varied from 162 m to 347 m (mean 265 m). The AP1 station (commercial pot station) and one IMR 2016 station (nr. 237) had a sample size of 50 and 17 egg-bearing crabs respectively, the other stations had a sample size of between 1 and 7 crabs (mean 2.3 crabs/station) (Figure 3 A). The mean size of the females collected at a given station (or the size of the female at stations with only one crab) ranged from 52 mm to 86 mm CW (mean 71 mm) (Figure 3B).

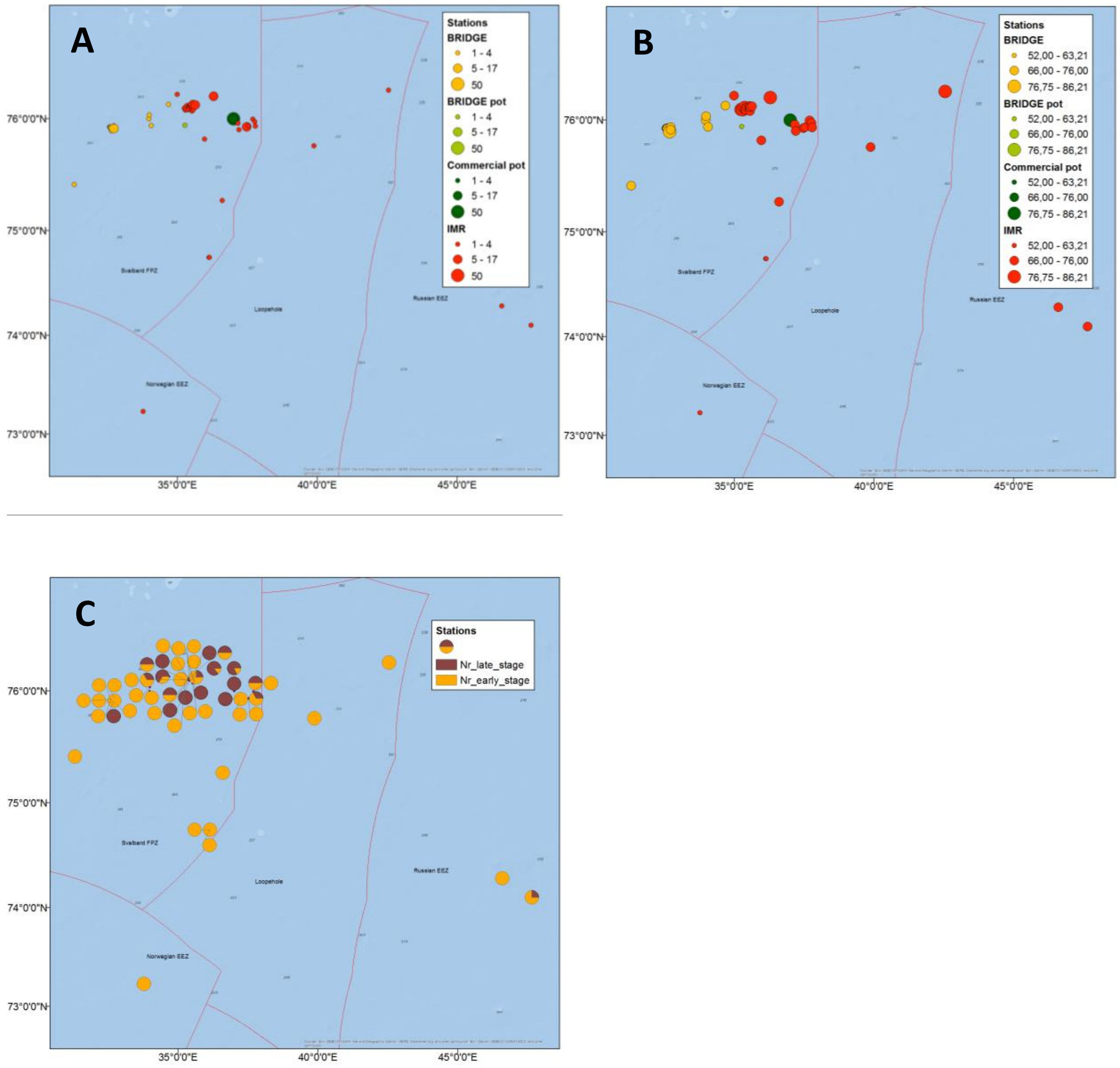

Figure 3: Maps of sampling stations with mature females. A: Size of the point on the map corresponds to the sample size (number of females caught) at a station, colors according to cruise type. B: Size of the map point corresponds to the mean size of the females collected at that station (or size if only one female was collected). C: Distribution of females with early and late egg development stages of the clutch.

2.2.3 Biological data

All crabs collected were assigned an individual number and several qualitative and quantitative measurements were taken; carapace width (CW), abdomen width (AW, females), shell condition, sex, maturation stage (females), clutch fullness and color of the egg mass (modified from Jadamec et al. (1999)). For males, only CW was used in this study.

The carapace width (CW) was measured at the widest part of the carapace, and the abdomen width (AW) was measured at the widest part of the abdomen. Measurements were done using a digital caliper, and rounded to the nearest mm. The shell condition was determined by visual inspection of the individual, according to Jadamec et al. (1999) and Sainte-Marie (1993). The shell condition stages used were based on color, epi-growth and wear of the shell and dactyls and are further described in Table 3.

Table 3: Shell condition stages with criteria used to determine the stage of a crab. Based on Jadamec et al. (1999) and Sainte-Marie (1993).

Stage	***Description***
1	New, clean and **soft** shell.
2	New but hard shell. No epi-growth. Evenly distributed color of carapace, white to pink dorsal side, both sides without brown spots. Iridescent chelae and sometimes carapace. Pointy dactyls. No grasping marks.
3	Hard shell with possibly some epifaunal growth. Cream colored dorsal side with some spots/marks. Grasping marks on pereiopods visible in females (from mating, most evident on ventral side of posterior pereiopods). Slightly rounded dactyls.
4	Hard shell with some epifauna, mostly on carapace. Dark cream to yellow/brown dorsal side with brown and black sports and marks. Distinctly worn dactyls (rounded and often black tip).
5	Brown to black color. Soft shell from decay. Epi-growth and marks. Rounded dactyls.

Sex was determined by the shape of the abdomen; females having rounded abdomens, and males having triangular shaped abdomen (Alunno-Bruscia and Sainte-Marie, 1998, Jadamec et al., 1999). It can be difficult to determine the sex of very small crabs, but no crabs smaller than 7 mm CW were recorded in this study and all crabs could be sexed. Abdomen allometry was used to determine whether a female was morphologically immature or mature; abdomen of an immature female does not cover the entire ventral side of the crab, whereas in morphologically mature females, the abdomen covers the entire ventral side (Figure 4A). All but one of the morphologically mature females in this study also had eggs attached to the pleopods (Figure 4B-D). This means that morphologically mature females are virtually equivalent to functionally mature females and will sometimes just be referred to as "mature females". The shell stage was used to differentiate between the maturation stages of the female; mature females with shell stage 1-2 were defined as primiparous and mature females with shell stage 3-5 were defined as multiparous (Jadamec et al., 1999, Webb et al., 2016).

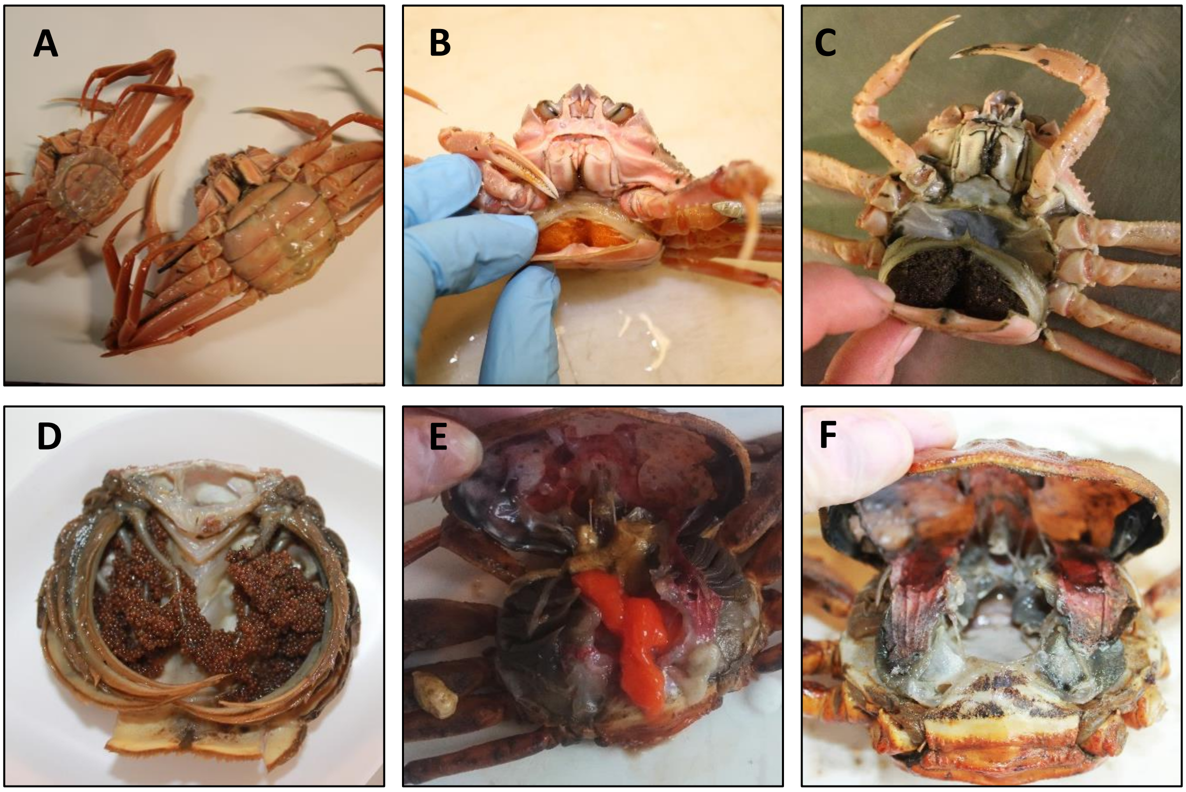

Figure 4: Illustrational pictures documenting different reproductive stages of female snow crab; A: Abdomen allometry of juvenile (left) and mature (right) female snow crab. B: Full clutch of early stage eggs (orange in color). C: Full clutch of late stage eggs (dark in color). D: Lower clutch fullness (~20%). E: Bright orange ovaries, partially lifted out of the female. F: Senescent female with undistinguishable ovaries.

Clutch fullness (Figure 4B-D) was assessed either in the field or in the lab, by visual determination (Jadamec et al., 1999), and was estimated in percentage; 100% clutch fullness meaning that the egg mass completely filled the abdomen, and 0% meaning no eggs or merely traces of egg were detected. The estimate was rounded to the nearest 10%. The appearance of 100% clutch fullness would differ between a female with early stage and late stage eggs, with the late stage clutch making the abdomen bulge out and expose parts of the clutch as seen in Figure 4 B and C.

The egg clutch was assigned one of five different categories, described in Table 4 according to the color of the clutch and the developmental stage of the eggs (modified from Jadamec et al. (1999), Alunno-Bruscia and Sainte-Marie (1998), Comeau et al. (1999) and Moriyasu and Lanteigne (1998)). Degenerate eggs were not found in this study. For some analyses the three categories “eye spot”, “eye spot to hatching” and “hatching” was grouped together and treated as “late stages” and the orange eggs were called “early stages”.

Table 4: Egg developmental stages according to color and development of the embryo, Categorized based on Moriyasu and Lanteigne (1998) and Comeau et al. (1999).

Egg color/stage	***Egg development***
Orange	No internal structures to some structure but no eye spot
Eye spot	The eggs were still clearly orange, but eye spots were visible in the microscope
Eye spot to hatching	Brown to purple in color, embryo clearly visible to close to hatching
Hatching	Empty egg shells mixed with brown to purple eggs
Degenerated eggs	empty egg shells and/or dead eggs

All egg-bearing females, and females larger than ~20 mm CW from BRIDGE cruises were frozen whole onboard the research vessel and brought to the laboratory, in some of the IMR cruises only abdomens with the attached eggs were frozen and brought to the laboratory. The females from the commercial fleet were not measured and characterized at sea, but frozen directly and measured later in the laboratory.

2.2.4 Laboratory data collection

In the lab the fecundity and individual egg weight of each female was investigated as done by e.g. Hjelset et al. (2012) for red king crab and Jewett (1981) for snow crab. The weight of the weighing boat was later subtracted from the dry and wet weight of the sample. All the eggs were detached from the pleopods and weighed to the nearest 0.001 g. Three subsamples of approximately 200 eggs each were then taken out and weighed to the nearest 0.0001 g, before being counted under the stereomicroscope. Eggs were placed into variously sized (different for large and small egg clutches and sub-samples) plastic weighing boats that were pre-weighed. The counting was done by help of a transparent counting chamber with transmitted light. Some of the eggs had to be gently pulled apart to be countable, and some eggs broke in this operation. Egg shell fragments were not counted, but more or less intact embryos (with two eye spots) were. Both the main egg clutch and the three subsamples were then dried for at least 24 hours at 60°C, and then cooled down (on the lab counter) before dry weight was recorded to the nearest 0.001 g for the main clutch and to the nearest 0.0001 g for the subsamples. Individual egg weight (IEW) was calculated according to equation 1, for every subsample (i) as the subsample dry weight (SSD) divided by the number of eggs in the subsample (N). The female (x) fecundity (F) was then estimated according to equation 2, by dividing the total brood dry weight (TBW) by the mean individual egg dry weight of the subsamples (the number of subsamples, n, was three for every female).

1) $$IEW_i = \frac{SSD_i}{N_i}$$

2) $$F_x = \frac{TBW_x}{\left(\frac{\sum_{i=1}^{n} IEW}{n}\right)}$$

Egg diameter of 10 eggs was measured in each of the three subsamples taken for fecundity estimation, using a measuring ocular on a Leica MZ12 stereomicroscope at 10 times magnification. The diameter was measure from the base of the funiculus and across the egg (Moriyasu and Lanteigne, 1998). Some eggs were encountered that were obviously oval in shape, these eggs were skipped, and only eggs that were practically circular were measured. Mean egg diameter was calculated for each female.

Two stages of ovary development may be identified by color; in the pre-vitellogenesis stage the ovaries are “rosy-white to lilac” and in the succeeding vitellogenesis stage they are “yellow-brown to bright orange” (Alunno-Bruscia and Sainte-Marie, 1998). The ovaries of all adult females, and juveniles larger than ~20 mm were dissected out and weighed to the nearest 0.001 g and the color was noted. For the smallest females the ovaries could not be detected visually. Some ovaries had a paler orange color than the rest, and although the difference to orange colored ovaries were not very pronounced these were kept out of analyzes of ovary weight. The ovaries were then dried at 60°C for at least 24 hours, cooled, and then weighed again.

2.3 Data analysis

The data from all cruises and all years (Dataset A, Table 5) were used to generate size frequency distribution plots for the population sample as a whole, to estimate size of 50% maturation for females and explore the abdomen allometry of immature and mature females. Data from the 2014-2017 IMR cruises, the BRIDGE cruises and the commercial boats (dataset B in Table 5) were used for female fecundity analysis and investigations of the egg incubation cycle of snow crab.

Table 5: Overview of the two datasets used in this study, its origin, content, usage in this study and sample size.

Data-set	***Cruises***	***Content***	***Usage***	***Sample size***
A	IMR 2006-2017, BRIDGE 2016 & 2017, Commercial boats	Sex, CW, AW, shell condition, maturation stage, clutch fullness and egg mass stage (last three for females)	Description of the populations through e.g. size frequency distribution plots. Estimate size at 50% maturity and explore abdomen allometry for females.	4133 (1803 females)
B	IMR 2014-2017, BRIDGE 2016 & 2017, Commercial boats	As above, and additionally: fecundity estimates, egg diameter measurements and ovary weight	Investigation of various aspects of female reproduction, such as fecundity and egg incubation cycle.	235 females

Several statistical procedures were explored to unravel how size frequency distribution was affected temporarily and by sampling method but found inappropriate given the unbalanced sampling regime.

A logistic regression was made on the basis of 1 803 females between CW as a continuous predictor variable and the binary outcome variable, immature or mature. The size of 50% maturity was calculated from the model (using the dose.p function in the R package MASS)

(Venables and Ripely, 2002). All ovigerous females, regardless of clutch fullness, were included in this analysis.

Next, fecundity to CW relationships were analyzed using linear regressions, and using only females with 100% clutch fullness. Data were $\log_{10}$ transformed to enhance analytical simplicity and account for the known allometric relationship between fecundity and size (Somers, 1991). The relationship between the $\log_{10}$ transformed variables were described by linear regression (lm – linear model in R, (R Core Team, 2017)). The relationship between fecundity (Y) and carapace width (X) on the log scale was described by equation 3:

3) $\log_{10} Y = \log_{10} a + b^* \log_{10} X$

For multiple linear regressions, the slope and intercepts were tested for equality by analysis of variance and covariance. Multiple linear regressions were used to investigate potential differences in the size-fecundity relationship between females with broods in early and late developmental stages. To compare my result to earlier studies where the size-fecundity relationship was described using power curves, the relationship was also plotted at the non-logarithmic scale according to the function:

4) $Y = aX^b$

In most plots, the $\log_{10}$ scale was used, but back transformed labels were added to ease the interpretation, as the $\log_{10}$-transformend values may be difficult to relate to. The 95% confidence interval is shown as a grey shaded area around most of the regression lines.

Differences in mean fecundity between full-clutch females and females with lower clutch fullness, and between egg diameter of early and late developmental stages were tested using a Welch two-sample t-test. Assuming the size distribution of ovigerous females from this study is representative of the Barents Sea population, the theoretical percentwise contribution of different size classes of females to the populations total egg production was calculated for groups of size intervals of 5 mm CW. Pearson’s chi square test (χ^2-test) were used on data from March to test for independence between maturation stage and egg developmental stage.

To account for the expected ovary growth over time, only females sampled in February or March, who also had orange ovaries (n = 93) were included in analysis regarding ovary weight according to brood developmental stage.

The significance level used for all statistical analyses was p = 0.05. All statistical analyses were carried out using R software (R Core Team, 2017), ant the graphics were made using the R package “ggplot2” (Wickham, 2009). Maps were made in ArcMap 10.5.

3 Results

3.1 Size frequency distributions

In total, 4 133 female and male crabs were sampled between February 2006 and September 2017. Of these crabs, 1 803 were females, and the size distribution ranged from 10-100 mm carapace width (CW), with a mean of 26 mm and a median of 18 mm. For comparison, the size of the 2 330 male crabs ranged from 7 to 145 mm CW with a mean of 43 mm and a median of 19 mm. Maximum size of females was smaller than that of males. About 54% (2 233) of all crabs (female and male) were between 15 and 20 mm CW (Figure 5). Crabs < 15 mm CW were relatively scarce (n = 148), and the smallest sized crabs (<7 mm CW) were absent.

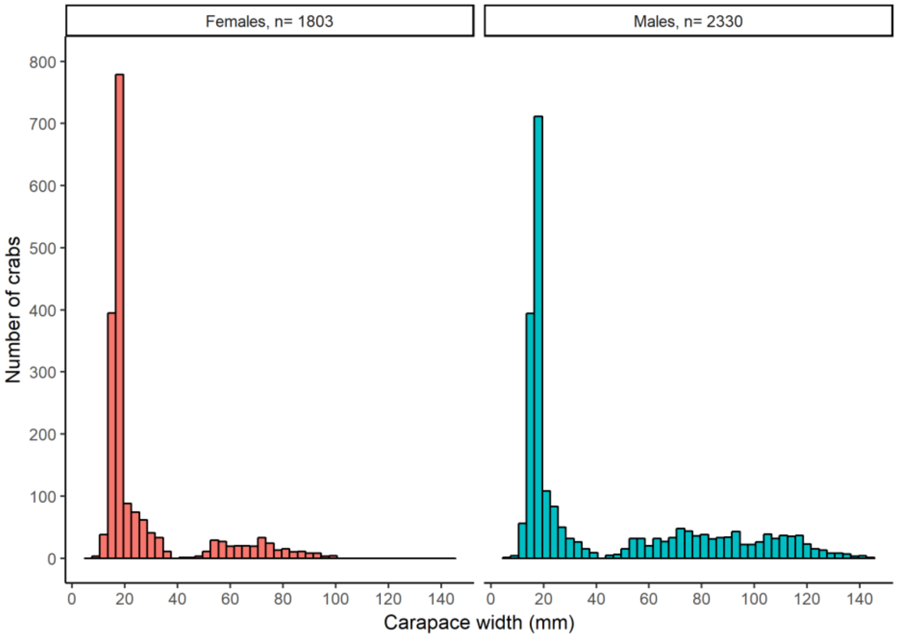

Figure 5: Size-frequency distribution of snow crab caught in the Barents Sea between February 2006 and September 2017.In this plot all data are grouped together regardless of year and month sampled, and gear used. Females (n=1803) are represented with red bars in the left plot, and males (n=2330) with blue bars to the right.

Visual inspection of size distribution plots suggest that they differ between the months and gears (as is illustrated in Appendix figure 1 and Appendix figure 2). The samples were considered to be complementary and are grouped together in this study. As can be seen in

Table 2, a substantial proportion of the crabs in this study were collected in March using a Campelen 1800 shrimp trawl with the crab bag attached. Many of these crabs (n=1 835) were collected at only four stations and were very small (mean size at the four stations was 18.5 mm CW). The four stations were very close together, and the depth was between 210-224 m.

3.2 Size at maturity

Based on n=1 803 female crabs, the size of 50% maturity (±SE) was estimated by logistic regression to be 62 ±0.87 mm CW (Figure 6). The smallest mature female in the dataset was 48 mm CW, the largest was 100 mm. The smallest immature female was 10 mm and the largest immature female was 77 mm CW, yielding a substantial size overlap between mature and immature females (Figure 7). In Figure 7, the distinct shift in abdomen allometry (AW to CW relationship) associated with the molt to maturity of female snow crabs is obvious.

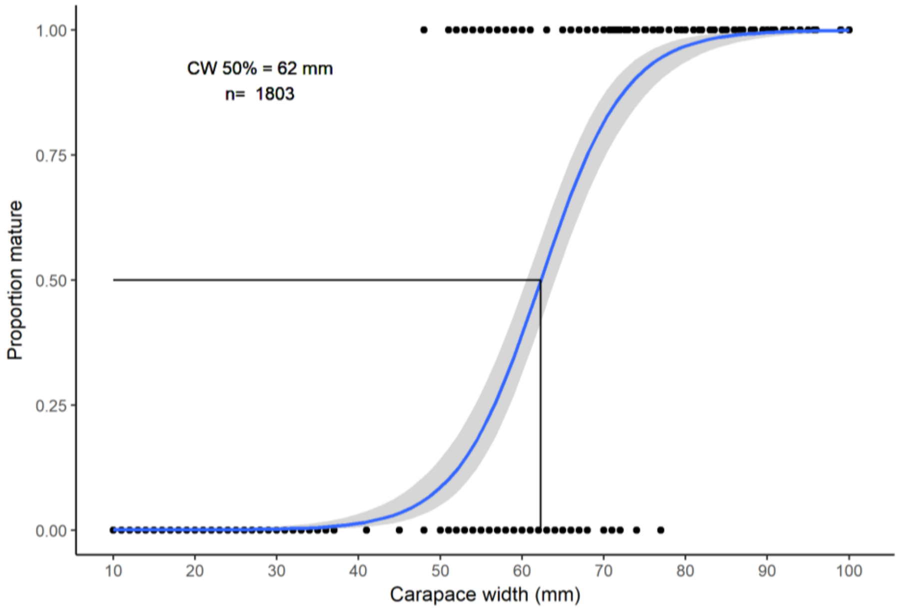

Figure 6: Size at 50% maturation of female snow crab from the Barents Sea. The black points represent individual females with and without eggs and the blue line is the fitted model, the 95% confidence interval is illustrated by the grey shaded areas. The size of 50% maturity was estimated to be ≈ 62 mm CW, and this is illustrated by the black lines.

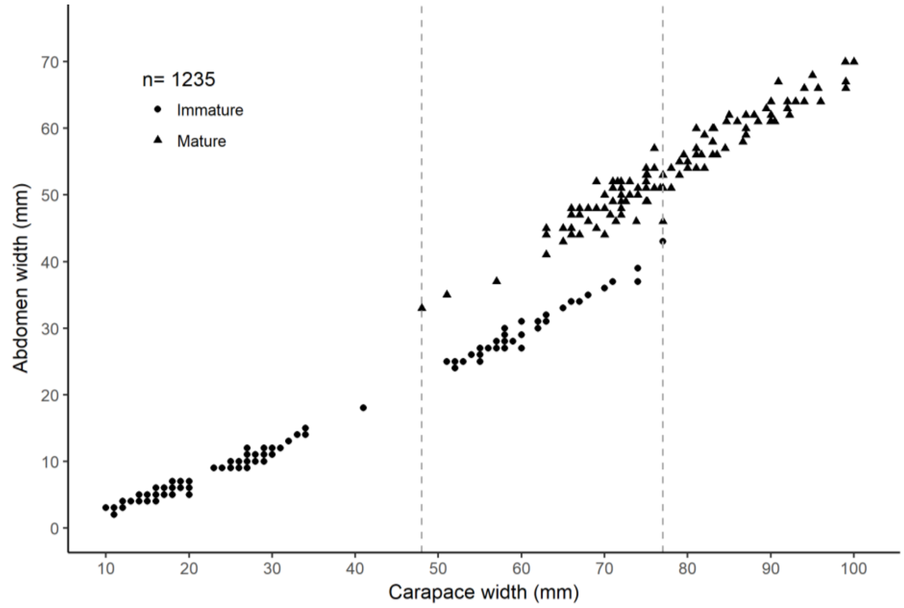

Figure 7: Abdomen allometry (AW to CW relationship) of immature and mature female snow crab from the Barents Sea. Presumed mature females are plotted as triangles, immature females as dots. The overlap in size of mature and immature females (48-77 mm) is marked with the vertical grey stippled lines. The sample size is smaller in this figure compared to figure 5 and 6, due to missing AW measurements for some females caught before 2014.

All but one of the 186 morphologically mature females that were used for fecundity analysis were ovigerous (egg bearing). The carapace width range of ovigerous females is, therefore, essentially the same as for morphological mature females, it ranged from 48 to 100 mm, with a mean of 75 mm (SD = 10.4 CW, CV= 13.9%) and median of 73 mm CW. Figure 8 shows the size distribution by intervals of 3 mm CW.

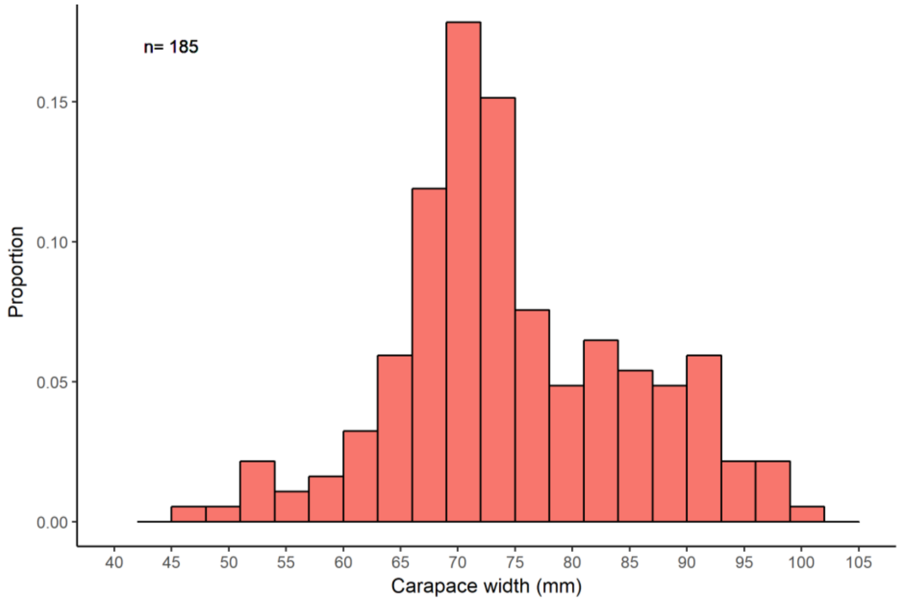

Figure 8: Size distribution of ovigerous female snow crab from the Barents Sea from 2014 – 2017, all sampling gears and seasons pooled together. The bin width used is 3 mm CW.

3.3 Fecundity

All but nine (95%) of the females had 100% clutch fullness (Table 6). Of the nine with less than100% clutch fullness, two were estimated to have as little as 10% clutch fullness and one had no eggs, and these three also had shell condition 4 (old shell) and the ovaries were not detectable or not recognizable. As expected, the fecundity was significantly lower in the females with low clutch fullness compared to the females with a full clutch (Welch two sample t-test; t statistic = 6.61 on 8.7 degrees of freedom, p-value= 0.0001, box plot in Appendix figure 3).

Table 6: Sample size of Barents Sea female snow crab according to clutch fullness and shell condition. For 94 females, shell condition was not recorded (shell condition = NA (not available)).

		Clutch fullness (%)								
		0	***10***	***20***	***50***	***60***	***80***	***90***	***100***	***Sum***
Shell condition	***2***	0	0	0	0	0	1	0	33	***34***
	3	0	0	0	0	0	0	0	25	***25***
	4	1	2	1	0	0	0	0	31	***34***
	NA	0	0	0	1	1	0	2	88	***92***
	Sum	***1***	***2***	***1***	***1***	***1***	***1***	***2***	***177***	***186***

On the $\log_{10}$ scale fecundity showed a significant linear increase with carapace width (ANOVA: F-value = 506.43, p-value = $2.2e^{-16}$) (Figure 9 and Figure 10). The relationship on $\log_{10}$ scale was: y = -0.61 + 2.93x. The 95% confidence intervals of the intercept and slope ranged from -1.10 to -0.13 and from 2.68 to 3.19, respectively. On the non-linear scale, the relationship can be described by the equation $y= 0.24 * x^{2.93}$ (Figure 10). The modeled relationship gives an estimated fecundity of a mean sized female (75 mm CW) of ~ 77 000 eggs in one reproductive cycle.

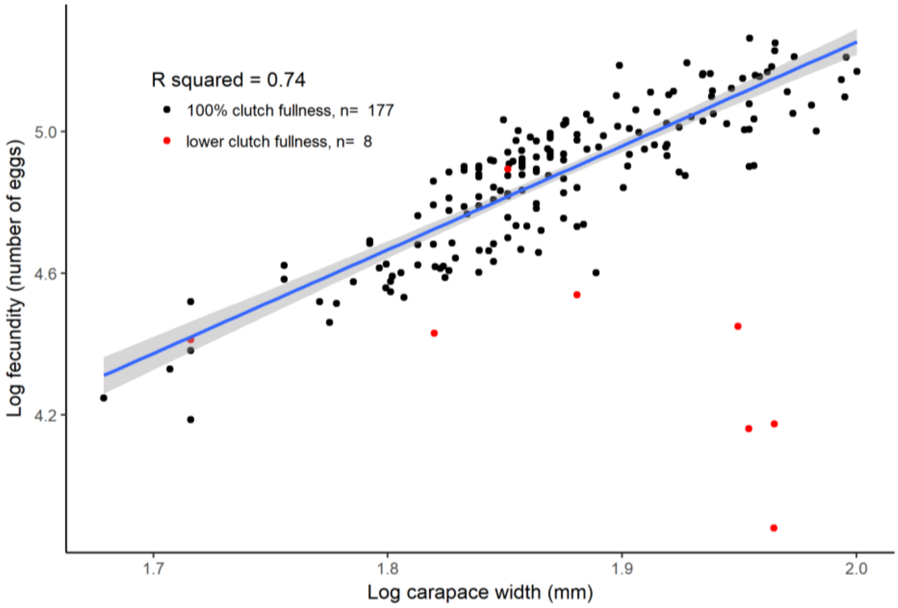

Figure 9: Relationship between fecundity and carapace width on $\log_{10}$ transformed data in female Barents Sea snow crab. Black points represent the observed values from females with 100% clutch fullness. The red points represent females with less than 100% clutch fullness, these were not included in the linear model, but are included in the figure for reference. The blue line represents the linear regression with the equation y= -0.61 + 2.93x. The gray shaded area indicates the 95% confidence interval of the linear regression.

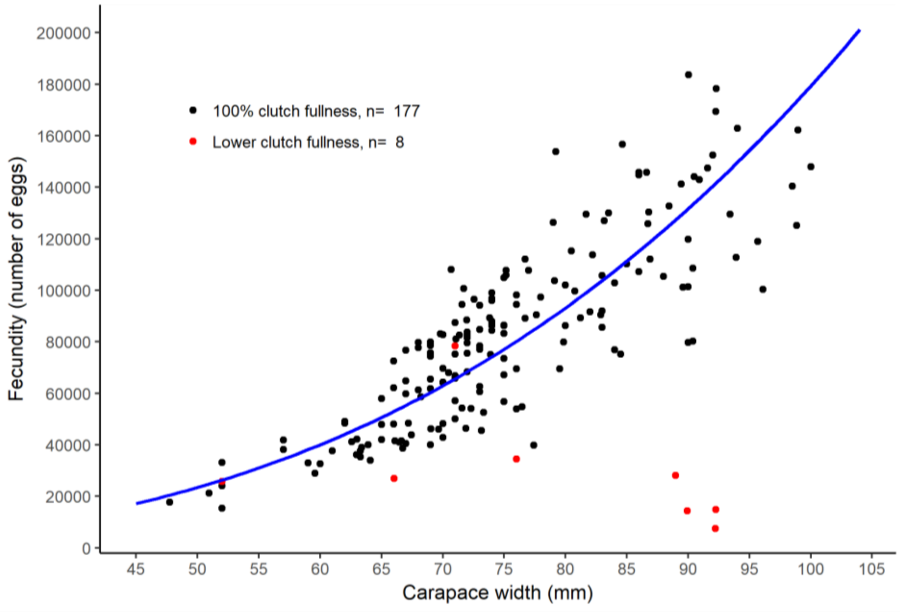

Figure 10: Fecundity to CW relationship plotted with non $\log_{10}$*-transformed data. Black points represent the observed values from females with 100% clutch fullness. Whereas red points represent females with less than 100% clutch fullness, which were not included in the linear model, but are included in the figure for reference. The blue line represents the relationship between fecundity and CW modeled on the* $\log_{10}$*-transformed data and has equation* $y= 0.24 * x^{2.93}$.

The calculations of percentwise contribution of egg production by size class (Table 7) show that females at intermediate sizes (70-74 mm CW) have the highest percentwise egg production at 26% of total egg production. More than 50% of the eggs are produced by females at sizes between 65 and 79 mm CW (combined size interval of 15 mm CW). The second smallest and the second largest size group from this study (50-54 and 95-99 mm CW) constitute similar proportions of the total abundance of mature crabs (2.3 and 2.8% respectively), but the smallest crabs produce only about 23 000 eggs each per cycle, contributing less than 1% of the total egg production, whereas the largest crabs produce more than five times as many eggs (129 000), thus contributing >4% of the total production despite the low abundance.

Table 7: Potential egg production and contribution of different size classes of female snow crab to the Barents Sea population by CW intervals of 5 mm. Standard deviation (SD) is given in brackets behind the mean group fecundity. In the first and last size group there was only observed individual, the fecundity given for these groups are thus the observed fecundity, and no SD could be calculated (NA).

Carapace width (mm)	*Sample size in this study*	*Percent of total abundance of mature females*	*Mean fecundity in thousand eggs (±SD)*	*% Contribution to total egg production*
45-49	1	0.6	18 (NA)	0.1
50-54	4	2.3	24 (7.4)	0.6
55-59	4	2.3	36 (5.7)	1.0
60-64	12	6.8	39 (5.2)	3.2
65-69	30	17.0	59 (15.0)	12.0
70-74	51	28.8	76 (16.4)	26.2
75-79	24	13.6	90 (24.8)	14.7
80-84	18	10.2	104 (21.4)	12.8
85-89	12	6.8	125 (17.2)	10.2
90-94	15	8.5	134 (33.2)	13.7
95-99	5	2.8	129 (23.2)	4.4
100-104	1	0.6	148 (NA)	1.0

The mean CW of multiparous females (66 mm) was larger than that of primiparous crabs (84 mm) (Figure 11), tested by a Welch two sample T-test which showed a significant difference in the mean size (CW) between the groups (t statistic = 10.9 on 78.9 degrees of freedom, p-value= $2.2e^{-16}$). The difference in means was estimated to be 18 mm CW (95% confidence interval ± 3 mm). Most primiparous females in this study (having low CW and accompanying low fecundity) therefore grouped together in the lower left corner of the fecundity to CW plot (Figure 12) while the multiparous females grouped together in the top-right corner of the plot.

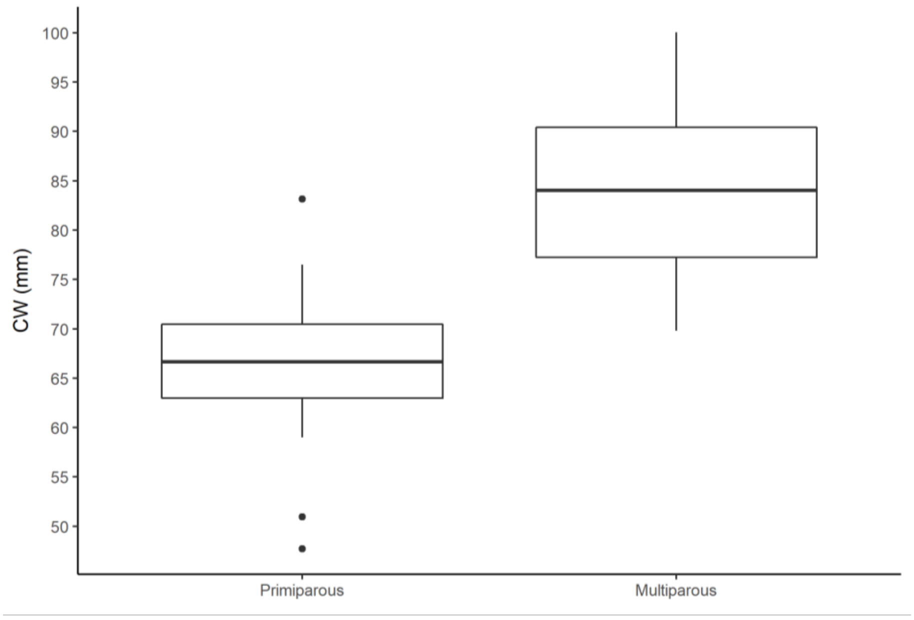

Figure 11: Box plot of mean carapace width (mm) of primiparous (n=33) and multiparous (n=56) female snow crab. Horizontal line indicates the median, the "top" and "bottom" of the box corresponds to the first and third quartiles, the whiskers extends from the box to the highest/lowest value within 1.5 times the interquartile range and outliers are plotted as points.

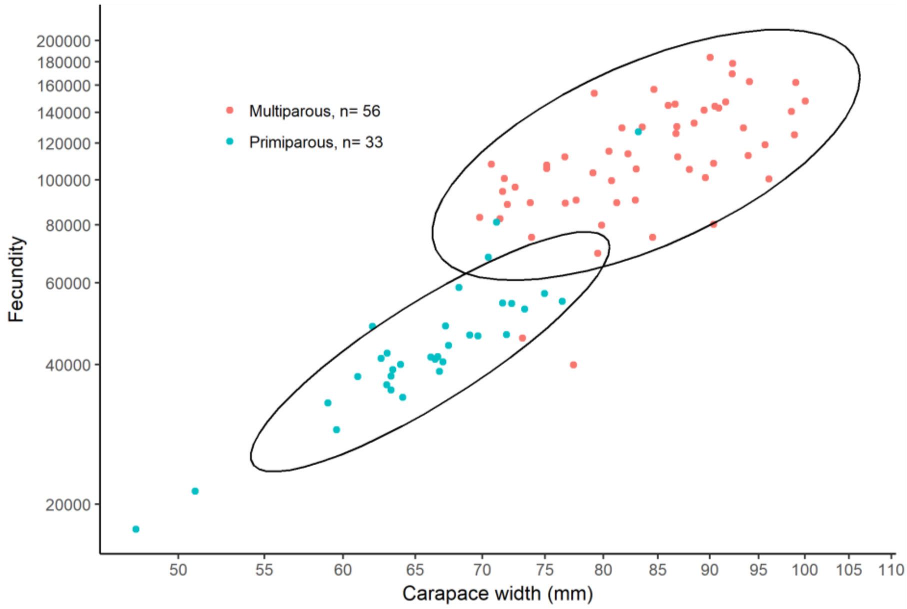

Figure 12: Fecundity by CW for primiparous and multiparous female snow crab. Red and blue points represent the females who were categorized as multiparous and primiparous respectively. The ellipses mark the 95% confidence intervals of the two groups (in both dimensions). Log$_{10}$ scale, with back transformed labels for easier interpretation.

There was a significant difference in the fecundity-at-size between the females with eggs in early and late developmental stages (ANCOVA: F-value= 9.14, p-value=0.0029). Females with late stage eggs had a higher fecundity-at-size compared to females with early stage eggs (Figure 13). No spatial segregation between females that were close to hatching and females that were not could be seen from the station map (Figure 3C).

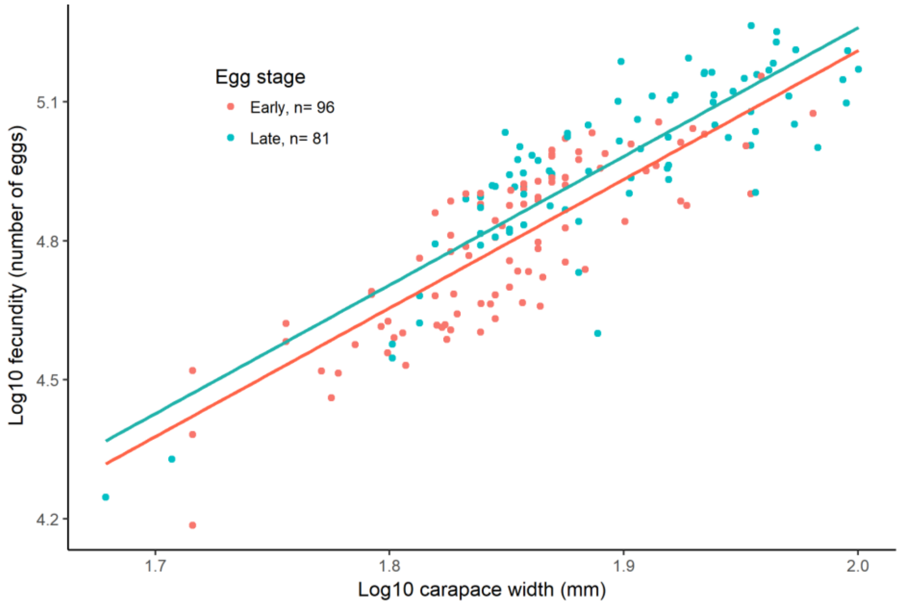

Figure 13: Fecundity related to carapace width by egg stage for female Barents Sea snow crab. Log_{10} scale. Red points correspond to females with early stage eggs, and blue points to females with late stage eggs. The linear regressions with equal slopes and different intercepts are plotted with the corresponding colors. The relationship on the log_{10} scale for females with early stage broods were y= -0.34+2.78x, and for late stage is was y= -0.29+2.78x).

Egg diameter was positively correlated with carapace width in the late egg stages, but not in the early egg stages. There was no significant difference (ANCOVA: F=0.6, p-value=0.5) in mean egg weight between the early and late stages (Figure 14). There was a slight positive correlation (ANOVA: F value= 12.32, p-value= 0.0005) between the mean egg weight and female carapace width (Figure 15).

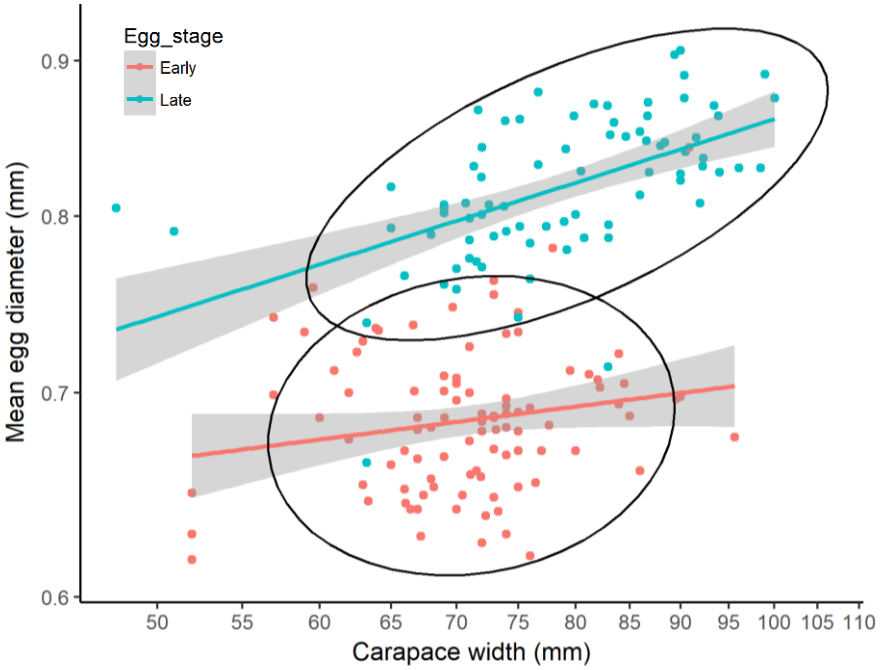

Figure 14: Mean egg diameter to carapace width. Early egg stages are marked with red dots, and the regression line is red (y= -0.32 + 0.09x). Late eggs stages are represented with blue colored dots and regression line (y= -0.5 + 0.22x). Gray shaded area and ellipses indicate the 95% confidence interval of the regression and means, respectively. Log$_{10}$ scale, with back transformed labels for easier interpretation.

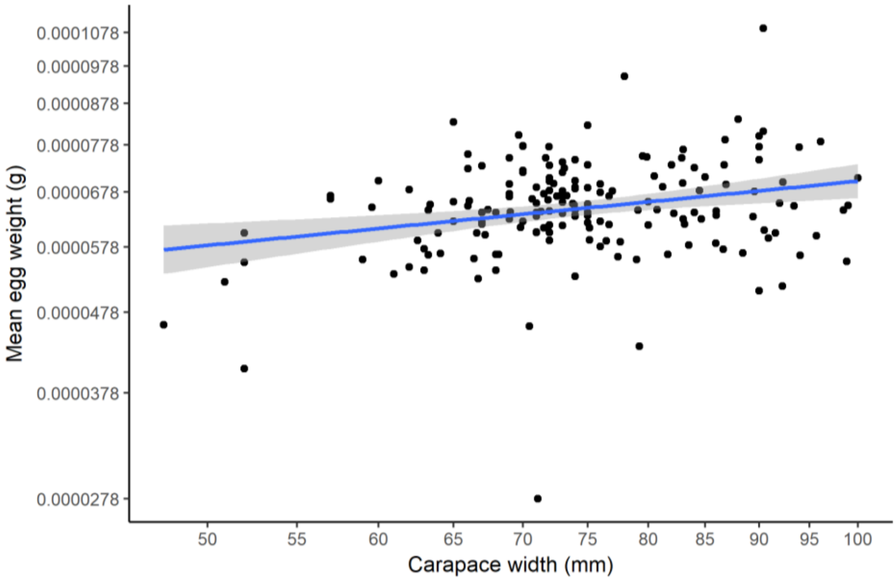

Figure 15: Mean individual egg dry weight (g) versus carapace width (mm) for Barents Sea female snow crab. Log$_{10}$ scale, with back transformed labels for easier interpretation. Gray shaded area indicates the 95% confidence interval of the regression (y= -4.69+ 0.27x).

3.4 Reproductive cycle

All the 13 ovigerous females caught in September had orange eggs indicating early development stages. Females with eggs in both early and late development stages were observed simultaneously during the late fall and winter season (November, February and March, Figure 16). In November, ~17% of the 29 females had eggs with emerging eye spots, the rest of the eggs were orange. Three different stages of development were observed in February, including both orange eggs (60%), “eye spot to hatching” (30%) and “hatching” (10%). In March, the majority of egg clutches (~69%) were in late development stages “eye spot” or “eye spot to hatching”, and about one third (31%) were in the early development stages.

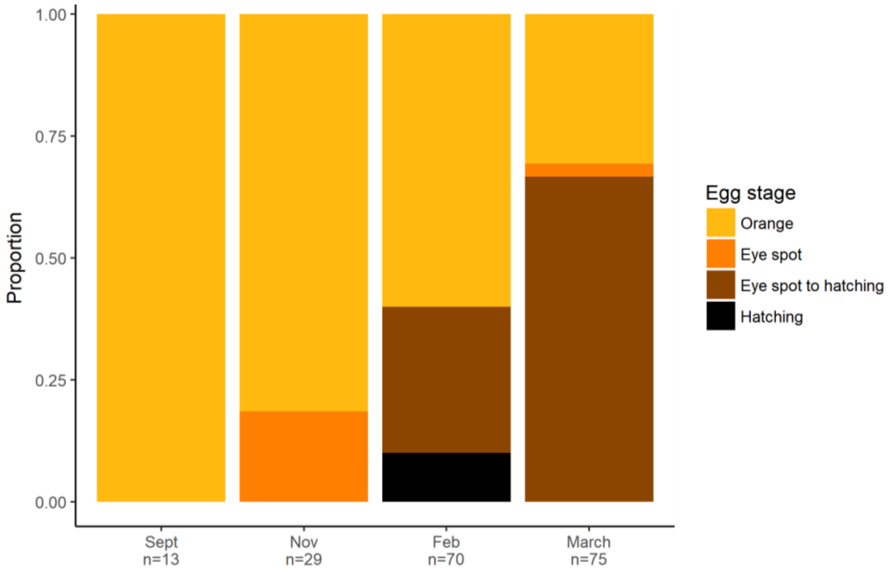

Figure 16: Egg development stages by months for Barents Sea snow crab females. The figure starts with September, which is considered to be the first sampling month after the mating season and should consequently have the least developed eggs.

For females sampled in March (75), the distribution of early and late development stages was not independent of the maturation stage (Table 8, Pearson’s Chi-squared test: $\chi^2 = 22.1$, degrees of freedom = 1, p-value = $2.574e^{-6}$).

Table 8: Number of females with early and late egg stages according to maturation stages for snow crab from the Barents Sea sampled in March.

	Multiparous	*Primiparous*
Early	9	13
Late	46	4

In the smallest, immature females and some mature females, the ovaries could not be detected visually. Out of the 124 females were data on ovaries were available, only seven did not have bright orange color of the ovaries. One of the seven had white/cream colored ovaries (CW =54 mm), this female was immature. Three females had paler orange ovaries (CW = 72, 86 and 90 mm), two of these had early developmental stage eggs, and one had late stages, and they were all sampled in March. Three large females had orange to black ovaries with deformities in the form of hard lumps (CW = 95, 92 and 92 mm). An analysis of covariance showed that there was significant difference in the ovary weights between the groups (F-value = 62.5, p-value = $2.2e^{-16}$). Multiple comparisons were not done, but by visual inspection it may be deduced that females with late stage eggs had larger ovaries at a given CW than females with early stage eggs, whereas pubescent females grouped together at an ovary-weight-at-size higher than that of females with late egg stages, and lower than or possibly the same as females with early stages (Figure 17).

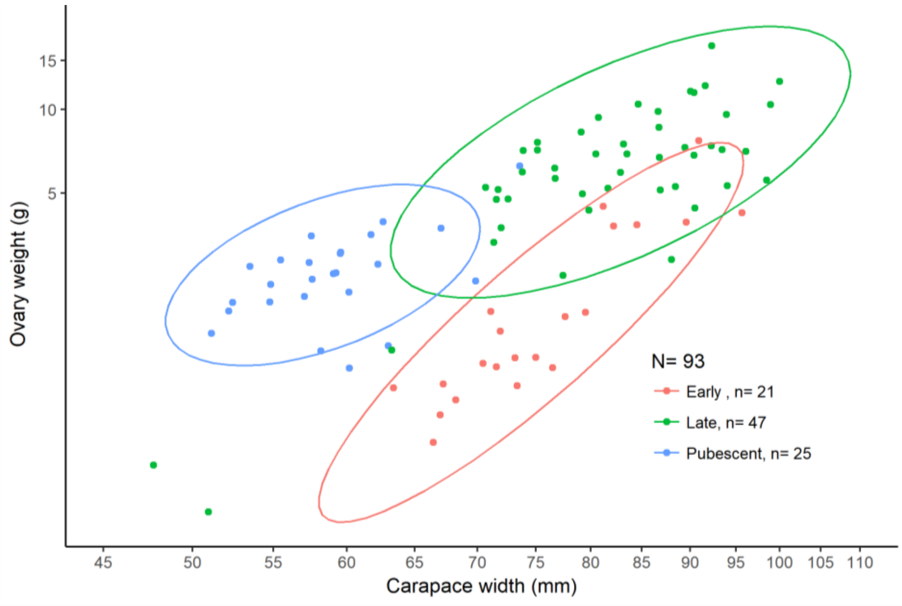

Figure 17: Ovary dry weight to carapace width in Barents Sea female snow crab by egg stage and for pubescent females. Only females that were sampled in February and March and had orange ovaries were included in plot. Females with early development stages of the egg clutch are represented by red points, females with late stage eggs with green points, and pubescent females with blue points. Log$_{10}$ scale, with back transformed labels for easier interpretation.

4 Discussion

4.1 Data collection

Although the dataset that this study is based on is an assemblage of samples from different institutions, years, areas and seasons (which is not ideal), it is valuable, as to give the first leads on the reproductive ecology of the female Barents Sea snow crab. Some of the results from this study is directly applicable to the management and the study might also serve as a baseline study for future comparison.

Some methodological problems aside from the patchy nature of the dataset was encountered. During the fecundity estimation, some eggs broke during handling. This might have influenced the estimation differently for early and late stage females, as relatively whole embryos from late stage eggs but without a complete egg shell were still counted, whereas remnants of the early stage eggs could not be counted. This would lead to a lower estimate of individual egg weight for late stage eggs and thus a higher fecundity estimate. Yet this is contradicted by the missing difference in mean individual egg weight between early and late stages. The egg staging method used in this study, although convenient in its simplicity, has its constraints, especially towards separating the recently extruded eggs from eggs close to the eye pigmentation stage, which are both orange in color but may be more than a year apart in developmental time (given a biennial brooding cycle) (Moriyasu and Lanteigne, 1998). Some eggs were staged as "hatching" these eggs had embryos partially outside the egg-shell and empty eggs occurred simultaneously in the clutch. Keeping in mind that no females were caught in the expected main period of hatching (April-May), the investigator might not have encountered hatching eggs at all, and thus have miss-staged some broods as "hatching" in the absence of a standard of comparison. The staging of shell condition for snow crab is a subjective method and might easily be biased by the experience of the examiner on this topic. Staging crabs that has been frozen is not advisory as the appearance change significantly and the criteria used for staging are no longer applicable. Some of the criteria suggested such as biofouling is likely to be site specific, and criteria from other areas might not be directly adoptable to the Barents Sea population. The data collected in this study indicates a significant difference in the size of primiparous and multiparous females, which is hard to explain biologically and are more likely to be caused either by the sampling regime, or by a tendency to stage larger females as multiparous and smaller females as primiparous. The absence of grasping marks was a criterion used to identify primiparous females (or more precisely shell stage 1), presuming that mating in the soft shell condition (as would be the case for first time spawning females (Watson, 1970)) would not lead to these marks (Donaldson and Adams, 1989, Jadamec et al., 1999). It has previously been suggested that the absence of smaller females staged as multiparous could indicate that small multiparous females mate without, or with less visible grasping marks (Donaldson and Adams, 1989, Comeau et al., 1999). Rugolo et al. (2005) also recognize this problem and reports that they suspect multiparous females with a one-year old shell were staged as primiparous due to low wear and biofouling on the shells. Thus, it is likely that also in this study, some multiparous females may have wrongly been staged as primiparous. Many of the larger crabs had been frozen prior to staging (crabs from commercial boats), which caused the color to change somewhat and damages to appear more clearly. This might have led to some primiparous females being staged as multiparous, although other criteria such as the wear of the dactyls are not likely to have been affected by freezing.

The gear used by IMR during their annual Barents Sea Ecosystem survey (Campelen trawl) is probably not the most suitable equipment to catch snow crab (Bakketeig et al., 2016), and the suggested solution is to use the “crab bag” in some areas. All though the crab-bag should be more appropriate for catching snow crab, the sustainability of this method could be debated, as the damage to the bottom substrate might be considerable.

4.2 Size frequency distributions

The general shape of the size frequency distribution plots (Figure 5) was as expected for both females and males; there was a high frequency of small crabs, and fewer large crabs, presumably due to natural mortality for both sexes and fishing mortality for large males. The smallest sizes (<15 mm) are also expected to be abundant in the population but were not sampled with the gear used in this study. This was expected given the mesh sizes of the trawls (≥ 12.7 mm).

Few crabs between the size of 40 and 50 mm CW were recorded (Figure 5 and Figure 7) in this study (only 16 individuals). Some size intervals are expected to have lower frequency due to molting increments creating a distance between the peaks of instar modes. For example Comeau et al. (1998) report size increments at instars in this size range of up to 37% of pre-molt size for males, and 28% for females, resulting in a difference in mean instar size of up to 12 mm. In the mentioned study (from Bonne Bay, Newfoundland), instar VIII and IX of juvenile males had mean CWs of 38.3 and 50.2 mm respectively, which interestingly corresponds to the size gap observed in data from the Barents Sea. Nevertheless, the largest sized crabs of one instar and the smallest crabs of the next instar are expected to overlap in size to some extent, and I would expect to find at least some frequency of snow crabs at all body sizes within the observed size range. Interannual variation in year class strength (as discussed by Ernst et al. (2012)) and mean size at instars might also account for some of the observed pattern, e.g. if an abnormally large-sized year-class is followed by a small-sized year-class. For this study it was not considered appropriate to investigate interannual variability further, due to the small sample size in some years. A larger sample size is expected to reveal the finer patterns (frequency peaks at instars) of size frequency that is expected for species growing by ecdysis.

The large number of small crabs found at four stations in March 2017 indicate that young stages of snow crabs occur at high densities in some areas of the Barents Sea, and implies that strong year classes might be recruiting in the coming years to the part of the stock that resides on the Norwegian shelf . Comeau et al. (1998) also report aggregates of immature crabs of 9-20 mm CW in some areas in Bonne Bay in Newfoundland. For the Barents Sea, high densities of juvenile snow crab was first reported from the Goose bank area (Alvsvåg et al., 2009).

4.3 Size at maturity

The size range of mature females found in this study (48-100 mm CW) was relatively broad (CV = 13.9), and the largest female found was quite large compared to findings in the Bering and Chukchi Sea and the Gulf of St. Lawrence (Figure 19). The finding of such large females was surprising, given that the size at terminal molt is temperature dependent (Burmeister and Sainte-Marie, 2010), and low temperatures that persist in the bottom waters of the snow crabs main distribution area in the Barents Sea (mean temperatures between -1 and 1 °C, Figure 18) (Jørgensen et al., 2015). Large sized females (as large as 103 mm CW) have also been reported from Western Greenland (66-69°N, in bottom temperatures of -0.8 to 3.2 °C) (Burmeister and Sainte-Marie, 2010), where the median size of adult females is reported to be 61.9 to 72.8 mm CW depending on the area. The median size of mature females from this study (73 mm) matches that reported from western Greenland.

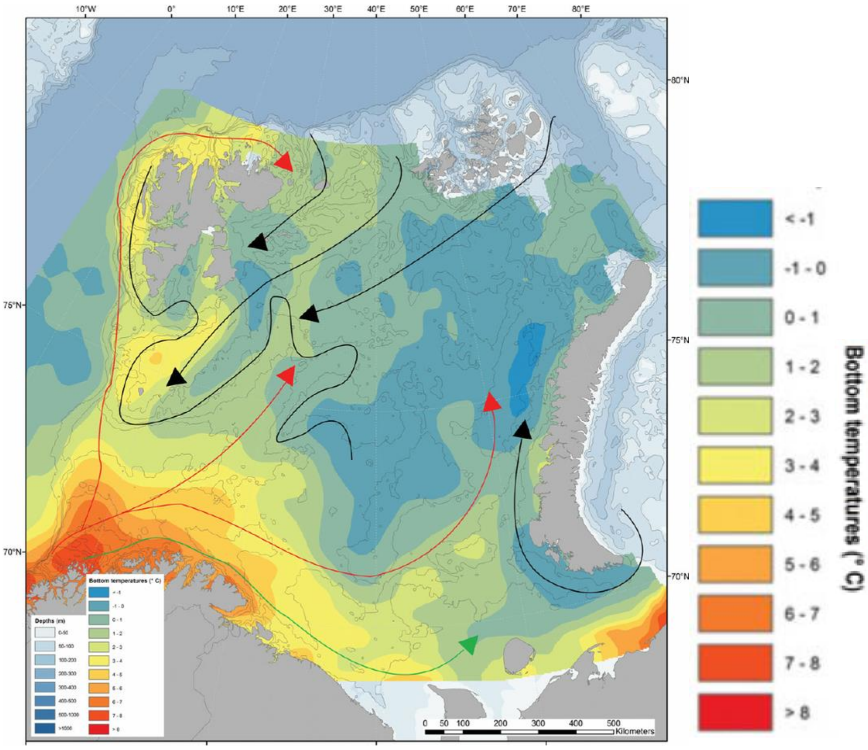

Figure 18: Bottom temperatures in the Barents Sea, averaged from 2000-2010 Seabird CTD vertical casts. The black line represents the oceanographic polar front, and the arrows indicate currents of coastal water (green), Atlantic water (red) and Arctic water (blue). The figure is from Jørgensen et al. (2015).

The relatively wide size range of mature females in this study compared to other studies (except that from Bonne Bay in the Gulf of St. Lawrence) could maybe be explained by the fact that several different gear types were used, as the smallest and largest mature females were caught with a small-meshed pot with a small-opening, and a commercial pot, respectively. As we know that size at maturity molt is (at least to some extent) temperature dependent (Burmeister and Sainte-Marie, 2010), the broad size range might be an indication that the females are utilizing areas with differing temperatures within the distribution area (Figure 18), e. g. at the border of the benthic polar front. It is likely that a further expansion of the distribution areas westwards, and thus possibly into warmer waters will keep up or enhance this effect, and in future studies the size range should be investigated in relation to the temperature distribution.

Size at 50% maturity is reported to be around 50 mm carapace width in the southern Chukchi Sea (Jewett, 1981), which is considerably lower than the findings in this study. Size of 50% maturity has not been reported for many populations of snow crab, to my knowledge, limiting comparison to other studies. The terminal molt in snow crabs makes this parameter less useful than for species that continue to grow after the first mating event. For such populations (e.g.

red king crab) it is a more useful parameter in management, as setting the size of total allowable catch above the size of 50% maturity would allow most individuals to participate in at least one mating event. For snow crab in the Barents Sea, this is not so relevant as females rarely grow to the least size of allowable catch (100 mm CW) (Hvingel et al., 2017). However, it should be kept in mind that females that potentially reach this size (as has been reported from Greenland (Burmeister and Sainte-Marie, 2010)) might be important for the population's reproductive potential in terms of their high fecundity and also for the genetic diversity of the population. For male crabs who are targeted in the fishery it is important to have a good estimate of the size of maturity to set the appropriate least size of allowable catch, as has been done for the Barents Sea snow crab by Hvingel et al. (2017).

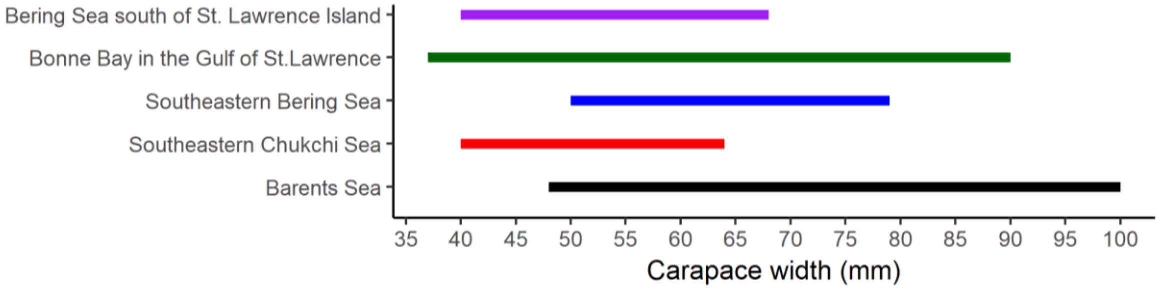

Figure 19: Size range of mature females of snow crab in the Barents Sea compared to other distribution areas. Data from the Chukchi Sea and southeast Bering Sea are from Jewett (1981), data from Bonne Bay are from Comeau et al. (1999), data from the Bering Sea south of St. Lawrence Island are from Kolts et al. (2015).

The observed gap in size of the largest immature female at 77 mm CW, and the largest mature female at 100 mm CW was a bit larger than expected. The size increment of females at the maturity molt is reported to be between 14.7 to 20% of pre-molt CW (Alunno-Bruscia and Sainte-Marie, 1998, Comeau et al., 1998), from this I infer that a mature female of 100 mm CW (the size of the largest female in this study) could not have been smaller than approximately 83 mm CW at the last instar prior to maturity molt. As the largest immature female found in this study was 77 mm CW, it seems like we have not been able to sample the entire size span of immature females. Similar differences in size of largest immature and largest mature female has been reported previously, and used as an argument to question the terminal nature of the maturity molt (Elner and Beninger, 1995), supported by the (rare) reports of mature (multiparous) females undergoing molt (Hooper, 1986). Alunno-Bruscia and Sainte-Marie (1998) contradict these arguments, reporting that in well studied areas immature females of sufficient sizes have been found, and that no multiparous females have been found that showed signs of upcoming molting.

The size distribution of mature females in this study (Figure 8) is likely to be biased by the difference in selectivity, efficiency and sampling effort of the gears that were used. Females caught in commercial pots were large (range 70-100 mm CW with a mean of 85 mm, standard deviation =8.4 mm). This was expected since these pots are designed to catch male crabs at the commercial size of 100+ mm CW. Due to the large proportion of the sample coming from the commercial industry (58/185), the observed size frequency distribution of mature females (Figure 8) is likely to be skewed to the right (more larger females) relative to the true distribution in the population.

4.4 Fecundity

Fecundity in female Barents Sea snow crab scales to body size, as has been reported in other areas (Figure 20 and later discussion). Given the size distribution of females, we can deduce that the larger-sized fractions of females contribute more to the total production than would be expected from their abundance (Table 7). In contrast, the smallest fractions of females are both low in abundance and fecundity and contribute relatively little to the total egg production of the population. If further studies of the population should reveal size specific spatial distribution of mature females, the above information should be taken into consideration in management. This could be used e. g. to identify potential refugee areas (no-trawl zones or no-fisheries zones) to ensure high recruitment. The calculations of percentwise contribution of egg production were based on the assumption that the observed size frequency distribution of mature females was representative for the population as a whole. I recognize that this assumption might not be valid, but it is worth presenting anyhow given the information scarcity for this population.

The size-fecundity relationship seems fairly similar to other areas (Figure 20) though with slightly yet consistently higher fecundity-at-size than in the compared areas, except the Gulf of St. Lawrence for females larger than ~65 mm CW. In the Barents Sea and the Gulf of St. Lawrence the maximum fecundity estimates are higher than the other areas. In the Barents Sea this seems to be mainly a consequence of the large size of the females found, whereas in the Gulf of St. Lawrence the line is steeper, resulting in higher fecundity for females larger than ~65 mm CW in this area.

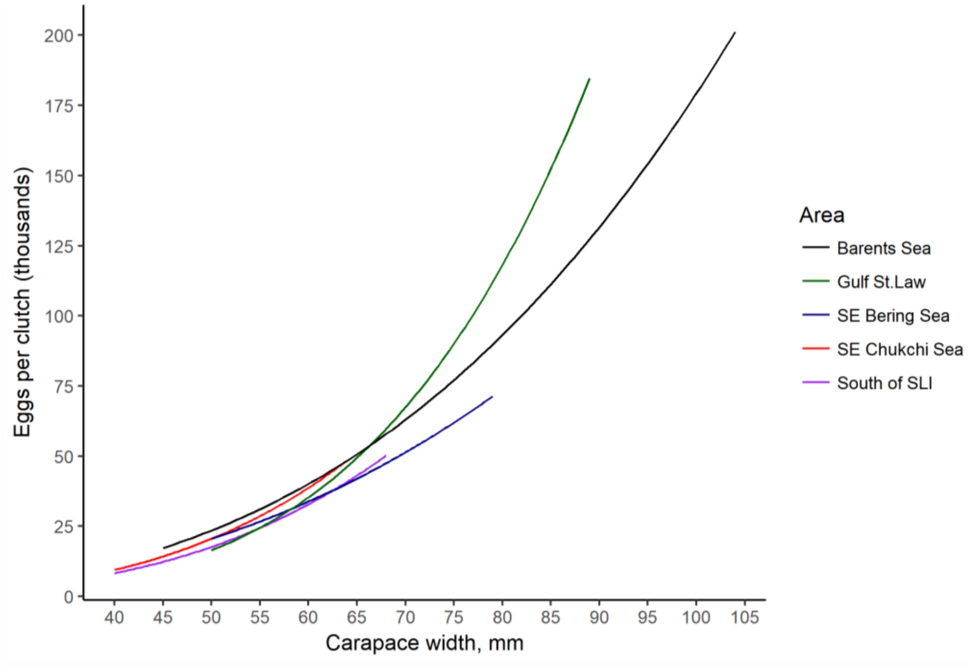

Figure 20: Comparison of fecundity estimates of female snow crab from this and other studies. Black line represents the relationship in the Barents Sea population as described in this study, all other data are from (Kolts et al., 2015) who presents a similar figure. The equations for the relationships are as follows: Barents Sea, $Y=0.24*X^{2.93}$; *Gulf of St. Lawrence,* $Y=0.0012*X^{4.20;}$ *Southeastern Bering Sea,* $Y=0.49*X^{2.72;}$ *Southeastern Chukchi Sea,* $Y=0.025*X^{3.48}$; *Bering Sea south of St. Lawrence Island (SLI),* $Y=0.029*X^{3.4}$.

A significant difference in fecundity between primiparous and multiparous females has been reported both in Newfoundland (Sainte-Marie, 1993) and in the Bering Sea (Webb et al., 2016). Webb et al. (2016) showed that in fact it is only the young multiparous females that has higher fecundity than the primiparous females, and the multiparous females with very old shell had even lower fecundity than primiparous females. Lower fecundity in primiparous females might be explained by the smaller size of the body cavity of primiparous females prior to the molt to maturity which might restrict the size of the ovaries and thus the number of eggs produced or possibly also the higher energetic need of the pubescent females directed towards molting which is then not available for ovary growth (Sainte-Marie, 1993). Unfortunately, it was not considered appropriate to compare the potential difference in fecundity between primiparous and multiparous females in this study due to the observed size difference between the two groups (Figure 11 and Figure 12), which is (given the relationship between fecundity and CW) likely to obscure the potential difference in fecundity between primiparous and multiparous females. The differing size of primiparous and multiparous females was unexpected and is difficult to explain but might be caused by some sampling bias as discussed above. Although the data in this study might be biased, the fecundity of primiparous females is likely to be lower than for multiparous females, deduced from visual inspection of the data and indices from other studies. This should be considered in management. The overall estimated relationship between fecundity and crab size from this study is based on both primiparous and multiparous females and thus is likely to represent some intermediate state between of the true relationship for the two groups separately, which justifies the use of this estimate for management purposes.

Egg mortality during brooding of about 20% (measured as the difference in size specific fecundity between females with early and late stage broods) has been reported (Comeau et al., 1999), whereas other authors did not find significant egg mortality (Sainte-Marie, 1993, Webb et al., 2016). This was also the case in the Barents Sea, where the females with late stage eggs actually had a higher estimated fecundity-at-size relative to females with early stage eggs. The findings in this study suggests that the Barents Sea snow crab population is not largely affected by the proposed causes of egg mortality, such as predation, parasitism and low fertilization rate (Elner and Beninger, 1992, Sainte-Marie et al., 2002). There is no logical biological explanation for higher fecundity in females with late stage eggs, and the observed pattern is likely to be caused by something other than a true biological effect, possibly by bias in fecundity estimation or type I error during the statistical analysis. It seems like females with early stage broods in this study tended to also be primiparous. Thus, the observed difference in fecundity-at-size between females with early and late stage broods might be an artifact of the confounding effect of lower fecundity-at-size for primiparous compared to multiparous females.

Mean individual egg dry weight was positively correlated to the carapace width of the female, suggesting that larger females might invest more into the eggs, although the effect is likely to be minor. Webb et al. (2016) found that egg volume, weight and elemental composition varied somewhat between females within different shell condition groups but not with maternal size and concluded that large variation in embryo quality with maternal characteristics was unlikely.

The two females who had 10% clutch fullness, old shells and deformed ovaries were probably senescent females. Sainte-Marie (1993) and Ernst et al. (2005) also reports multiparous females with un-proportionally small clutches and argues that this could be caused by senescence. The other females from this study with lower clutch fullness are more likely to have lost parts of the clutch, either during brooding, or during handling or transport (some of these were not frozen individually). In nature, female carbs might lose parts of the clutch during brooding because of e.g. predation or failure in fertilization or development (Elner and Beninger, 1995).

4.5 Reproductive cycle

This study contributes to the debate on annual versus biennial reproductive cycles, my findings support the theory of a biennial cycle occurring in the Barents Sea. Although my data does not contradict that both may occur.

The presence of both early and late developmental stages of eggs in the same month shows that the egg development is clearly not synchronous for all female snow crab in the Barents Sea, indicating a biennial (two-year) egg development/ brooding cycle (Figure 21). Females with different egg stages were at several occasions found at the same station at the same time, suggesting the pooling of data over several years was not responsible for this pattern. Other authors (Sainte-Marie, 1993, Moriyasu and Lanteigne, 1998, Comeau et al., 1999) report the same bimodal distribution of egg development stages and argue that this indicates a biennial cycle. In March there were still some females that did not have eye-spot stages of the eggs, indicating that they would not hatch prior to the following mating season, as the development from un-eyed eggs to hatching takes about 7 months in the wild (Moriyasu and Lanteigne, 1998), which would leave the eggs to hatch no earlier than September. It might be that the primiparous females from this study, having early developmental stages of the brood in March had recently extruded the eggs. However, there was no evidence of recent molting (soft shelled females) detected during the winter and early spring seasons when the sampling was carried out, contradicting the theory of a mating season for primiparous females in that period. Overall, I find the presence of females with early stage broods in March is a strong indication of a biennial brooding cycle.

Comeau et al. (1999) reports brown (ergo late stage) eggs of multiparous females in Bonne Bay, Newfoundland, as early as September and August (consecutive years, 1991 and 1992, respectively) and that hatching mainly occurs in May and June. Both Sainte-Marie (1993) and Moriyasu and Lanteigne (1998) report first occurrence of females with eyed eggs in August and hatching from April till June in the Gulf of St. Lawrence. In this study, no females with late stage broods were found in September, and the first occurrence of females with late stage broods was in November, keeping in mind that there was no sampling in October and that the sample size from September is small. This indicates that hatching might occur later than that reported from other areas where late stage broods were found in August and September. On the other hand, some egg clutches in this study were defined as “hatching” and several as “eyespot to hatching” in both February and March, indicating a main hatching period in early spring. However, it is possible that broods staged as “hatching” have been wrongly staged as such, as discussed above. The findings of Comeau et al. (1999) indicate that interannual variations of timing of egg development do occur and should be taken into consideration. This difference in the time of first occurrence of late stage eggs between populations should act as a note of caution of interpreting the findings of this study relative to other areas, as there does not seem to be a widespread synchronous pattern in reproductive cycle.

Among ovigerous females sampled in March, most of the multiparous females (46 of 55) had broods in late developmental stages, whereas most of the primiparous females (13 of 17) had early developmental stages of the broods (Table 8). This might be caused by most multiparous females having mated earlier in the season than most primiparous females, and thus the eggs having had more time to develop. However, this is inconsistent with the findings of Sainte-Marie (1993) who state that primiparous females extrude eggs earlier (in February-April) than multiparous females (April-June). Under the assumption that primiparous and multiparous females mate at the same time, a possible explanation might be that multiparous females have resided in warmer waters than the primiparous females, resulting in a faster developmental rate compared to the primiparous females. It is also possible that the pattern is obscured by the observed relationship between maturation stage and size, nut the mentioned arguments would also apply in that case. A study of the population with emphasis on spatial distribution, especially in relation to temperature, might yield a better understanding of the reproductive ecology of females of different size classes and maturation stages.

The indices for the occurrence of a biennial reproductive cycle is further supported by the data on ovary weight. The females with well-developed broods generally had the highest ovary weights, indicating that they are preparing to extrude a new clutch the following mating season. On the other hand, the females with early developmental stages had lower ovary weight, indicating that they were not ready to mate again this season. They also had lower ovary weight than the immature females, which support this theory. Sainte-Marie (1993) report that females with early development stages of the brood had ovaries less than half the weight of females with well-developed eggs and he also argued that this is a good indication of a biennial cycle.

Figure 21 gives an overview of the expected patterns in an annual and a biennial reproductive cycle. The conceptual model assumes a synchronized mating season in April, but as has been described earlier several authors report a longer period of hatching and mating from April to June, which further complicates the picture. Nevertheless, the simple model laid out in Figure 21 is useful to understand the reasoning behind the proposed biennial reproductive cycle. Two consecutive “cohorts” (females maturing and going through primiparous mating in the same year) of crabs are put into the model to illustrate how early and late stage eggs would co-occurrence in this scenario. Crabs of the first cohort will be in the second year of egg development (have late stage eggs) at the same time as the next cohort is in the first year of egg development (and thus have early stage eggs). It may also be seen from the conceptual model how an annual cycle may co-occur with a biennial cycle without this being detected, as it would not change the composition of egg stages at any time of the year. If there was only an annual cycle, there would not be a bimodal composition of egg stages close to the hatching season, as was observed in this study, thus this seems unlikely.

If the distribution of the snow crab population keeps spreading westward, which is expected, it is possible that parts of the population will reside in relatively warmer waters than what is the current situation (Figure 18). In this instance it seems likely that females in warmer areas adapt to an annual incubation cycle.

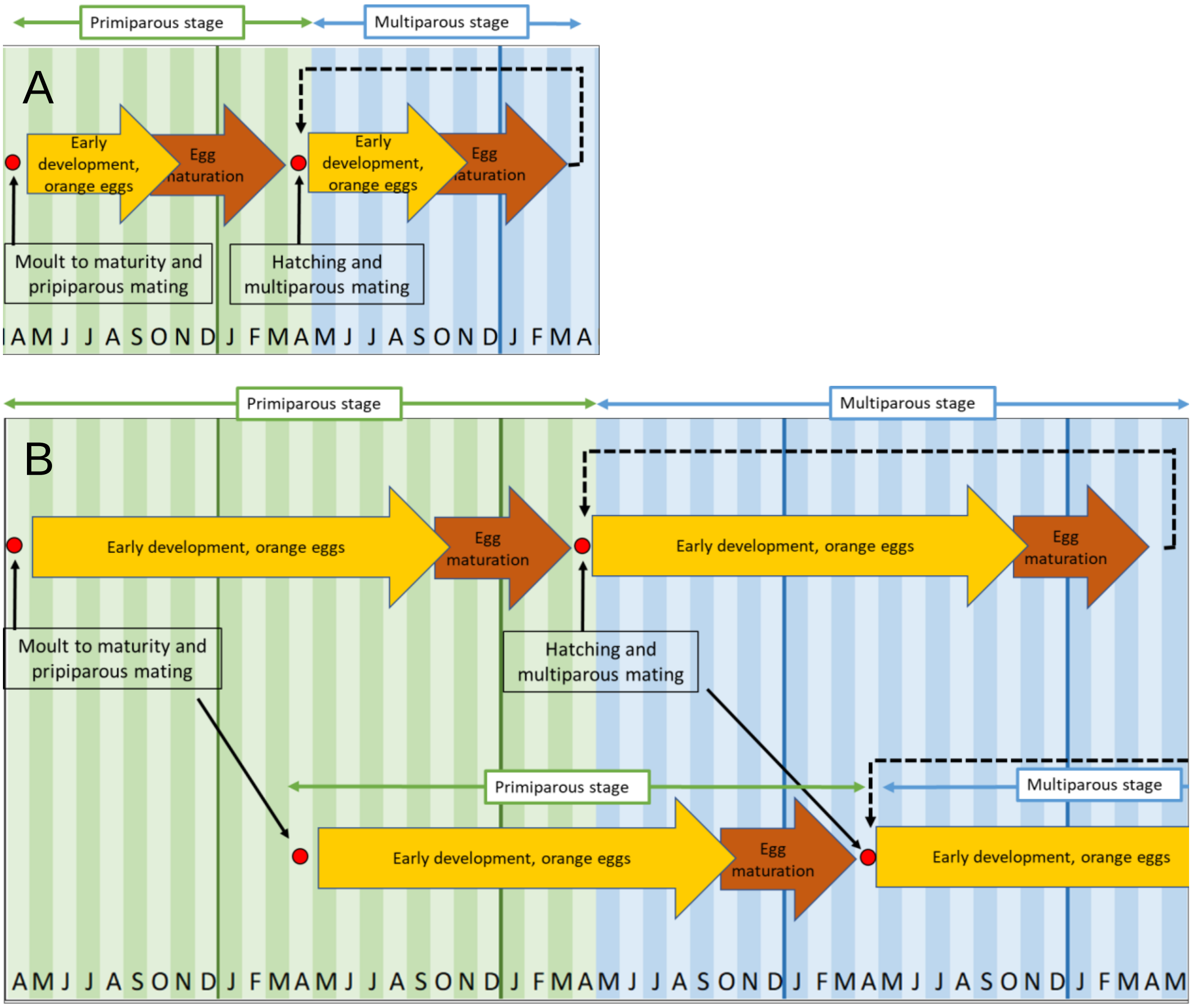

Figure 21: Conceptual models of the proposed annual (A) and biennial (B) brooding cycle for female snow crab from the Barents Sea. Both models assume a mating (indicated with a red dot) period in April, and the models start then. The months are indicated with different shades of green and blue and the first letter of the name of the month in the bottom of the panels. In the biennial cycle we expect to se both late stage eggs and early stage eggs simultaneously in the winter and spring season, as was seen in this study.

The length of the reproductive cycle is important for management purposes, especially in the estimation of the populations reproductive potential. Female snow crabs are estimated to live 5-6 years after the terminal molt (Alunno-Bruscia and Sainte-Marie, 1998, Comeau et al., 1999), and therefore might produce only two (assuming a biennial cycle) (Sainte-Marie, 1993, Comeau et al., 1999), or as much as six broods (assuming an annual cycle) during their lifetime. These extremes correspond to a potential life-long reproductive output of a mean sized female (75 mm CW) of about 154 000 and 462 000 eggs, respectively. Scaling these coarse estimates up to the population level give a substantial difference in the reproductive potential, stressing the importance of clarifying the likelihood and proportions of annual versus biannual cycles.

The findings of Ernst et al. (2005) and Webb et al. (2016), who showed that fecundity was lower in very old-shelled multiparous females, suggests that the two first brooding events are the most productive, and this should be investigated also for the Barents Sea population.

Even if a biennial cycle were to occur in the Barents Sea it is virtually impossible to completely dismiss the possibility that some females complete the cycle in one year. The more conservative assumption of a biennial cycle or the dominance of a biennial cycle should be chosen for management purposes, as the implications of underestimating the populations reproductive potential and on that basis set a lower quota for the fishery intuitively has smaller negative consequences to the population than over-estimating the reproductive potential.

5 Conclusions and future research needs

This study gives the first estimates of size at maturation and fecundity of female Barents Sea snow crab. It also shows evidence towards the existence of a biennial incubation cycle in the Barents Sea, although a co-occurrence of an annual cycle cannot be rejected. This new knowledge is directly applicable to management in that it can improve the estimation of the population’s productivity. More studies of the egg and ovary development, especially in spring are necessary to define the length of the egg incubation cycle and the time of hatching and mating more precisely. And the hypothesis of the co-occurrence of annual and biennial cycles should be further addressed with the aim of revealing if both cycles indeed co-occur, and if so, to establish the proportions of females from the population that have a biennial cycle. Findings in this study indicate that different gears have different size-selectivity for snow crab, and this issue should be further addressed to ensure representative sampling for stock assessments.

As the Barents Sea snow crab population spreads further it is essential to investigate the spatial distribution of and usage by the various parts of the population to identify important areas for nursing, egg brooding females, and mating. It is also critical to delineate where mature females and males reside during different periods of the year, and if they have an ontogenetic or mating migration as present in other areas. This information is important for crab stock management, as it might be necessary to protect certain areas from e. g. trawling at certain times of the year, if the management goal is to keep a population size that can support sustainable and profitable fishery in the future.

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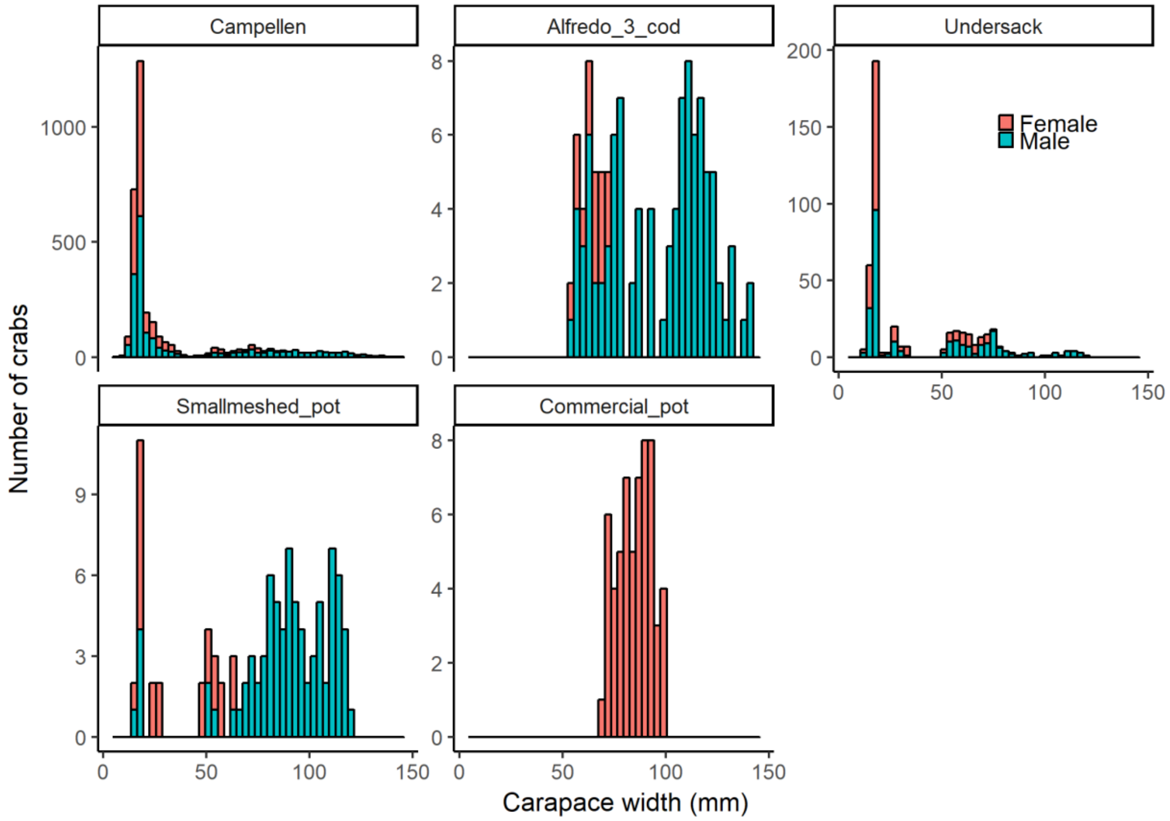
Appendix A – Supplementary table

Appendix table 1: Station table of stations with ovigerous females. For every station the date, source, position, depth, number of mature females caught, and the mean CW of those females are given.

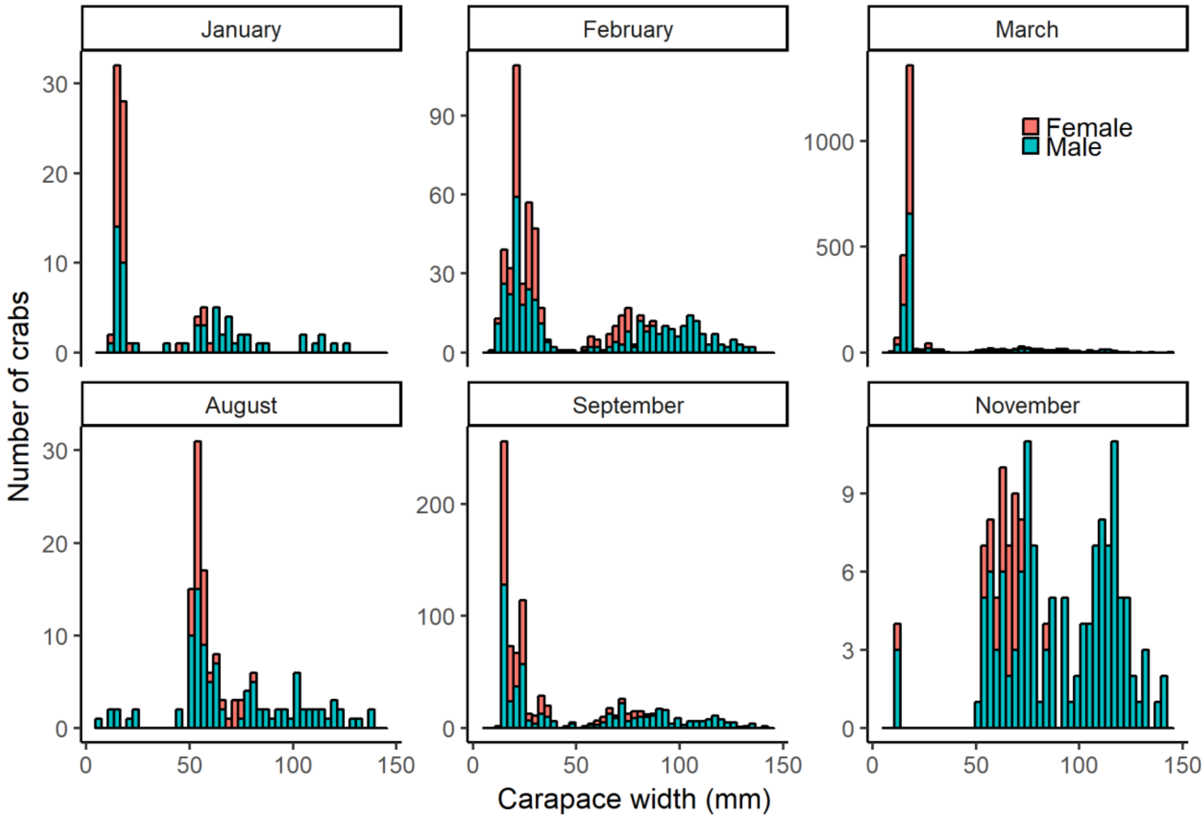
Station name/ number	***Date***	***Source***	***Latitude***	***Longitude***	***Depth (m)***	***Number of ovigerous females***	***Mean carapace width***
1931	26.11.2016	BRIDGE	75.4238	31.3140	225	1	69.0
195	01.03.2017	BRIDGE	75.9294	32.5800	260	2	71.5
201	01.03.2017	BRIDGE	75.9320	32.5871	180	1	70.5
197	01.03.2017	BRIDGE	75.9318	32.6012	229	2	70.8
203	02.03.2017	BRIDGE	75.9271	32.6026	222	2	72.1
228	04.03.2017	BRIDGE	75.8976	32.6377	237	1	71.1
191	01.03.2017	BRIDGE	75.9006	32.6976	231	1	77.4
194	01.03.2017	BRIDGE	75.9396	32.7252	224	1	75.0
204	02.03.2017	BRIDGE	75.9177	32.7263	231	5	68.5
2645	25.09.2017	IMR	73.2340	33.7772	207	2	61.8
1924	25.11.2016	BRIDGE	76.0014	33.9818	316	1	67.4
1849	13.11.2016	BRIDGE	76.0350	33.9878	295	1	66.1
1865	17.11.2016	BRIDGE	75.9427	34.0562	321	1	69.7
1864	17.11.2016	BRIDGE	76.1250	34.6800	329	3	71.0
192	19.02.2016	IMR	76.2115	34.9890	331	2	73.0
261	27.02.2016	IMR	76.0930	35.2452	327	1	85.0
158	28.02.2017	BRIDGE pot	75.9440	35.2625	220	3	54.0
211	21.02.2016	IMR	76.0755	35.2738	314	1	52.0
205	21.02.2016	IMR	76.0903	35.2965	256	4	76.8
219	22.02.2016	IMR	76.1018	35.3262	276	1	66.0
217	22.02.2016	IMR	76.1092	35.3658	257	2	84.0
223.1	22.02.2016	IMR	76.0973	35.3682	284	4	71.3
223.1	23.02.2016	IMR	76.0973	35.3682	271	2	70.5
221.1	22.02.2016	IMR	76.1018	35.3720	268	3	73.3
227	24.02.2016	IMR	76.0975	35.3878	275	2	60.0
257	27.02.2016	IMR	76.0908	35.4058	267	1	75.0
241	25.02.2016	IMR	76.1077	35.4478	278	2	74.5
235	24.02.2016	IMR	76.0680	35.5197	265	1	52.0
220.1	22.02.2016	IMR	76.1062	35.5397	272	1	72.0
222.1	22.02.2016	IMR	76.1180	35.5398	317	6	74.5
216	22.02.2016	IMR	76.1238	35.5492	254	5	74.0
246	25.02.2016	IMR	76.0787	35.5642	271	1	75.0
206.1	21.02.2016	IMR	76.1105	35.5657	279	1	69.0
237	24.02.2016	IMR	76.1203	35.6370	274	17	72.5
101	19.11.2014	IMR	75.8240	35.9682	261	2	71.5

2641	25.09.2017	IMR	74.7513	36.1228	269	4	63.2
2642	25.09.2017	IMR	74.7515	36.1333	272	1	62.6
2637	24.09.2017	IMR	74.7513	36.1395	315	3	62.0
236	27.02.2016	IMR	76.1955	36.2830	300	7	80.9
2620	23.09.2017	IMR	75.2778	36.5952	277	1	66.0
AP1	15.03.2017	Com. pot	76.0000	37.0000	301	50	84.6
K1	15.03.2017	Com. pot	76.0000	37.0000	264	7	86.2
108	20.11.2014	IMR	75.9618	37.1625	282	1	76.0
110	20.11.2014	IMR	75.9052	37.2007	348	2	66.0
102	19.11.2014	IMR	75.9317	37.4730	162	5	66.2
107	20.11.2014	IMR	75.9409	37.5275	205	4	72.5
106	20.11.2014	IMR	75.9996	37.6841	246	1	75.0
105	19.11.2014	IMR	75.9755	37.7631	249	2	68.0
103	19.11.2014	IMR	75.9362	37.7846	208	3	73.0
409	04.09.2012	IMR	75.7650	39.8667	225	1	70.0
413	04.09.2012	IMR	76.2450	42.5333	225	1	78.0
99	20.02.2015	IMR	74.2892	46.5772	218	2	69.0
100	20.02.2015	IMR	74.1018	47.6305		4	70.8

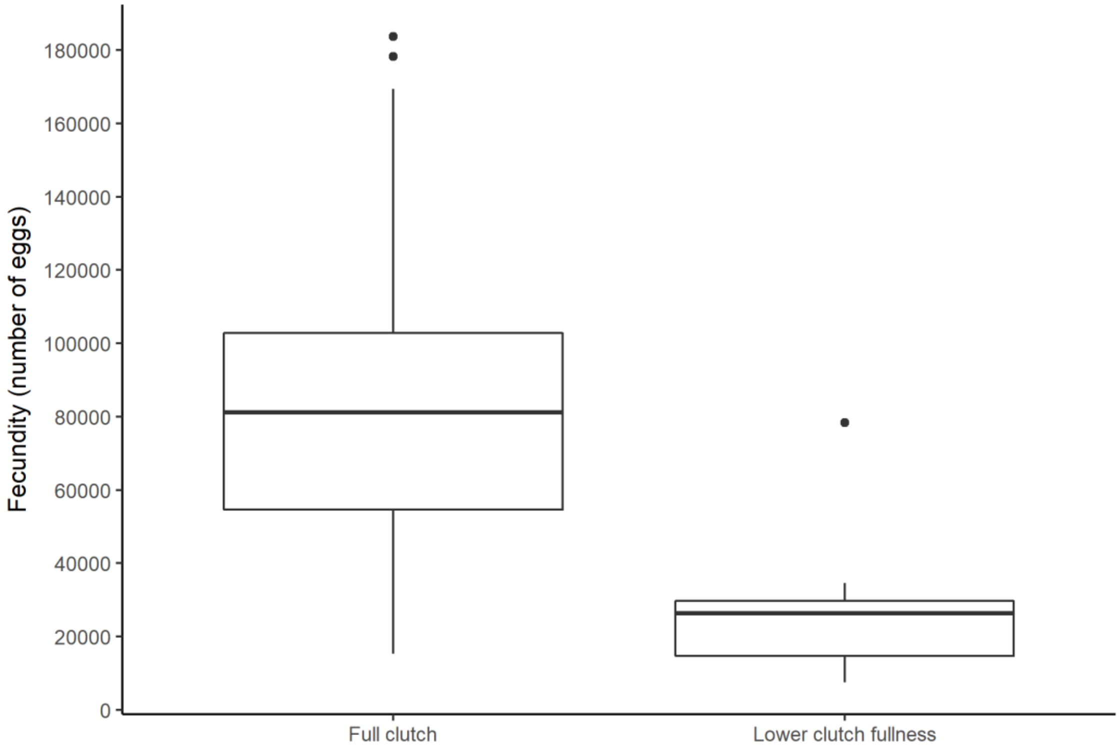
Appendix B - Supplementary figures



Appendix figure 1: Size distribution of snow crab according to the gear used. Crabs were caught in the Barents Sea in 2006-2017. Stacked bar graph, the height of the bar corresponds to the number of crabs caught in the respective group (bin width is 3 mm CW). The red areas of the bar represent the female portion of the population, and the blue areas represents the male portion. Be aware of the differences in the y axes. For the commercial pots, only females were recorded.



Appendix figure 2: Size distribution of snow crab according to the month of caption. Crabs were caught in the Barents Sea in 2006-2017. Stacked bar graph, the height of the bar corresponds to the number of crabs caught in the respective group (bin width is 3 mm CW). The red areas of the bar represent the female portion of the population, and the blue areas represents the male portion. Be aware of the differences in the y axes



Appendix figure 3: Box plot of fecundity in full and low clutch fullness females. Horizontal line indicates the median, the "top" and "bottom" of the box corresponds to the first and third quartiles, the whiskers extends from the box to the highest/lowest value within 1.5 times the interquartile range and outliers are plotted as points.