UiT THE ARCTIC UNIVERSITY OF NORWAY

Faculty of Biosciences, Fisheries and Economics

Department of Arctic and Marine Biology

Variation in egg size, fecundity and size structure in female red king crab (*Paralithodes camtschaticus, Tilesius 1815*) from Varangerfjorden over time.

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Rasmus Kristoffer Høyning

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Master's thesis

Variation in egg size, fecundity and size structure in female red king crab (*Paralithodes camtschaticus, Tilesius 1815*) from Varangerfjorden over time.

By Rasmus Kristoffer Høyning

Supervisors

Einar Magnus Nilssen

Ann Merete Hjelset

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1 Acknowledgement

When I first started studying biology at the university, I was always sure that I was going to be working with fish, until I did my bachelor's thesis with my supervisor Einar on shrimp. He opened my eyes to a completely different world of marine biology. When I started my master's degree and Einar had this thesis available, I was in no doubt of what thesis I wanted to write. His knowledge, enthusiasm and encouragement to think and speculate has helped me expand my mind and see the bigger picture in the world of marine biology. Thank you Einar!

The study could not have been done if the data had not been collected. A thanks to my supervisor at IMR Ann Merete for providing the data, showing an enthusiastic interest in my thesis and providing invaluable help during the thesis writing and graph making. The involved personnel at IMR and the crew on F/F Johan Ruud deserves thanks for gathering the data.

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2 Abstract

The introduced red king crab (*Paralithodes camtschaticus*) has successfully established in Norwegian waters since its release to the Barents Sea in the 1960's. It has become an important commercial resource contributing to the local coastal society in the eastern region of Finnmark. The fishery consists of one quota regulated area east of 26° (North Cape) and an open fishery west of 26°E. During the years of commercial fisheries multiple changes has been issued in the management regime. Change from a male-only fishery, a lowering of legal catchable sizes in both male and female crabs and quotas for female crabs have been applied with the intention that the red king crab should continue to be an important commercial resource as well as preventing further spreading west of 26°E. It has therefore been of great interest to study the development of the invasive red king crab. This study looks at fecundity, egg size and ovigerous female size distribution in Varangerfjorden in the period 2008-2017, comparing it with a previous study from the period 2000-2007 by Hjelset et al., (2012). The size-distribution of ovigerous females has changed as there are almost no big females > 150 mm left in the population. Individuals of 110-120 mm make up the biggest part of the ovigerous females population. Fecundity was found to be a function of size ($p < 0.0001$) and individual egg weight was not a function of size ($p > 0.05$). A mean sized female of 117 mm has increased number of spawning events by 20% based on lower calculated OL_{50}-values in the recent years. The fecundity upper range has declined due to the disappearance of the biggest females and therefore the potential egg production of the stock has declined. To maintain sustainable management, it is important to monitor the reproductive features such as fecundity, as it gives information about its reproductive potential. Thus, more work needs to be done to fully understand the reproductive biology of the red king crab in Norwegian waters.

Keywords: Ovigerous female, ovigerous length, egg production, life-history strategy, reproduction, Finnmark fjord, invasive species, management, fishery.

3 Introduction

3.1 Introduction and spreading

The red king crab (*Paralithodes camtschaticus*) is a non-native species to Norwegian waters, released by Russian scientists in the Barents Sea from 1961-1969 for harvesting purposes (Orlov and Ivanov, 1978). A total of 2609 adult individuals from 5-15 years old were released during the period, as well as 10 000 juveniles 1-3 years old in 1961 and about 1.5 million zoea stage 1 larvae (Orlov and Ivanov, 1978). It's native distribution ranges from the Sea of Japan, through the Bering sea and all along the coast to the area of Vancouver Islands in the north Pacific (Hjelset, 2012) and is known for its meat and size with a possible maximum size of 280 mm carapace length (CL) (Jensen, 2004). After appearing in fishermen catches in Norwegian waters for the first time in 1977, the species was left untouched and could continue to reproduce and spread undisturbed (Hjelset, 2012). As the red king crab mainly existed in the areas of Varangerfjorden in the beginning, it was not until 1992 due to by-catch and problems with local gillnet fisheries that it was given attention from Norwegian management and research institutions (Sundet and Hoel, 2016).

From 1994 a scientific fishery was initiated, and since the autumn of 2002 there has been a commercial fishery on the species, with males having the greatest commercial interest and value. With low exposure of predators on adult red king crabs (Rosecchi et al., 2001; Sakai et al., 2001; Weis, 2010; Amundsen et al., 2012; Chapple et al., 2012; Hjelset 2012), the population has spread throughout the Finnmark region and has fully established itself in the four most eastern fjords in Finnmark within the quota regulated area (QRA) east of 26°E (North Cape) successively, Varangerfjorden, Tanafjorden, Laksefjorden and Porsangerfjorden (Hjelset, 2012). West of 26°E there is an open fishery to avoid possible negative impact on the native marine ecosystem as it is considered an introduced species (Hjelset, 2012). The spreading of the crab further west in Finnmark has been monitored since 2011 on summer surveillance cruises documenting the spreading from the quota regulated zone (Sundet and Hoel, 2016). The spreading of the red king crab has gained a lot of media attention, sightings and catches has been reported in the media from all the way down to the south-western coast of Norway (Institute of Marine Research, 2016). In 2007 the first documentation of king crab in Balsfjorden was reported in the media (Benjaminsen, 2007), a sub-arctic fjord south of the city of Tromsø. Recent sightings and documented catches suggests enough evidence that the red king crab is reproducing in the area (Sundet and Hoel, 2016).

Since 1994 red king crab has been sampled annually in the autumn season during scientific cruises in the eastern fjords of Finnmark (Hjelset, 2012). This annual sampling gives an opportunity to monitor the population and study the development and adaptations based on other data than fisheries catches. In the PhD of Hjelset (2012), she investigated size at maturity in female king crabs, egg size and fecundity. This study made up a time series of carapace length frequencies from 1995-2010 as well as a fecundity data time series from 2000-2007 in Varangerfjorden. Another study estimated mortality rates, total mortality (Z), fishing mortality (F) and natural mortality (M) from 1995-2012 (Windsland, 2014). The PhD study of Windsland (2014) also suggested a weight-based von Bertalanffy growth curve and a biomass distribution of age in the red king crab of the coastal area in the periods 1995-2001,2002-2007 and 2008-2012.

3.2 Fisheries and quotas

The commercial fishery of the red king crab is divided into two periods, 2002 to 2007 and from 2008 till today, which makes it a young fishery. Up until the 2006/2007 season Norwegian and Russian governments managed the red king crab fishery together, but has split into separated national managements since (Anon., 2007). When the fishery was initiated, the average weight of the crabs caught in Norwegian waters was approximately 1 kilo higher than the native crabs in Alaska (Institute of Marine Research, 2016). Since then, the average weight of individuals caught in commercial fisheries has declined (Institute of Marine Research, 2016) and in 2011 the minimum legal catchable size was reduced from 137 to 130 mm to increase available catches for the fisheries (Anon., 2015). Originally in the beginning of the fisheries in the quota regulated area (QRA) east of 26°E, the vessels that were prioritized to be allowed in on the fisheries, were the once most troubled with bycatch of king crab in other fisheries, with 184 out of 264 of the vessels in 2006 having local affiliation (Anon., 2007). In 2008 they changed the system of who was allowed quotas and by the season of 2013/2014, a total of 551 vessels were registered for the red king crab fisheries (Anon., 2015). At the same time, the aim of the management plan given in 2007 was to have a long-term management plan to secure business and jobs within the regulated area.

Since 2002 the quotas for the crab increased, peaking in 2008/2009 with a total of 2610 ton as well as opening for commercial catches on both female and male king crab (Anon., 2015). The Russian management on the other hand, has not opened for a female crab fishery. The year after, the quota was reduced to about half the size and has then varied around a 1000 ton with the season 2014/2015 having a quota of 1100 tons male crab and 50 tons female crabs. Landings in the area had a value of 100-150 million NOK and in 2015 Norwegian red king crab had an export value close to 365 million NOK (Sundet and Hoel, 2016). In 2017, the value of landings within the QRA was 279 million NOK (Norges Råfisklag, 2018). In the open fishery west of North Cape since 2010, fishermen fishing in areas that are non-profitable get compensated (Windsland, 2014), and landings outside the QRA had a value of 12.7 million NOK (Norges Råfisklag, 2018). To create a more attractive commercial market for female crabs, the Norwegian fisheries department reduced the catchable size of female king crab to 120 mm in 2017 (Norwegian Ministry of Food and Fisheries, 2016). The total quotas for 2018 consists of 1575 tons of male red king crab, 100 tons of females and 175 tons of injured male crabs within the regulated area (Norwegian Directorate of Fisheries, 2017). From the total quota 1 ton is given to science catches, 1 ton to recreational fishing and 16 tons to the tourist fishing industry. By law all the crabs caught within this area must be delivered to local fish landing sites within the regulated area, which continue to secure local jobs and business.

3.3 Invasive species

Historically land and latitude have been natural barriers for marine species, restricting them to various parts of the earth's ocean. With human activity these barriers have been broken down intentionally and unintentionally. Today introduction and spreading of new species is the second most important reason for endangerment and extinction of species (Lowe et al., 2000). Of the 170 species in the IUCN (International Union for Conservation of Nature) database that had a documented cause of extinction, 54% were found to be related to invasive species (Clavero and García-Berthou, 2005). The intentional release of the red king crab made it an invasive species that has thrived in Norwegian waters, suggesting a strong ability to cope with changing conditions during the establishment phase (Hjelset, 2012). Invasion and establishment can be split into two phases of 1; density-independence, where density is low and there is a low expectation of intraspecific competition. And 2; density-dependence where the species density has reached a point where intraspecific competition is expected to increase (Hjelset, 2012). During a period of rapid population growth within an invasive species, plasticity within relevant life-history traits might then result in changes in phenotypes (Reznick et al., 1997; Hjelset, 2012). In the scientific community there is a debate regarding the use of terminology on invasive species. There are many different words and terms related to invasive species (e.g. alien, non-native, toxic, tropic) and therefore a framework to help defining terms within invasion studies was suggested (Colautti and MacIsaac, 2004). Looking at the spreading of the red king crab, this framework gives a tool to understand succession of the invasion, as well as understanding the terms used. To explain the different steps of invasion of the red king crab, Windsland (2014) used a sigmoid curve to describe three steps of invasion 1; arrival and establishment 2; spread and 3; equilibrium (Williamson, 1996; Windsland, 2014). The sigmoid curve described how there was an acceleration in dispersal after establishing in Varangerfjorden and how there was a sudden reduction in expansion after the spreading to Porsanger (Windsland, 2014).

3.4 Life history strategy

The life history strategy of a species is composed by several factors; somatic growth rate, age and size at maturity, age- and size-specific reproductive effort, age- and size-specific fecundity, egg size, age- and size-specific mortality, larval development type and time, and adult lifespan (Wilbur et al., 1974; Rose, 1983; King and Butler, 1985; Olive, 1985; Stearns, 1992; Winemiller, 1992; Winemiller and Rose, 1992; Eckelbarger, 1994; Jaeckle, 1995; Hadfield and Strathmann, 1996; McCann and Shuter, 1997; Ramirez-Llodra, 2002). The habitat and ecosystem where a species is present, breeding sites, competitors, food, temperature and refugia will also shape the plastic life-history strategies of a species (Stearns, 1976). Life-history traits that are highly plastic are important within a species for populations to adapt to local variations. However, within reproductive biology, the reproductive strategies of a species are fixed (e.g. batch versus total spawners, determinate versus indeterminate spawners) (Morgan, 2008). A common classification of the reproductive strategy and life-history characteristics of a species is the terms r-/k-selection named by MacArthur and Wilson (1967) based on the hypothesis of Dobzhansky (1950) (Pianka, 1970). Where K-selection is a qualitative adaptation towards high density effects, competition and stable environments with high effort into fitness and parental care of individual off-springs, while r-selection is a quantitative adaptation towards low density effects, no competition, putting all energy into reproduction and minimum effort into individual off-springs (Pianka, 1970). The king crab is in literature defined as a K-selected species because of its maximum size and highly developed reproductive behaviour (Hjelset, 2012)

3.4.1 Reproduction

The red king crab has internal fertilization and since the female crab is unable to store the sperm, the males need to be present when the female extrudes her eggs (Hjelset, 2013). For the male to be able to deposit his sperm, the shell of the female needs to be soft, which leaves them vulnerable and dependent on males to guard them (Hjelset, 2013). When the female moults, male spermatophores are deposited on the female's ventral surface during copulation. The ova are fertilized at the time of spawning, and the developing eggs are incubated on the pleopods (Adiyodi and Subramoniam, 1983; Nelson, 1991; Ramirez-Lodra 2002). Eggs are incubated from 10-12 months and they reproduce every year (Stevens and Swiney, 2007). They mate in shallow waters and the spawning event is directly linked with the red king crabs' migration between deep and shallow waters throughout the year (Stone et al., 1992), a behaviour that has been documented both in native waters as well as in the present study area Varangerfjorden (Sundet and Hjelset, 2010). After moulting and mating in spring, they migrate to deeper water for feeding, before returning to shallower waters early winter. Slowly they start going to intermediate depths in late winter/early spring to pre-moult before mating in shallow waters again (Stone et al., 1992). All the energy spent in reproduction (e.g. spawning migrations, producing egg structures, protecting mates and parental care) is defined as reproductive effort (RE) (Clarke 1987; Thessalou-Legaki and Kiortsis,, 1997; Ramirez-Llodra, 2002). RE however, is difficult to quantify accurately and therefore reproductive output (RO) has been favoured as an estimate instead (Ramirez-Llodra, 2002). RO is the weight specific gonad production, the total biomass of reproductive products on the biomass of the female (Clarke, 1987; Thessalou-Legaki and Kiortsis, 1997; Ramirez-Llodra, 2002).

3.4.2 Fecundity

Fecundity is defined as the number of offspring a female individual produce within a given time-period (Ramirez-Llodra, 2002). It is a parameter representing a lived life as well as the start of a new one. There are distinct categories of fecundity (Anger and Moreira, 1998) and thus it is important for every individual study to define the fecundity explicitly to obtain maximum amount of information from the data analysed (Ramirez-Llodra, 2002). The realized fecundity was applied in Hjelset (2012) and it is defined as the number of eggs carried on the pleopods (Anger and Moreira, 1998). Fecundity is a non-conservative parameter that varies within a species based on food availability, population density and age and size at adult stage (Eckelbarger, 1986) and it is directly limited by bioenergetics and life-history strategies (Ramirez-Llodra, 2002). Standalone differences in populations such as skewed sex-ratios and reduced abundance of spawners may cause a decline in fecundity even if e.g. the food availability is high (Murua et al., 2003). Size at maturity and egg size directly restricts the fecundity parameter because the space available for eggs a restricted by the size as the red king crab is a brooding species.

The red king crab can carry hundreds of thousands of eggs, with reported numbers ranging from 25 000-390 000 eggs in Kachemak Bay in Alaska (Haynes, 1968), 73 000-704 000 in the Barents Sea (Gerasimov and Kuzmin, 1995), 18 000-560 000 in the fjords of eastern Finnmark (Hjelset et al., 2012) and 7 900-450 000 in Bristol Bay, Alaska (Swiney et al., 2012). A significant number of eggs per ovigerous female with carapace length has been documented in Finnmark fjords (Hjelset et al., 2012), while other studies also have reported an increase with female size, they report a decline at 138 mm CL in fecundity rate, suggesting that decline in the slope after 138 mm is due to senescent (Swiney et al., 2012). In addition, greater brood loss is reported in red king crabs with greater loss in females >138 mm by 4% compared to smaller female crabs from spring to autumn Swiney et al. (2012). In the Finnmark fjord Porsanger a trend has been found in egg loss from May to October in red king crab, but the results were not significant (Lindberg, 2012).

Males that moult pre-mating season do not participate in the coming mating season (Rodin, 1990; Dew and McConnaughey, 2005) and a male-only fishery might give rise to a skewed sex ratio and a reduction in mean male size leading to reduced fertilization due to sperm limitation (Sato and Goshima 2006, Swiney et al., 2012). With the current catchable size of males 130 mm in fisheries, some males might not even be able to participate once before being caught (Windsland, 2014). Lack of larger males on the mating grounds due to moulting (Dew and McConnaughey, 2005) and sperm limitation would affect the fecundity possibly both in the long term and in year to year variation.

Investment in egg production is mainly affected by food quality and quantity, and influenced by some environmental factors, of these are temperature maybe the most important one, and toxic substances in the local habitat (Ramirez-Llodra, 2002). Egg production is the result of reallocation of energy in a trade-off between individual growth and reproduction, and thus enables a lot of strategies that are directly influential on the fecundity parameter such as size and age at maturity and first reproduction, egg size and reproductive effort (RE) (Ramirez-Llodra, 2002). Of these strategies the size of eggs is often a less variable parameter (Stearns, 1992). Trade-offs, the links between traits that constrain the evolution of two or more traits (Stearns, 1992), is essential in fecundity studies as the primary goal of all species is to survive and reproduce (Hjelset, 2012). When two physiological functions are generating energy from the same resource storage it is defined as a physiological trade-off, if resources gathered for this resource pool are limited, an increased transport of resources to one function must result in reduced resources to another (Stearns, 1992). During periods of limited resources, increasing reproductive effort will reduce somatic growth. The increased reproductive output (RO) will be seen as either increased fecundity or increased egg size, (Ramirez-Llodra, 2002). Optimizing the balance between reproductive effort and somatic growth is to maximize the fitness of a species, deciding when to mature and how much to invest in reproduction up against chances of survival after spawning and survival of the offspring. The red king crab in Norwegian waters mature at an estimated age of 5-7 years (Windsland, 2014; Sundet and Hoel, 2016) and is a species that benefits from size as fecundity increases with size on successful reproduction. When invading the coast of Finnmark with high food availability, low predation and fishing pressure, it enabled the king crab to maintain somatic growth and have a high reproductive output.

3.5 Larvae and juveniles

The red king crab has an indirect life cycle with a pelagic larva and benthic juvenile and adult stages, with the pelagic larval stage being the most critical phase (Hjelset, 2012). Little research has been done on the larval stages of the red king crab (Michelsen et al., 2017), as well as studies on the juveniles due to its behaviour (Hjelset, 2012). Being pre-adapted to low food availability and to tolerate low temperatures (Anger, 2006), the red king crab has the possibility to release their larvae at a wide time range making it resistant to differences in the habitat. It has been shown that the king crab larvae was present in the water column from January to May in Porsangerfjorden (Michelsen et al., 2017), fitting the pattern of its successful establishment in Norwegian waters. The pelagic larvae live in the upper water column for up to two months before settling in shallow waters <20 m, staying there as juveniles until they migrate to deeper waters as the grow bigger and eventually mature (Sundet and Hoel, 2016). Cannibalism occurs within the species and especially in between the early stages 0-3 year old juveniles which share the same habitat. Experimental studies have been done on the survival of glaucothoe, the settling stage of the red king crab, together with cannibalistic predation from juvenile king crabs 1-3 years old, showing a highly reduced survival with predators present, with a dampened effect by available refuge (Stevens and Swiney, 2005). A similar study performed argues that 1 year old juveniles potentially can have a strong impact on the 0 year class, and that the larger crabs have less effect on the smallest crabs (Long et al., 2012).

3.6 Feeding

Due to its large body size and multiple ways of feeding, the red king crab has a wide range of benthic prey in their diet (Oug et al., 2011; Pavlova, 2015; Fuhrmann et al., 2017). In a study done by Sundet et al. (2000) they found a highly omnivorous diet with polychaeta, bivalves and algae as the three highest prey groups in the stomach respectively, followed by gastropods and multiple groups of Echinoderms. Recent studies also show that polychaeta and bivalves dominate the stomach content and explain the huge variation in diet with different depth and areas of foraging (Fuhrmann et al., 2017). Besides being a highly effective predator on especially sessile and slow-moving benthos (Falk-Petersen et al., 2011), other events such as spawning in capelin (*Mallotus villosus*), which feeds in the open Barents Sea and migrate to shallow waters to spawn, both eggs and post-spawning capelin has shown to be highly present in stomach samples of red king crab when available (Mikkelsen, 2013).

3.7 Current knowledge status

It has been showed that the red king crab in Finnmark have a higher mean ovigerous length (OL_{50}, the size where 50% of female crabs carries eggs), compared to ovigerous females in studies from native areas (Hjelset et al., 2009). They found mean OL_{50} of 108,9 ± 0,2 mm for Varangerfjorden, with non or minor significant difference with the neighbouring fjords and only a difference of 0,1 mm between the periods before and after onset of the commercial fisheries. Findings of spatial and temporal changes in the size at maturity in Norwegian waters is probably explained by a varying year-class strength within the stock (Hjelset et al., 2009). Additionally, the fisheries did not seem to impact the size at maturity in the short period of time it has been active, but a reduction in potential egg production in the stock is suggested related to fisheries (Hjelset, 2013).

Fecundity data for the studied population of Varangerfjorden in the period of 2000-2007 ranged from 23 000-560 000 eggs, having a mean (±SD) of 176 000 ± 82 000 eggs and a CL mean (±SD) of 129 ± 19 mm. No annual differences in size-dependent fecundity was shown in Varangerfjorden during the 2004-2007 period, but during the whole study period, the total number of eggs in a standard sized female had dropped by 30000 eggs. The individual egg weight (IEW) was not influenced by the size of the female, but annual changes in IEW was significant. The total mortality estimates (Z) for the population also suggests that mortality is too high for crabs to reach old age and great size (Windsland, 2014), thus indicating a further reduction in mean stock egg production is to be expected due to lack of high fecund reproducing female.

In this master thesis fecundity data from 2008-2016 from Varangerfjorden has been analysed, extending the already available time series from Hjelset et al., (2012), making it a 16-year fecundity timeseries. Along with supplementary data from the annual scientific cruises by The Institute of Marine Research (IMR), I will be discussing the further potential development of the female red king crab stock and the species adaptation to the environment and fisheries in Varangerfjorden with focus on fecundity, size and weight of eggs. As important background it is also crucial to study how the size structure of female red king crab affects the reproductive potential as well as study if there are any long-time trends within Varangerfjorden.

4 Material and Methods

4.1 Study area

Varangerfjorden is the eastern most fjord along the Norwegian coast. It has a west-east direction with a wide opening towards eastern oceanic waters (Hjelset et al., 2009). The fjord has a depth of 300 m at the mouth and several smaller fjords and side-inlets on the southern side of the fjord, with depths down to 200 meters (Oug et al., 2011). It holds cold water temperatures in winter and reaches surface temperatures of 10-12 °C in summer time (Nilssen and Sundet, 2006). Similar to other northern Norwegian fjords it has a quite high water exchange with the Norwegian Coastal Current (NCC) (Wassmann et al., 1992), however the surface currents consist of a counter-clockwise gyre in the outer parts, which suggests a minor water exchange (Nilssen and Sundet, 2006). Even though the red king crab is found throughout the whole fjord, it seems like the silty to sandy sediment bays and inlets in the south are favoured (Oug et al., 2011).

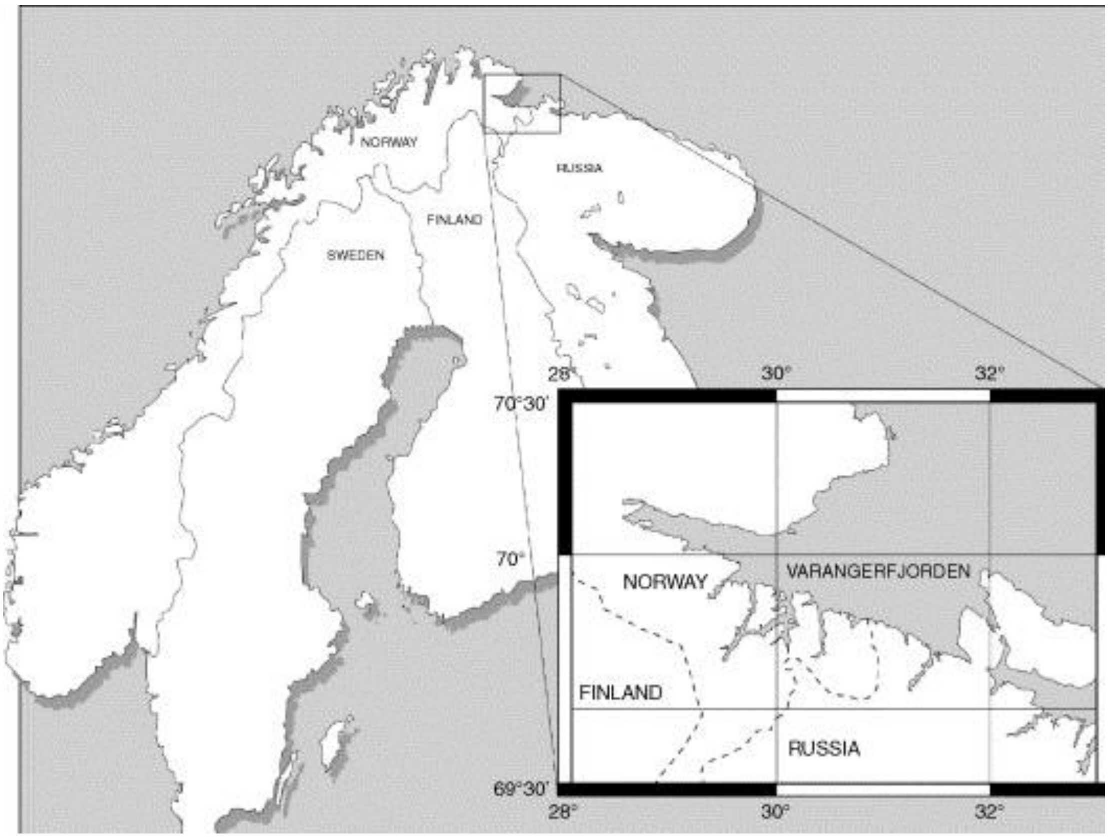

Figure 1: Map of the study area Varangerfjorden (from Nilssen and Sundet, 2006)

4.2 Sampling method

In annual autumn cruises conducted from 2008-2016 by the IMR crabs have been sampled in Varangerfjorden on board R/V Johan Ruud (Figure. 1). Using baited traps and a beam trawl, bottom areas spanning from 25- to 400-meter depths has been covered during the yearly sampling, covering a variety of bottom types. When brought to the surface, crabs were put in tubs stored on deck and brought into the laboratory where they would be measured for size and weight and other morphological measurements. Further the ovigerous females with roe would be turned on their backs, opening the abdomen and the pleopods with eggs would be cut of gently with scissors and transferred into zip-lock bags and put in the freezer.

4.3 Lab work

Samples from 5 years (2008,2010,2011,2015,2016) were analysed in the laboratory at The University of Tromsø, while the sample from 2013 has been analysed earlier by IMR.

The frozen king crab eggs were defrosted in a refrigerator at 2-4°C and processed within 24-48h. Weighing boats were prepared with numbering and weighting before the eggs were carefully separated from the pleopods in the larger weighing boats. Other organisms found in the egg clutches as amphipods and bivalves were removed and noted. For subsamples, three small samples were taken from the egg clutches on the smallest pleopods and put in individual smaller weighing boats. The separated pleopods were also put in weighing boats and weighed. Everything is then weighed on balances, 0,001g accuracy for the main clutch and 0,1mg accuracy for subsamples and pleopods. The subsamples were then counted in a Bogorov-tray, put under a dissecting microscope, carefully using water and pins to spread them out. Dead eggs in the samples were also noted down while counting. After counting, they are transferred back to the weighing boats. All the egg samples were then put in a heating cabinet at 60°C for >24h depending on the number of samples put there at the same time, for it to dry properly. When fully dried out, they were again weighed on the same weights.

Subsamples were taken from 10 crabs evenly spread within the different size classes in each yearly sample, to compare and ensure no statistical difference in egg size within a sample. (King and Butler, 1985; Clarke, 1993b; Ramirez-Llodra, 2002). The subsamples consisted of 3 small weighing boats with an approximate number of 300 eggs in each. From these subsamples the mean individual egg weight (IEW) was calculated. F-test regression lines were then applied to see if there was a relation between individual egg weight (IEW) and carapace length (CL) for all years. Fecundity was then calculated for all the crabs using the total dry egg mass (TEM) divided with the mean IEW measured from the subsample.

4.4 Statistical analyses

All statistical analyses and creation of figures was conducted with RStudio, Version 1.1.423 – © 2009-2018 RStudio, Inc. (R Core Team, 2017), while tables and raw data treatment was done in Microsoft Office Excel, Microsoft Office 365 ProPlus.

Regression models of individual egg weight (IEW), total dry egg mass (TEM) and fecundity (F) were fitted to log10-transformed data both for the response variables and explanatory variable (CL) to stabilize the variance and to achieve the assumptions of normality and homogeneity of variance in a linear regression model (Hjelset et al., 2012).

$$log_{10}F = log_{10}(a) + b\ x\ log_{10}(CL) \tag{1}$$

All statistical results from the calculated regression lines to look for a relationship with CL are presented in tables. Analysis of covariance (ANCOVA) was run looking for a year effect in the dataset. A standard sized female from Hjelset et al. (2012) of CL = 125 mm was calculated (F ± SD) with Equation (1) for the period 2008-2016 for comparison. The 95th percentile was generated by describing the data with the Hmisc package in R.

The value at which 50% of randomly selected female king crabs had a chance to be ovigerous, the OL_{50}-value, was calculated using the method from Hjelset et al., (2009) Equation (2).

$$Proportion\ ovigerous = \frac{1}{1+exp(\alpha CL - \alpha OL_{50})} \tag{2}$$

The dataset is robust as removing outlayers did not affect the results and thus, they are therefore included in all the statistical analyses.

Reproductive output (RO) was calculated using Equation (3) and is illustrated in Appendix Figure 3., total wet egg mass (WW) and total weight of the female (TW).

$$RO = \frac{WW}{(TW - WW)} \times 100 \tag{3}$$

5 Results

5.1 Female red king crab size distribution

The length-frequency distribution of all female red king crab from Varangerfjorden in the period 1994-2017 is presented as to periods in Figure 2.

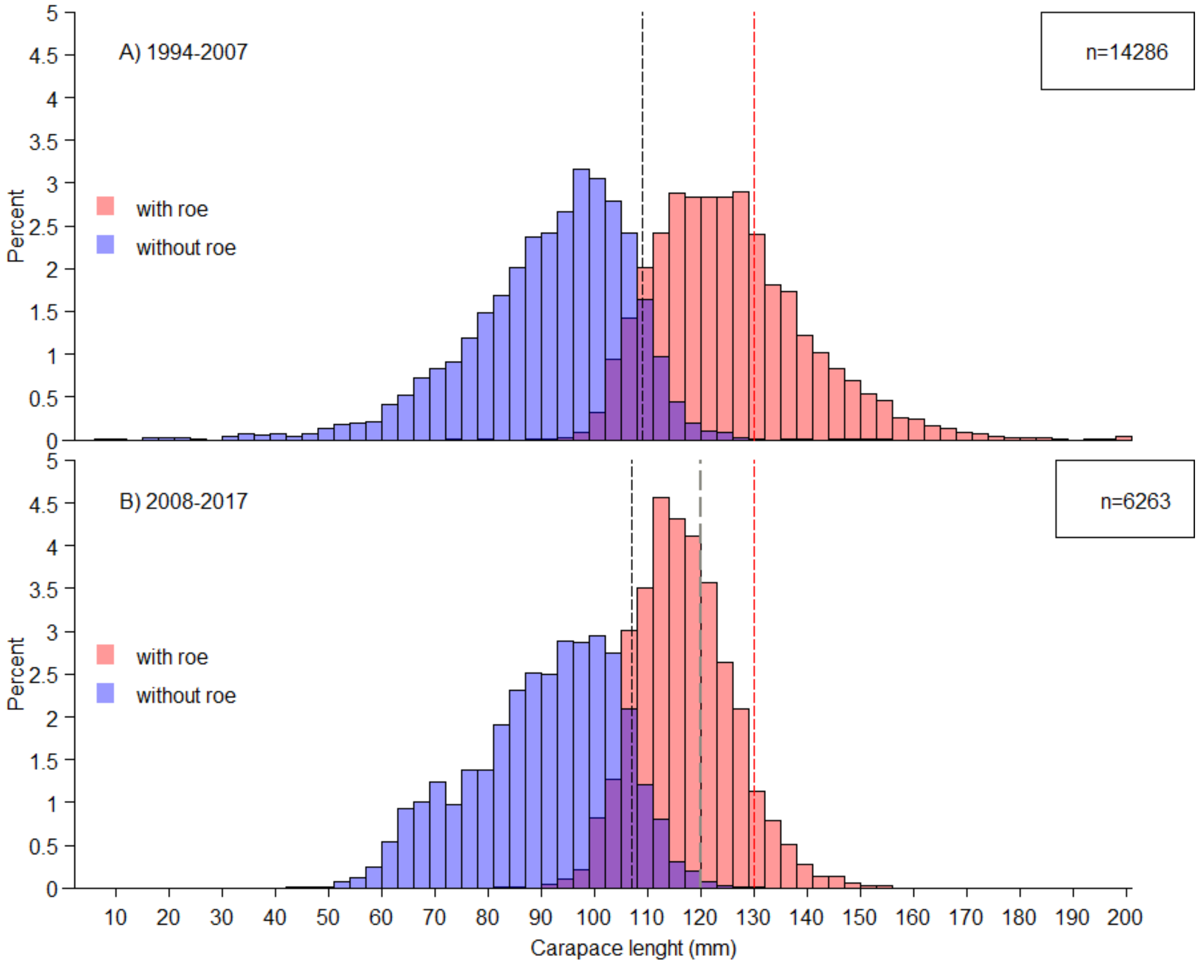

Figure 2: Female red king crab (Paralithodes camtschaticus) from Varangerfjorden. Length frequency (3 mm grouping) distribution from a) 1994-2007 and b) 2008-2017. Female without roe (blue), female with roe (pink) and the overlap of the two groups (purple). Black dashed line is the OL_{50} value calculated for the different periods a) 109 mm CL and b) 107 mm CL. The red dashed line is the minimal legal catchable size set for female crabs as of 2008 = 130 mm CL. Grey thick dashed line is the minimal legal catchable size set for female crabs in 2017 = 120 mm CL.

The size distribution in the female red king crab has changed between the two periods and mostly in the roe carrying population. In the period of 1994-2007 (Figure 2 a) the ovigerous crabs are characterized by a wide mode between 115 – 130 mm (median = 125 mm) compared with ovigerous females in 2008-2017 (Figure 2 b) with a sharp mode at 110-115 mm (median = 117 mm). The period of 1994-2007 has mean of 127 mm with a large tail going all the way up to 200 mm, while the tail of the 2008-2017 period is short and barely reaches the 155 mm CL with a mean of 117 mm. The 95th percentile length for the whole 1994-2007 period was 154 mm and in the period 2008-2017 there were no crabs above 160 mm with a 95th percentile length of 133 mm. The OL_{50} value (± SD) decreases with 2 mm from 1994-2007 to 2008-2017 with 109 ± 0.2 mm to 107 ± 0.2 mm respectively. There is not much change in the population of non-ovigerous females except from a shorter range of the head (30-50 mm) in 2008-2017.

5.2 Individual egg weight

The relationship between individual egg weight (IEW) (g) and carapace length (CL) (mm) is illustrated in Figure 3 from 2008 until 2016. The individual egg weight results presented in Figure 3. illustrate some variability between individuals, and for some years the egg size increases with CL and some years there is a decrease in egg size with length. The egg size data from 2015 indicates that the egg size is larger than the other years, the combined pooled regression seems to indicate no trend (black dashed line).

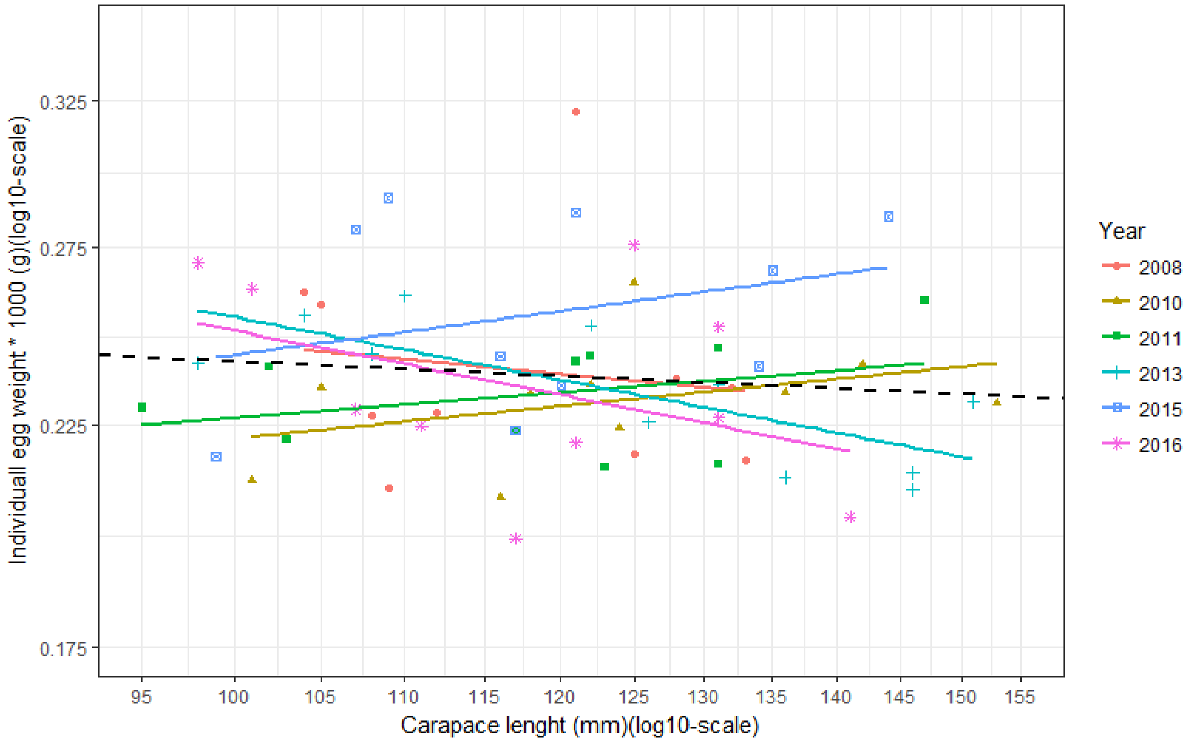

Figure 3: Red king crab (Paralithodes camtschaticus) from Varangerfjorden (2008-2016). Individual egg weight (IEW) and carapace length (CL) of the different years and the corresponding regression (dashed line). Log values have been replaced by the actual CL.

The results from the single year regression and pooled year analysis are presented in Table 1. and from the result presented, the IEW has a non-significant relation with CL for all years pooled, the change in IEW is not significant from zero. For the single year regressions, 2013 has a significant relation between IEW and CL and all the other years show insignificant values

(P>0.05). An analysis of covariance (ANCOVA), indicate no difference in slopes and height (size), see Table 4.

Table 1 Regression analyses of the individual egg weight (g)(on a log10-scale) on carapace length (mm) (on a log10-scale) of the female red king crab (Paralithodes camtschaticus) from Varangerfjorden, 2008-2016.

Year	n	intercept	slope	SE slope	r^2	F-value	P-value	range CL (mm)
2008	10	-0.231	-0.189	0.458	-0.102	0.17	0.691	100-133
2010	10	-1.056	0.201	0.174	0.036	1.34	0.281	101-153
2011	10	-0.963	0.159	0.157	0.003	1.03	0.341	95-147
2013	11	0.185	-0.390	0.112	0.527	12.15	0.007	93-151
2015	10	-1.159	0.273	0.324	-0.033	0.71	0.424	91-144
2016	10	0.198	-0.400	0.312	0.066	1.64	0.236	98-141
Pooled	*61*	*-0.439*	*-0.089*	*0.104*	*-0.005*	*0.73*	*0.396*	*95-153*

5.3 Total dry egg mass

Total dry egg mass (TEM) (g) as a function of CL (mm) from Varangerfjorden 2008-2016 is illustrated in Figure 4 and the results from the regression analyses are shown in Table 2. All regression results are highly significant (P< 0.0001, Table 2) meaning that log10 total egg dry weight is increasing with size for all years.

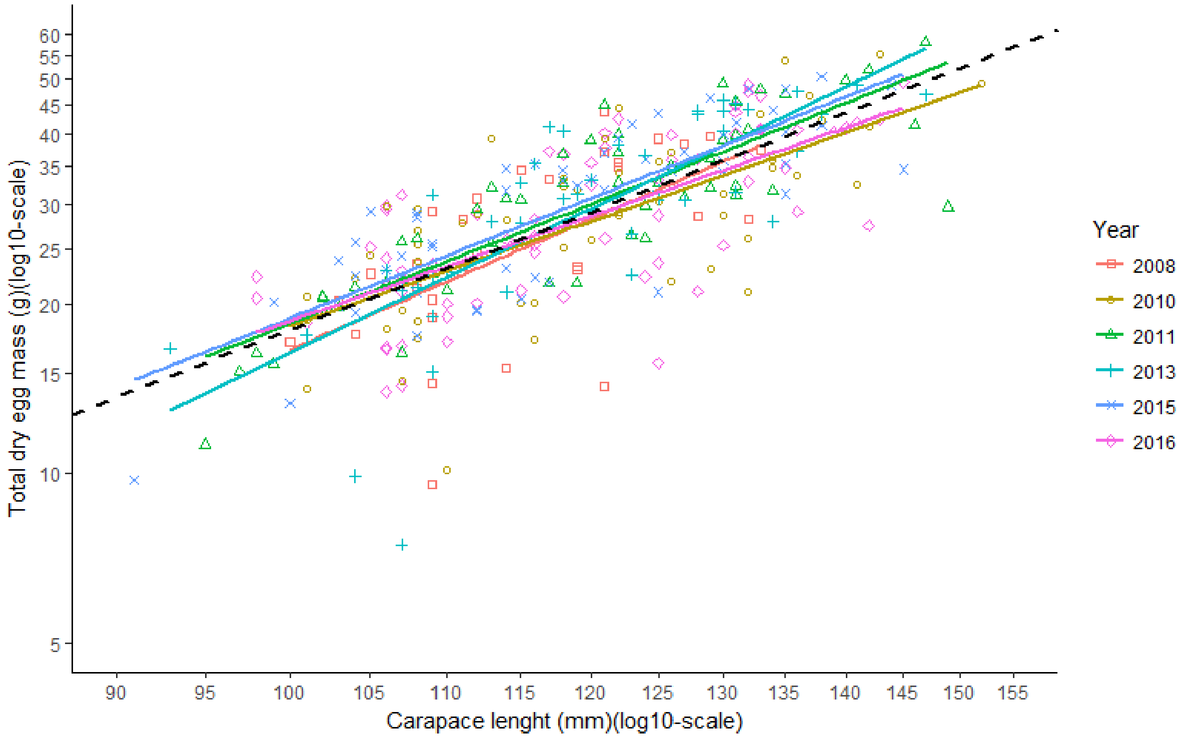

Figure 4: Red king crab (Paralithodes camtschaticus) from Varangerfjorden, 2008-2016. Total dry egg mass as a function of carapace length of different years, with pooled regression line (black, dashed). Log values have been replaced by the actual CL.

The total range in TEM is 7.46 g to 58.12 g and has a mean (±SD) of 30.16 ± 10 g. An analysis of covariance (ANCOVA) clearly indicates no difference in slope between years (P > 0.05, Table 4). This means that it was possible to make a common regression line (black dashed line in Figure 4) representing all years.

Table 2 Regression analyses of total dry egg mass (TEM) (g) (on a log10-scale) on carapace length (CL) (mm) (on a log10-scale) of the female red king crab (Paralithodes camtschaticus) from Varangerfjorden, 2008-2016.

Year	n	intercept	slope	SE slope	r^2	F-value	P-value	range CL (mm)
2008	31	-4.652	2.935	0.707	0.351	17.26	< 0.0001	100-133
2010	57	-3.434	2.348	0.317	0.491	54.96	< 0.0001	101-153
2011	52	-4.086	2.676	0.235	0.716	129.4	< 0.0001	95-147
2013	44	-5.235	3.225	0.410	0.586	61.79	< 0.0001	93-151
2015	56	-4.105	2.690	0.253	0.671	113	< 0.0001	91-144
2016	68	-3.426	2.348	0.282	0.505	69.26	< 0.0001	98-141
Pooled	*308*	*-4.010*	*2.633*	*0.132*	*0.564*	*398*	*< 0.0001*	*95-153*

5.4 Fecundity

The fecundity as a function of carapace length (CL) (mm) of female red king crab from Varangerfjorden 2008-2016, is illustrated in Figure 5, and the results from the regression analyses are presented in Table 3. All regression results are highly significant (P < 0,0001, Table 3) meaning log10 fecundity is a function of size and increasing with female crab size. For the whole period of 2008-2016 an ovigerous female has a mean fecundity (±SD) of 126000 ± 42000 and a mean CL of 117 mm. A standard sized female of 125 mm has mean fecundity (±SD) of 136000 ± 5700. An ANCOVA-test does allow for pooling the data set for fecundity (P > 0.05 Table 4), representing fecundity with one common regression line (black dashed line in Figure 5). The high IEW of 2015 (Figure 3), reduces the fecundity numbers which are lower than the other years with the same size range (Table 3) except from 2013, which did show a relationship between IEW and CL (Table 1).

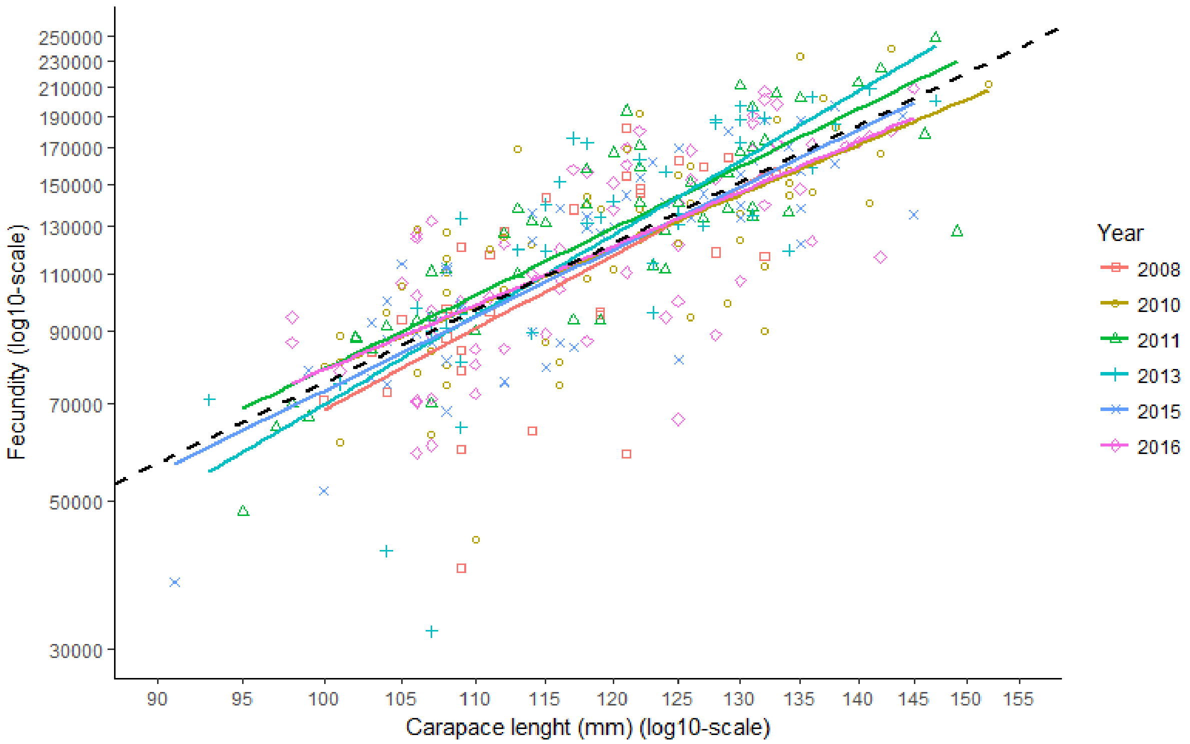

Figure 5: Red king crab (Paralithodes camtschaticus) from Varangerfjorden, 2008-2016 total number of eggs per female crab as a function of carapace length, with pooled regression line (black, dashed). Log values have been replaced by the actual CL.

Table 3: Regression analyses of fecundity (on a log10-scale) on carapace length (mm) (on a log10-scale) of the female red king crab (Paralithodes camtschaticus) from Varangerfjorden, 2008-2016.

Year	n	intercept	slope	SE slope	r^2	F-value	P-value	range CL (mm)	Range Fecundity*1000
2008	31	-1.034	2.935	0.707	0.351	17.26	< 0.0001	100-133	40-182
2010	57	0.277	2.310	0.319	0.480	52.61	< 0.0001	101-153	44-240
2011	52	-0.454	2.676	0.235	0.716	129.40	< 0.0001	95-147	48-249
2013	44	-1.605	3.225	0.410	0.586	61.79	< 0.0001	93-151	32-209
2015	56	-0.515	2.690	0.253	0.671	113.00	< 0.0001	91-144	38-197
2016	68	0.201	2.348	0.282	0.505	69.26	< 0.0001	98-141	59-209
Pooled	*308*	*-0.413*	*2.645*	*0.132*	*0.566*	*401.90*	*< 0.0001*	*95-153*	*32-249*

Residuals of the pooled fecundity regression (Figure. 5, Table 3) with a Loess-trend curve ± 0.95 CI is illustrated in Figure 6. It shows that there seems to be a trend of the small crabs (<100 mm) and the bigger crabs (>135 mm) to have lower fecundity while the middle group of 110-120 mm seems to have a high fecundity. Removing the six most extreme visual outliers (Appendix Figure 2), the ± 0.95 CI > 0 for the 110-120 mm group and CI < 0 for crabs > 140 mm.

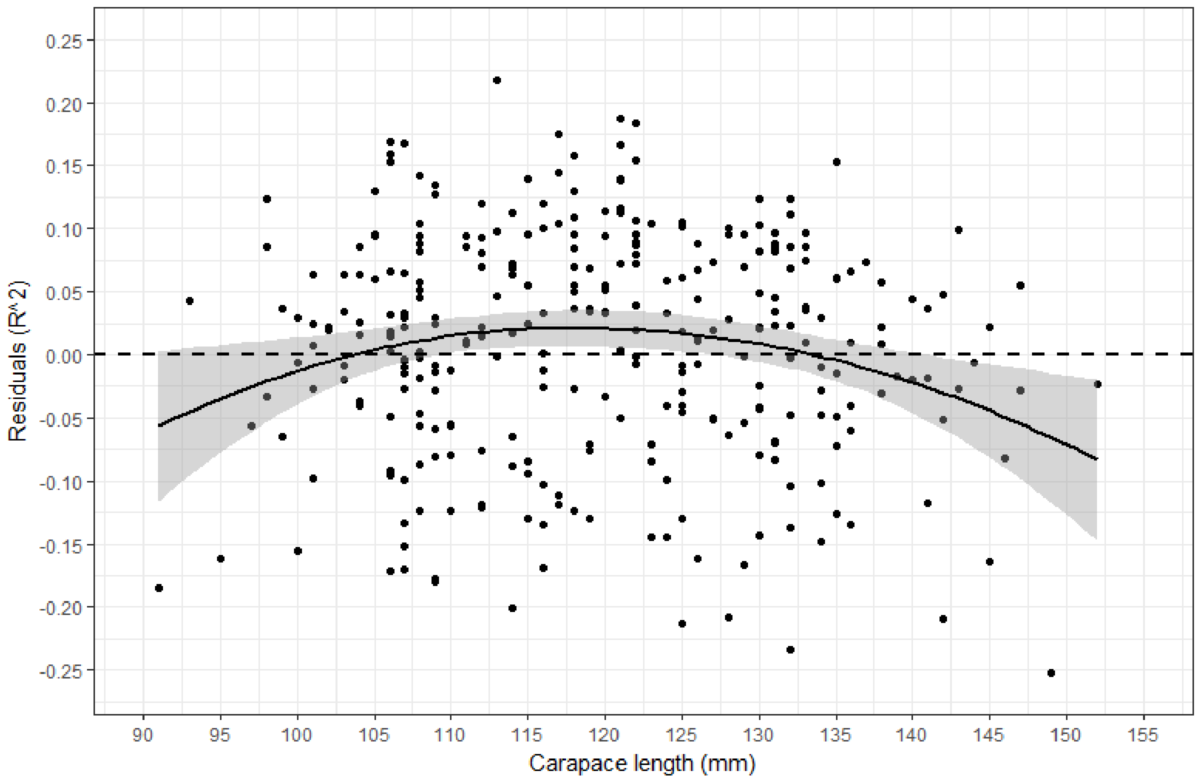

Figure 6: Residuals of the pooled regression (Figure 4, Table 3) on carapace length (mm) of the red king crab (Paralithodes camtschaticus) from Varangerfjorden 2008-2016. With a Loess-trend curve (solid) ±0.95 CI (grey coverage) and 0 residual line (dashed). Visual outliers n=6 showed in Appendix Figure 2.

Results from the ANCOVA-analyses are presented in Table 4. It shows there is a non-significant relationship with CL on IEW and a strong significant relationship with CL for both TEM and fecundity. There is no significant relationship with year or the interaction between CL and year.

Tabel 4: ANCOVA of total dry egg mass individual egg weight (IEW), total dry egg mass (TEM) and fecundity against listed parameters from Varangerfjorden in the period 2008-2016

Variable	parameters	df	F-value	P-value
Individual egg weight	CL	1	0,8	0,375
	Year	5	1,54	0,195
	CL:Year	5	1,61	0,174
	Residuals	49		
Total dry egg mass	CL	1	400,1	< 0,0001
	Year	5	1,32	0,254
	CL:Year	5	0,99	0,427
	Residuals	296		
Fecundity	CL	1	402,7	< 0,0001
	Year	5	1,08	0,37
	CL:Year	5	1,03	0,399
	Residuals	296		

6 Discussion

The Barents Sea red king crab has been of governmental interest since 1992 and has become an important local commercial species (Sundet and Hoel, 2016). To maintain a sustainable stock to harvest for future generations, it is important to have biological knowledge about of the species and to manage it thereafter.

In this study, I have found that there has been a change in the ovigerous females size distribution (Figure 2) with a noticeable reduction in the proportion of bigger females. There was no significant year effect in fecundity or individual egg weight, but there seems however to be a negative trend over time in fecundity. Due to the lack of big females and the nature of red king crab of having increased fecundity with size, showed by multiple earlier studies (Johnson et al., 2000; Swiney et al., 2010; Hjelset et al., 2012; Swiney et al., 2012), the total potential egg production (PEP) of the population has gone down (Hjelset, 2013). The size of the ovigerous female stock, showed an increase up until 2009, but since then a decline has been observed (Hjelset, 2013).

The relatively most fecund female individuals in the population of this study belong to the middle-sized group (Figure 6) and they also seem to have a relatively high reproduction output (RO) (Appendix Figure 3). Still however, 10 females of 135 mm are contributing more than 10 females of 115 mm to the population. From this study, an average 135 mm crab produces 166 622 eggs versus 109 030 egg of an average 115 mm crab. This gives a 57 593 eggs difference per crab i.e. 575 930 eggs more every 10 female crabs. With lower PEP, the population fecundity can still be maintained if 10 lost 135 mm ovigerous females are replaced by 16 ovigerous females of 115 mm. Though it is still uncertain if the red king crab is exceeding the carrying capacity of its habitat, the red king crab is most likely narrowing in on the equilibrium phase suggested by Windsland (2014). If they produce more eggs than the carrying capacity allows, it might not be how many that spawns, but rather when they spawn due to match-mismatch with food availability (Cushing, 1990).

Even though male crabs make up most of the commercial quota, the female fishery that previously almost targeted only the biggest 5% of females, is now targeting 34% of the biggest females. The Norwegian government reduced the female quota in 2018 with 50 000 tons (150 000 tons to 100 000 tons) reducing it with 33% compared to a reduction in the male quota of 12,5% (Norwegian Directory of Fisheries, 2017). Alongside this quota reduction, their intention is still to have high harvest pressure to reduce spreading outside the quota regulated area (QRA) (Norwegian Ministry of Food and Fisheries, 2017). It has been suggested that spawning stocks of extremely high magnitude might cause a reduced recruitment (Zheng et al., 1995) and that harvesting females from abundant stocks may give higher recruitment and a more stable populations (Botsford, 1991). With future perspective it has been argued that lowering the catchable size limit in male king crabs can result in a higher spawning stock (Kruse et al., 2000).

The unwanted spreading of king crab is retained to the western part of the QRA, while fishermen within the QRA would target the highest density areas. Regular surveys in the QRA indicates that density is higher in smaller side-fjords compared to the main fjords (Oug et al., 2018). The crabs in the side fjords also seem to have little immigration and emigration (Windsland et al., 2014). High quotas could lead to a patchy high fishing pressure, which has been suggested for a small side-fjord in Varangerfjorden to cause reduced catches after the high quotas given in 2009 (Oug et al., 2018). If it turns out that the king crab is falling below the carrying capacity and the quotas are not adapted thereafter, we might see fishing community interested in lowering the catchable size to increase profit. As the legal catchable size of females has already been lowered to 120mm, we might experience even more changes in the size structure of the female red king crab stock in the years to come. That is why this study is important as it highlights the biology of a species, so that it is possible to understand how to harvest it in the most sustainable way without endangering a "healthy stock condition".

6.1 Invasive species and terminology

Management of non-native species is challenging and identifying how the species arrived is important. The red king crab was intentionally released in the Barents Sea by humans and is therefore considered a non-native species. It has later become an invasive species as it has managed to establish and become widespread and dominant in many Northern Norwegian fjords (Colautti and MacIsaac, 2004; Hjelset et al., 2012). Still, the same term is not used for the Barents Sea king crab. Some refer to it as a non-native species (Sundet and Hoel, 2016) and some as an introduced species (Hjelset, 2012). These two terminologies both indicates that it has not been present in an area before, but the non-native term does not specify how it arrived. In addition, with an introduced species, is it any different from reintroduction of a species that has gone extinct? They are both living organisms put in an ecosystem where they currently do not exist. As species expand their distribution due to climate change and human activity (Sundet and Hoel, 2016), at what point should they be considered native to an area if they came due to natural expansion. There is a clear cut between species introduced by humans and species that spread naturally, thus the red king crab is considered an introduced non-native species in the Barents Sea and international law gives Norway full rights to manage the resource (Sundet and Hoel, 2016). However, with the current management from the Norwegian government of the quota regulated are (QRA) and free fishery area (FFA), there is a clear intention of keeping the red king crab within an area of interest. It is uncommon for an introduced species like the red king crab, to be managed sustainably like it is being done in Norway and Russia. Outside the QRA the Norwegian government treat the species according to 8th article in the Convention on Biological Diversity (CBD); “Prevent introduction of, control or eradicate those alien species which threaten ecosystems, habitat or species”. This brings in the term alien species, which is not specified by the convention, raising the importance of a good terminology in the global marine science and fisheries community to deal with non-native species.

Another hot species these days is the snow crab (*Chionoecetes opilio*) which is also considered a non-native species, but is under a different management regime as its origin in the Barents Sea is still unknown (Hansen, 2016). The United Nations Conventions on Law of the Sea (UNCLOS) obligates nations to reduce and control intentional and accidentally introduced species, this does not apply for the snow crab (Hansen, 2016), which makes its current management regulations different from the red king crab.

The red king crab has established itself in Norwegian waters and is managed as a commercially important species in the QRA and is regarded as a pest in the FFA in Norway (Sundet and Hoel, 2016). With pest being either a species with a negative economic effect (Falk-Petersen, 2004) or an organism considered harmful to human activities (Falk-Petersen et al., 2006), you could argue that it is being managed as a native species within the QRA and a non-native species in the FFA. Then at what point is it not reasonable anymore to define the red king crab as an invasive, non-indigenous, non-native or alien species as it is naturally occurring at this point and wanted along the northern most fjords of Finnmark? Should we simply draw a line between the domain of classical biology and the domain of invasive biology (Falk-Petersen et al., 2006) and ignore the fact the ecosystem has changed?

Because of the natural northward flow of the Norwegian Coastal Current (NCC) along the Norwegian coast (Johannessen et al., 1989; Skagseth et al., 2011), the large scale spreading west and south from the quota regulated area (QRA) is not likely to be caused by larval drift. The main source of spreading would then be emigration of adult king crabs walking. Given that there is no lack of food, the amount of emigration and immigration from a habitat with physiological and topographic ideal conditions is low (Oug et al., 2018). Since the sea floor does not provide an obstacle and the management regime clearly works towards a skewed density, the grass will always be greener outside the QRA. Thus, there will always be king crabs finding their way west of the QRA. Findings suggest that there is no significant increase in abundance in the FFA, but findings further west indicate continuous spreading (Sundet and Hoel, 2016). This study has found a further slight decrease in fecundity in a standard sized female (125mm) and a lower fecundity range than earlier. Due to the continuous changes in quotas and legal catchable size, it is still inconclusive whether this is an environmental adaptation or a result of fisheries. There are clear indications however, that fisheries have altered the populations since it started in 2002. Monitoring fecundity in crabs caught outside the QRA for comparison, could be of high interest to identify trends in fecundity, as the fishing intensity declines the further away from the QRA you go, due to lower densities. Fecundity is important in invasive biology as high fecundity exploits low density dependence, therefore monitoring fecundity in crabs outside the QRA might be helpful to predict the stock condition of the further invasion and spreading.

6.2 Environment

It has been indicated that the presence of the king crab has changed the bottom fauna leading to a change in the sediment quality in Varangerfjorden (Oug et al., 2011). Recent studies show that the function of the benthic community has changed from suspension and surface deposit feeding strategies to more motile and predatory feeding (Oug et al., 2018). It has also been argued that the red king crab stock has surpassed its peak values with possibly more limited recourses available (Hvingel et al., 2012). With intra-specific competition and more evasive prey, reduced surplus resources might increase the trade-off between growth and reproduction, decreasing fecundity and survival. This supports the findings of Windsland (2014) of a great total morality rate (Z) in the population, as the natural mortality M seems to increase. The male only fishery in the initial stages and the lowering of the catchable size limit might have reduced the number of big males on the spawning grounds leading to an increasing number of smaller males possibly reproducing.

With males not participating in reproduction every year due to their own moulting (Dew and McConnaughey, 2005), lack of big male crabs protecting females on the spawning grounds may be a leading cause of increased mortality for female crabs (Hjelset, 2013). When the red king crab matures and starts to reproduce the carapace length growth in females is reduced, while the male growth rate does not change per moult (Nilssen and Sundet, 2006). This may lead to a skewed sex-ratio because they reach catchable size much earlier, thus, favouring reproduction of the male crabs that skips the most moulting processes before they reach catchable size. It has been shown that the likelihood of skipping moulting increases with size in males (Hayes and Montgomery, 1963; McCaughran and Powell, 1977). Probability of moulting is a function of food and energy reserves. There is now an ongoing work of change in moulting probability as a function of size and year, and preliminary analysis indicates a reduction in size where 50% of the males are moulting in Varangerfjorden (Nilssen, unpublished data). It has previously been shown that probability of moulting in males of 140 mm has decreased with 60% over time in Bristol Bay (Zheng et al., 1995). This change in moult probability might eventually lead to a change in life-history traits of the Barents Sea king crabs, as the genes of the males that mature early and moult at a slower pace get to reproduce. However, due to the relatively brief time span of its existence in Varangerfjorden and the species natural longevity, it could take multiple years before it comes into effect.

The red king crab stock in the Barents Sea is a healthy population as there has been no documentation of high occurrence of parasites or substantial egg predation. However, with rising sea water temperatures (Hollowed et al., 2018), they might be exposed to new parasites and encounter new predators that expand the range northwards. Some amphipods and bivalves were found within the egg clutches of my samples, but the numbers were low and there were no visual signs of impact of their presence. Other egg predation studies have found no correlation in egg mortality with amphipods species (Kuris et al., 1991) and suggest nemertean species to be a more important egg predator. There were however no nemertean species found in any of my egg clutches. Previously few dead eggs have been found in the egg clutches of Norwegian Barents Sea king crabs (Hjelset et al., 2012) and very few dead eggs were also found in this study during counting. The low amount could however be due to bias, as many of the clutches had a wide spectre of colours and the lack of experience in identifying dead eggs. Due to the high chance of flawed sampling, no data has been processed on that matter. If high brood loss were to be found in future studies in Varangerfjorden, it is suggested that egg predation is investigated as a likely explanation (Kuris, 1991).

6.3 Ovigerous female structure and size distribution

During the period 1994-2007, size distribution structure of egg carrying females changed drastically. The 95th percentile of ovigerous female crabs CL dropped 20 mm to ≈ 140 mm size in 2002 and stabilised for the rest of the period (Hjelset et al., 2012). In 2008 the 95th percentile made another drop down to 131 mm (Hjelset et al., 2012) and has varied between 131-137 mm (2009-2016) with a current 95th percentile of 134 mm (Appendix Table 1). The 5th percentile remained relatively stable throughout the whole study period 1994-2010 (Hjelset et al., 2012) and has since 2010 varied between 102-106 mm with a current 5th percentile of 103 mm in 2017 (Appendix Table 1). The ovigerous females have gained a narrower distribution structure in the 2008-2017 period, and it seems to accumulate within the size range just above the calculated OL_{50} value (Fig 2). Growth per moult in ovigerous compared to non-ovigerous females of Varangerfjorden showed a difference of 14.4 mm in non-ovigerous to 5.1 mm in ovigerous (Nilssen and Sundet, 2006). In female crabs that moult every year, this is a good way to determine an approximate age when we have good data on size at maturity.

The estimated OL_{50} from the period of 1994-2007 and 2008-2017 decreased with 2mm CL from 109 mm to 107 mm, which equals an increase in roe carrying crabs smaller than the former legal catchable size of almost 10%. Increasing the group of roe-carrying females from 109-130 mm (21 mm) to 107-130 mm (23 mm). With the new legal size for females (120 mm), the increase in amount of roe carrying crabs is almost 20%. The OL_{50} parameter shows some variation from year to year, but the main trend over time is reduction in OL_{50}, from around a 110 mm CL in the 90's and in the latest years 105mm (Nilssen, unpublished data).

As bottom fauna and food availability changes and density of crabs is high, the few millimetres change in OL_{50}-value might be of substantial impact for commercial fisheries as it might lower the likelihood of females reaching legal catchable size. The average ovigerous female crab from this study, with a mean size of 117 mm and OL_{50}-value of 107 mm has been participating in 2 spawning events. In 2011 Hjelset (2012) found the average female of 117 mm with the measured OL_{50} of 109 mm at that time to be 1,6 spawning events. This is an increase of 20% in my data, which suggests that 1 out of 5 mean sized ovigerous females in this study have participated in one additional spawning event based on the calculated OL_{50} for the period (2008-2016). This increase in reproduction might be a way to compensate for the lack of big females in the population to keep the reproductive output high, reflecting the plasticity of the red king crabs life-history traits that makes it such a successful invading species.

Given the estimated age at maturity of 5-7 years (Windsland, 2014; Sundet and Hoel 2016) and the smallest ovigerous female crabs of 91 mm sampled in this study, we can do an approximate estimate of their age when reaching legal catchable size. Given the change from 130 mm to 120 mm, we can expect the crabs to be 2 years younger at legal catchable size. With the two different regimes they would be around 11-14 years and reproduce 7 times and 9-12 years and reproduce 5 times until they reached the legal catchable size for 130 mm and 120 mm respectively. If we assume the 91 mm ovigerous female crabs are 5 years and they waited one year with reproducing, their size would fit the OL_{50} value of 107 mm at an age of 6. The non-ovigerous females above 107 mm would reproduce at a size around 120 mm and 7 years of age, supporting the 5-7 years maturity estimate as it fits the overlap in distribution of the female king crab population (Figure 2). As Hjelset (2013) suggested minor impact of high mortality in newly matured crabs and strong influence of year class strength, the accumulation of female red king crab in the size range of 110-120 mm may be explained by multiple strong year classes with different mean age at maturity potentially holding 3 different year-classes approximately within that size range.

With the reduced legal catchable size of female crabs and at the same time increase in quota (50 000 to 150 000 in 2017), we might see even more changes in the size distribution of the king crab population. Harvesting on a bigger part of the female crab population, number of crab pots needed to attain the full quota might be reduced (Kruse et al., 2000). Where fishermen previously had to release female crabs smaller than 130 mm, they are now keeping them, which might relieve some pressure of the biggest female crabs and handling mortality of females not big enough (Kruse et al., 2000). Thus, if it turns out that fisheries are one of the bigger impact sources on the female king crab's size distribution, we should expect to see an even steeper decline in crabs larger than 120 mm. We might however, see an increase in females larger than 130 mm as they are not the only targeted size range, which could enable a higher potential egg production in the future.

6.4 Individual egg weight

The individual egg weight (IEW) gave confirmation on the hypothesis that there was no trend in IEW with size. The sample from 2013 did show a significant relation, but chances are that it is a coincidence and therefore highlights the importance of looking at pooled data. It has earlier also been proven that IEW is not dependent on female size (Johnson et al., 2000; Hjelset et al., 2012). It has also been shown that within species of copepods, as for the red king crab, there were no correlation in egg size to the female size (Poulin, 1995). In polar shrimp it was suggested that there was a significant difference in individual egg volume both within an egg-batch and between individuals (Clarke, 1993a). There are many studies in crustaceans reporting different results related to egg size within species. It has been shown that egg size increases with latitude in e.g. *Pandalus borealis* (Clarke et al., 1991), *Ceratoserolis trilobitoides* (Clarke and Gore, 1992) and the opposite in a study done on parasitic and free-living copepods, where they found a negative correlation with latitude (Poulin, 1995). However, as there is no significant gradient of latitude in the Norwegian king crab stock, it is more likely to be individual differences as found in polar shrimp. Since the sample was processed elsewhere, it could be a methodical error or a bias as someone else did the counting of 2013 and therefore support the importance of pooling the data.

As for the other years, there was some variation in egg size within the year between individuals, but for a single individual the variation was quite small (Appendix Figure 1), and the variation may be due to natural variation or human error and bias during the counting process. Counting many eggs in a dissecting microscope for multiple samples can be exhausting after a while. The 2015 samples did show a quite high IEW compared to the other years and this can be explained from the counting process. A lot of eggs got destroyed during the separation process in the counting chamber, making it hard to pair up egg content and broken egg membrane. This meant the number of eggs were poorly estimated and compared to the other countings and from personal observations most likely underestimated. Thus, the sample showed the correct value of dry egg mass weight, but lower egg count. Why this applied only to the 2015 sample is uncertain, but as the eggs seemed to have a weaker membrane, it might be environmental or food quality related or it could also be human error related to freezing process and storing.

A high occurrence of plastic in the stomach content of red king crabs in Porsangerfjorden has been found (Fuhrmann et al., 2017), which resides in the western side of the regulated fishing zone for king crab. They suggest that it is likely the crabs ingest plastic while filtering sediments for prey, therefore it is likely that the same outcome is to be found in Varangerfjorden since the plastic most likely was not a targeted prey. With diverse diet (Sundet et al., 2000; Oug et al., 2011; Fuhrmann et al., 2017) and an opportunistic feeding strategy, quality of food might vary and thus reduce the quality of eggs (Ramirez-Llodra, 2002).

Few studies have been done on pollution and biomagnification in benthic food chains, but it seems to have lower values than the pelagic food chain (Evenset et al., 2016). Recent studies of pollutant levels in red king crab in Finnmark found levels of POPs and metals to be low in comparison with European regulations, but they did find positive relations with size for pollutants such as mercury (Julshamn et al., 2015). As the study of Julshamn et al., (2015) was the first study of its kind done on Barents Sea red king crab, no time series has been made and it is not possible to tell what impact it has, but future monitoring is of interest not only for food consumption purposes. Pollution has been showed to possibly have negative impact on reproduction in fish (Kime, 1995; Kime et al., 1996), other crab species (Rodríguez et al., 2000; Medesani et al., 2004) and possible inhibition of moulting (Rodríguez et al., 2007). Therefore, with management perspective, monitoring of pollutants could be important for future scenarios as it might have an effect on reproductive behaviour and egg quality.

6.5 Egg mass weight and fecundity

There is a strong relation between size of the female, the number of eggs and the weight of the egg mass as our data suggests, thus fecundity is a function of size. This is reported in multiple studies for a variety of crustacean species (Koop and Field 1980; Hines, 1991; Nazari et al., 2003; Swiney et al., 2010). However, the trend in the fecundity data of this study shows that crabs in the 110-120 mm range are relatively more fecund (Figure 6). This could be explained by the distribution of multiparous and primiparous crabs and senescence. Primiparous crabs (first time spawners) are less fecund than multiparous (not first time spawners) (Dew and McConnaughey, 2005; Swiney et al., 2010; Swiney and Long, 2015). Findings show that the primiparous crab moult increase is almost two times greater than the multiparous moult (Stevens and Swiney, 2007b), which might explain why it is less fecund as it invests more energy in growth at first time spawning. It has also been found in low sample sized lab experiment that primiparous crabs have a higher brood loss than multiparous (Matsuura and Takeshita, 1985). As multiparous and primiparous crabs are impossible to identify in the field (Hjelset et al., 2012), growth data (Nilssen and Sundet, 2006) and fecundity data (OL_{50}, fecundity-carapace length) can be used to make assumptions on some groups of crabs to be primiparous. With an OL_{50} of 107 mm and crabs being more fecund in the 110-120 mm range, it is likely that the effect is due to an increased amount of multiparous relatively more fecund crabs.

The bigger crabs (>135 mm) seem to be relatively less fecund, which could be explained by a trend of senescence. This is supported by findings suggesting senescence in crabs >138 mm (Swiney et al., 2012). It could also be that the increased number of smaller males and low number of big females makes it less likely for the big males to mate with the big females, possibly reducing the reproductive success (Sato and Goshima, 2006). Due to the small number of bigger females the effect of senescence might be negligible, and it has not been regarded as a major problem for the Barents Sea stock in earlier studies (Hjelset et al., 2012). However, Hjelset et al., (2012) described the size-fecundity relation visualized with a power model based on a significant increase in eggs per ovigerous female with carapace length (CL). The significant fecundity-size relation found in this study does not support the power model as it does not seem that the bigger crab exploits their increasing CL to its maximum potential. If the OL_{50}-value continues to drop, the significance of senescence might increase as bigger crabs of the same size now will be older.

With a strong year class of primiparous crabs, the total fecundity of the population will turn out lower (Hjelset et al., 2012), but might also lead to a lower recruitment the following years due to cannibalism (Stevens and Swiney, 2005; Long et al., 2015). However, it can be quite hard to identify strong primiparous year-classes in a fecundity study like this, as it is of interest to sample a relatively even selection of different sized crabs for the egg samples. When the amount of small (<100 mm) ovigerous crabs are low in the sample, as they should be based on the size distribution (Figure 2), it makes it hard to analyze individual small size-ranges for comparison. There are however possibilities to discuss, e.g. if the smallest 2 crabs in 2016 of 98 mm were primiparous or multiparous crabs from the same year-class as the 91 mm crab from 2015. They seem quite fecund, as they both have higher fecundity than multiple larger crabs in 2016 (Figure 5). 2016 has a bottom range value of more than 10 000 eggs more than any other year (Table 3), and the crabs in the lower fecundity range are 10 mm larger than the smallest in 2015. This leaves it quite likely that the two smallest crabs in 2016 of 98 mm are multiparous and arguably belongs to the same year-class as the 91 mm crab from 2015. Thus, it is important with the size structure of the ovigerous and non-ovigerous females and fecundity data, as it might reveal information of which groups are greater and what size range makes up the core of the ovigerous female stock.

A viable way to identify a strong recruitment of primiparous females could be to look at larvae in the water column. In laboratory experiments it has been suggested that primiparous crabs hatch their eggs earlier due to longer development time (Stevens and Swiney, 2007a). Based on the results they created a conceptual model to describe the reproduction cycle of primiparous and multiparous crabs (Stevens and Swiney, 2007a). This model supports the findings of Michelsen et al. (2017) of king crab larvae being present in the water column over a longer period in Porsangerfjorden. This variation could also be due to temperature as it has been suggested that incubation time is reduced with higher temperature (Shirley et al., 1990; Stevens and Swiney, 2007a). Based on the findings by Eilertsen and Skarðhamar (2006) of a variation of less than 3°C in Finnmark fjords within the range ovigerous females operate, it was regarded as unlikely that temperature would affect the fecundity and egg weight (Hjelset et al., 2012) especially in the Varangerfjorden area where the crabs seem to find their preferred depth and bottom temperature within the both the main fjord and the side fjords (Oug et al., 2018). Thus, it is fair to assume that the hatch timing of the red king crab should not be significantly affected by temperature, supporting the suggestion of larvae monitoring to identify strong year-classes of primiparous king crab. In addition, predictions of future fecundity can be underestimated with strong presence of primiparous crabs as they show significant increase in reproductive success and timing of their hatching the following spawnings as multiparous crabs.

6.6 Conclusions and future work

In this Master thesis I have shown the further development of size distribution and fecundity of the female red king crab in Varangerfjorden. I have found a further reduction in presence of big females and a lower fecundity range, thus lower fecundity in the population. The current ovigerous female stock has gained a higher contribution of medium sized crabs and they also seems to be the relatively most efficient reproducing individuals in the stock with high individual fecundity and reproductive output. My data confirm that individual egg weight does not change with female size while the fecundity is significantly increasing with size. Calculations suggests a slight decrease in fecundity for a female of 125 mm, lower OL_{50}-values and an increase in number of spawning events for a mean sized female compared to the former study of Hjelset et al. (2012). As a characterised K-selected species, their ability to showcase a wide upper range in fecundity when they are under a low-density regime which favours r-selected species, reflects their success as an invasive species. This thesis is showcasing their adaptation to a more high-density dependant regime with change in food availability and a strong fishing pressure, describing their progress stabilizing as a top predator and human resource in the fjords of Finnmark.

The method used in this study gave solid results and results that correspond to current knowledge and findings in earlier studies. The possible bias and errors discussed and theorised, never seem to challenge the significance of the overall results, indicating that it is a resilient method, but still viable to possibly identify errors and flaws within the processing of the samples. The laboratory procedure is time consuming, but the simplicity, low costs and reusability of the gear supports the use of it as the data obtained are good. I would also like to highlight the fact that the hands-on method with no distant operations in the form of chemical tests and analyses with advanced machines, has strong educational value as it gives good insight in the biology of a species and makes it easy to understand the raw data produced.

Further to truly understand the adaptation of the red king crab, I would recommend doing identical analyses of the fecundity for the other successively invaded fjords Tanafjorden, Laksefjorden and Porsangerfjorden, as they are all under the same fishing regime. In future studies I suggest drawing a line and treat the coming years as a third period of the fisheries on the red king crab in Norway (2002-2007, 2008-2016,2017-) due to the changes in legal catchable size of female crabs. As I have identified some of the ongoing changes following the PhD of Hjelset (2012), there is still much work to be done to fully understand the development and reproduction of the red king crab as it continues to spread further south along the coast.

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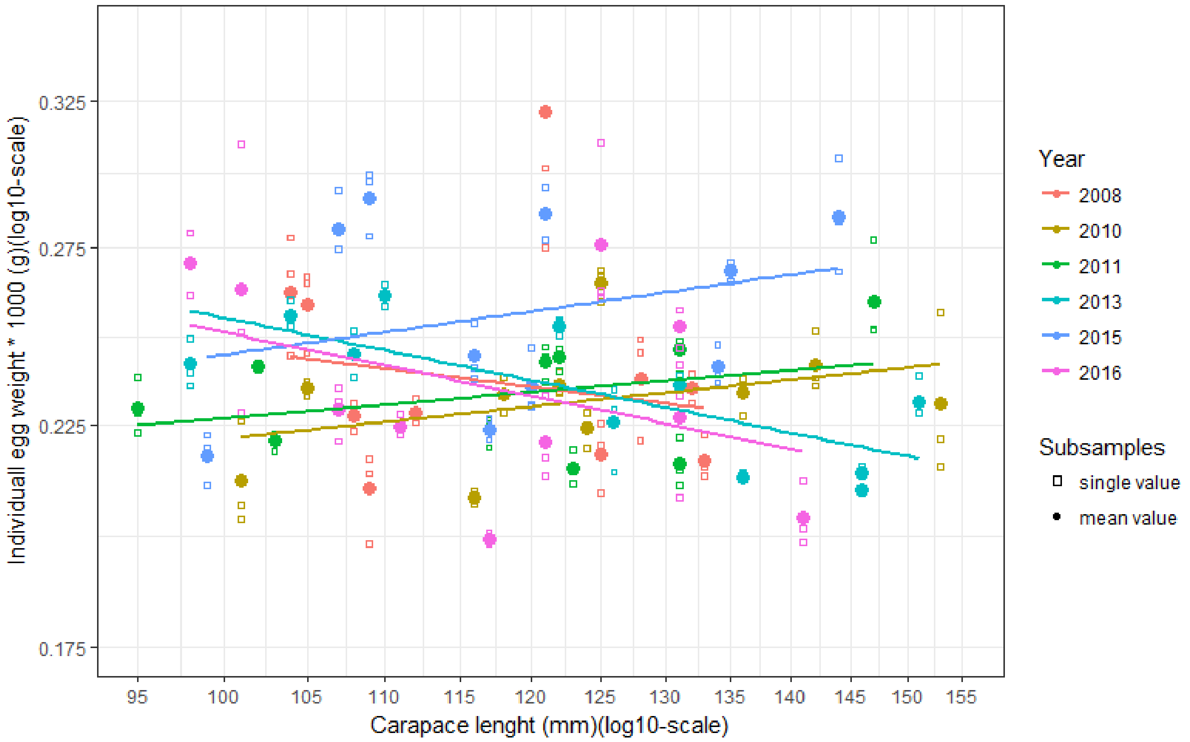
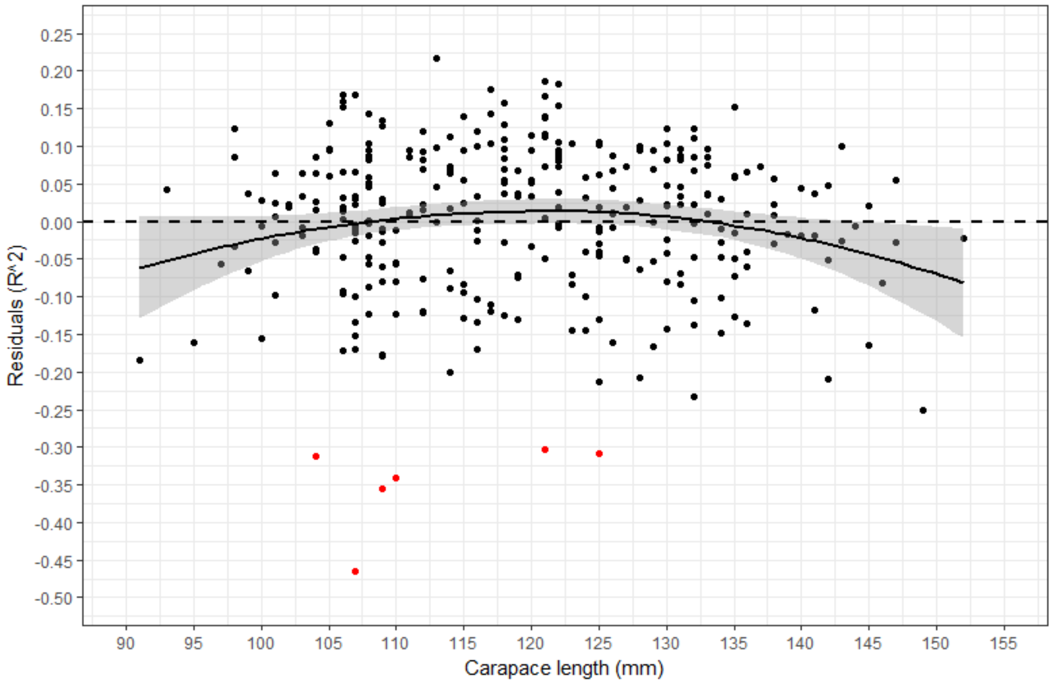
8 Appendix

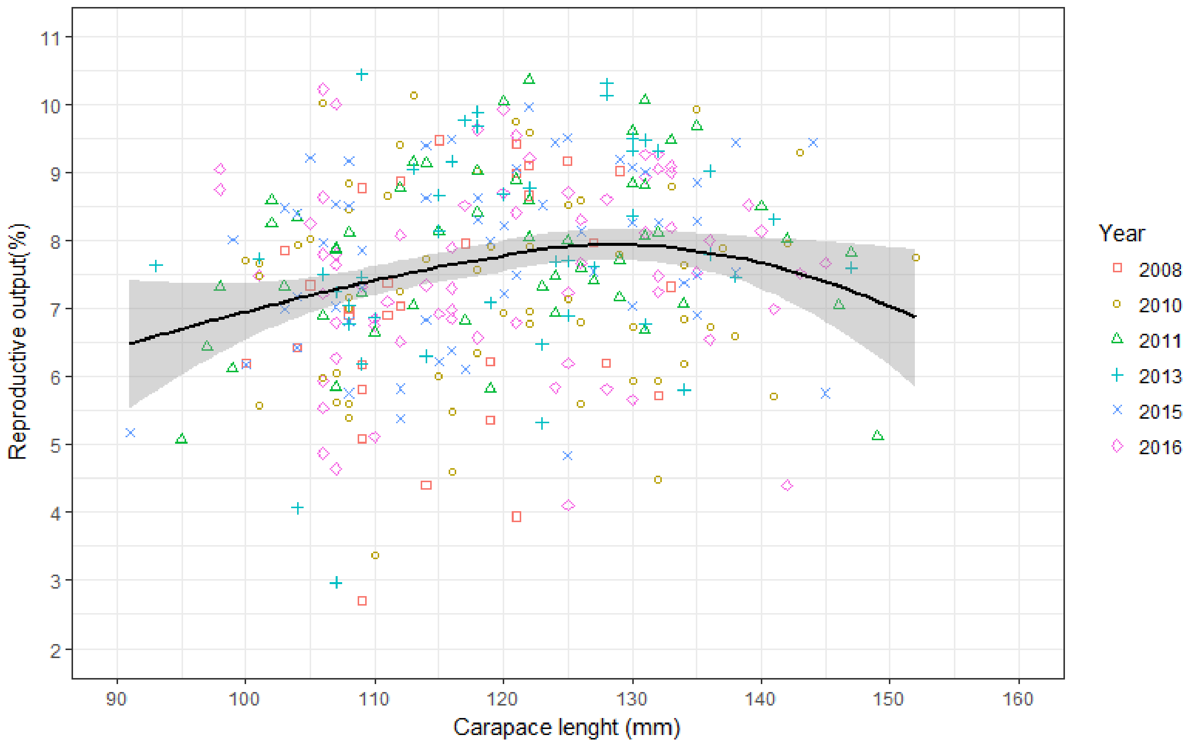
8.1 Appendix figures



Appendix Figure 1: Red king crab (Paralithodes camtschaticus) from Varangerfjorden (2008-2016). Individual egg weight (IEW) and carapace length (CL) of the different years. Square is individual values and circle is the mean value of the subsamples.



Appendix Figure 2: Residuals of the pooled regression (Figure 4, Table 3) on carapace length (mm) of the Red king crab (Paralithodes camtschaticus) from Varangerfjorden 2008-2016. With a Loess-trend curve ±0.95 CI (solid) and 0 residual line (dashed). Visual outlayers (n=7) from Figure 6 is red.



Appendix Figure 3: Red king crab (Paralithodes camtschaticus) reproductive output (total biomass of reproductive products(egg) on female body weight) on carapace length (mm) for the period 2008-2016. Solid black line is a Loess-trend curve ±0.95 CI.

8.2 Appendix tables

Appendix Tabel 1: Red king crab (Paralithodes camtschaticus) from Varangerfjorden (2008-2017) CL (mm) Median, 5th and 95th percentile

Year	median	5th	95th
2008	115	105	131
2009	116	102	134
2010	116	103	133
2011	114	103	131
2012	116	104	131
2013	116	104	131
2014	118	105	137
2015	118	103	135
2016	118	106	134
2017	119	103	134
Mean	*117*	*104*	*133*

Appendix Tabel 2: Red king crab (Paralithodes camtschaticus) from Varangerfjorden (2008-2016) 125 mm standard sized female fecundity

Year	Fecundity	Fecundity (rounded)
2008	131 957	132 000
2010	132 088	132 000
2011	143 658	144 000
2013	143 726	144 000
2015	133 564	134 000
2016	133 213	133 000
Mean	*136 367*	*136 000*