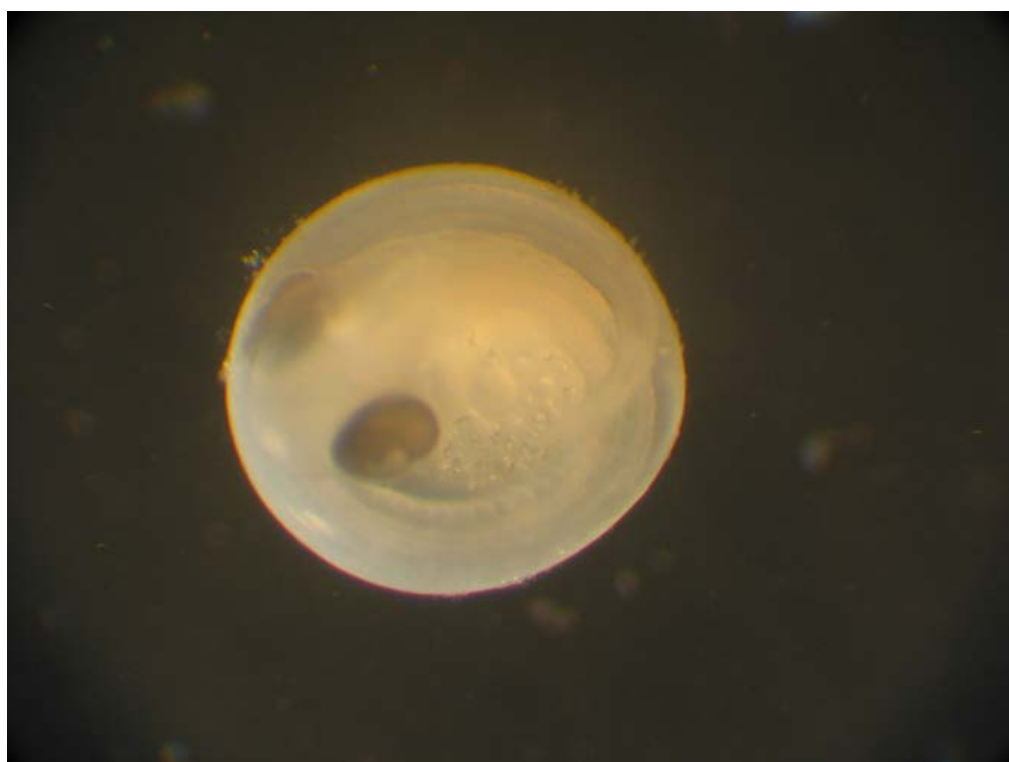


Predation on the demersal fish eggs of capelin *Mallotus villosus* and lumpsucker *Cyclopterus lumpus* in relation to recruitment



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A dissertation for the degree of Philosophiae Doctor
September 2013



Preface

My university studies started out with a randomly selected course in general ecology and I remember that predation - prey interactions instantly caught my attention. Further out in my studies this attention was awaked again in the course of fisheries biology where multispecies modelling was presented with Hamres hypothesis being mentioned as an example. This hypothesis attempts to explain the failure of capelin recruitment by the presence of strong year classes of young herring in the Barents Sea. As a result of this hypothesis, a research program called BASECOEX (Barents Sea Capelin Coexistence of Exclusion) was initiated, with the aim to establish new knowledge regarding the capelin – herring interactions in the Barents Sea.

Fortunately, by the time I was ready to write my master thesis; I was included in the BASECOEX program and did my thesis on the recruitment mechanisms and the recruitment function used in the assessment model for this species. This work was focusing on the life stage from larvae to one year old capelin. Mortality during the egg stage was not within the scope of my thesis although it is obvious that benthic fish eggs with no parental care, as is the case of the Barents Sea capelin, may experience high mortality.

As the research program was running, the introduced red king crab reached a maximum abundance in Varanger Fjord and the questions about the potential ecological impact of this species received attention both in public and in research communities in Norway and Russia. Also at a global scale, the impact of introduced species in general was -and still is a “hot topic”. The research program “Ecological impacts of the introduced red king crab” was initiated by the institute of Marine research and the effects on fish community were implemented in the program.

As the Barents Sea capelin spawns at shallow depth at the coast of northern Norway and Russia in spring the distribution may overlap the distribution of the invasive red king crab, a rising concern was given the potential impact of red king crab on the already highly variable recruitment of the Barents Sea capelin which also had experienced two stock collapses at the time. More knowledge about the potential impact of the introduced red king crab on commercial fish with benthic eggs was strongly recommended both by fisheries and research communities.

Acknowledgements

I wish to express my gratitude to my Supervisor Torstein Pedersen for excellent guiding throughout the work of this thesis. Torstein has provided great support and knowledge throughout all parts of this project and always keeping his door open for me. We have had numerous interesting discussions along the way. I also wish to thank my co supervisors Einar M. Nilssen (UIT) and Harald Gjøsæter (IMR). Einar has contributed to interesting discussions regarding aspects of red king crab research and some statistical challenges with regard to analysing stomach data from red king crab. Harald has contributed to several challenges regarding field work at capelin spawning sites and for inviting me to the ICES Benchmark assessment meeting on short lived species in 2009. Thank you to my co –authors Aril Slotte, Torstein Pedersen and Harald Gjøsæter.

Several colleagues have contributed to this project through field work, experimental work and laboratory analysis. I wish to thank Bjørn Erik Bye, Fredrikke Musæus, Berit Bendiksen, Els Cuveliers, Olav Nordgård, Bjørnar Seim, Helge Meissner, Emma Källgren and at last, but not least Trond Ivarjord for his invaluable effort during a challenging fieldwork collecting experimental animals in stormy weather and who assisted me during parts of the experimental work. I also wish to express my gratitude to Kjersti Fredheim who provided me research facilities at HiT Aquaculture Research Station on short notice when technical problems made experimental work impossible at the University of Tromsø in spring 2011. My deep gratitude to Sverre Hyttan at North Capelin fish plant in Honningsvåg, to ROV pilot and diver Jan E. Jenssen from Subsea Nor and to the crew onboard R/V Johan Ruud and M/S Leif Roald. Thank you to Frøydis Strand and Rudi Cayers for the artistic assistance during several parts of the project.

Thank you to all my colleagues at the Department of Marine and Arctic Marine Biology for good scientific and non -scientific discussions over lunch and coffee breaks. A special thanks to my roommates or neighbouring office mates over the years; Elvar Hallfredsson, Even Jørgensen, Marianne Frantzen, Tanja L. Hanebrekke, Mona Fuhrman, Ellen Kathrine Bludd, Jo J. Aarseth and Silje Ramsvatn for all the good times and discussions along the way.

I also want to express my gratitude to the Institute of Marine research for financial support of fieldwork collecting material for red king crab research. Special thanks to Jan Sundet who

encouraged me to work with ecological effects of red king crab on fish eggs, invited me to workshops on red king crab and provided literature at an early stage of this project. Ivan Ahlquist, thank you for your assistance during fieldwork and Hans Christian Strand for collection of red king crab for experiments.

Finally, thank you to all my friends and family that have been babysitting, picking up kids in kindergarten or at school, taking my place in voluntary work when needed, you all know who you are and you are amazing! A special thanks to my parents and my sister who are always ready to help out in everyday life and when the hard times hit.

The love of my life, my best friend and husband, Kenneth, thank you for everything! My accomplishments would not have been possible without your support. To my children, Ane Sofie, Njål, Pia Mari and Ada Kristin; thank you for adding joy and happiness to my life, making every single day worth living!

Tromsø

September 2013

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Abstract

Recruitment variability in marine fish is usually caused by high mortality in early life stages, and one important regulating mechanism is predation. Mortality of demersal fish eggs caused by predation was investigated in this research project. The selected prey species were the Barents Sea capelin *Mallotus villosus* and lumpsucker *Cyclopterus lumpus* L, while the selected predators were capelin itself by cannibalistic behaviour and the invasive red king crab *Paralithodes camtschaticus*. Both capelin and lumpsucker are commercially important species in the Norwegian fisheries, but capelin is also a very important forage fish for other species.

In this thesis, the main aim was to investigate if the predation mortality in demersal eggs of capelin and lumpsucker caused by the invasive red king crab hampers the recruitment of the species. It was also examined if egg cannibalism in capelin had a major effect on capelin recruitment as well. In addition, four sub-goals were defined to explore details around the egg predation by the red king crab. The first sub-goal was to investigate if the egg guarding lumpsucker was able to protect his eggs from the red king crab. Secondly, the response by red king crab to capelin egg density was explored. Thirdly, stomach evacuation rates for fish eggs in red king crabs stomachs were estimated from experimental work, for use in consumption models. Finally, the occurrence of post-spawn capelin, acting as alternative prey to capelin eggs in crab stomachs, was investigated.

The methods applied in this project were fieldwork (2002, 2003, 2005 and 2006), experimental work (2006, 2011) and modelling. All field work was carried out in the eastern part of Finnmark and predators were sampled for stomach analysis. The experimental work was carried out at the University of Tromsø and at the Aquaculture Research Station, Kårvika. The amount of eggs eaten by the crab was estimated by a consumption model and Monte Carlo (MC) simulations were applied to calculate consumption estimates with 95% confidence intervals.

The percentage of capelin egg cannibals increased during spawning season and cannibalism was most frequent in spent individuals and in males than in females, although the maximum number of capelin eggs in stomachs was higher in females than in males.

The egg guarding lump sucker male was not able to protect his eggs from the egg feeding red king crab, which pushed the guarding fish away with his leg and lump sucker eggs occurred in approximately 8% of the analysed red king crab stomachs in 2003. In 2005 and 2006, capelin eggs occurred in 10% and 23% of the analysed red king crab stomachs and capelin in 82% and 22% respectively. The red king crab showed no clear functional or numerical response to capelin egg density; but a logistic regression model showed that the occurrence of capelin eggs in red king crab stomachs increased with increasing capelin egg density. As post-spawn capelin occurred more frequently in crab stomachs than capelin eggs, they might have served as alternative prey to capelin eggs.

Average stomach evacuation time for lump sucker and capelin eggs were 9.97 and 5.38 h at 6.0°C and 2.9°C, respectively. No eggs could be detected in stomach after 14 hours for capelin and 17 hours for lump sucker eggs. The crab was more efficient feeding on the larger lump sucker eggs that stick more to each other than capelin eggs. The crab spilled a significant amount of prey offered in both experiments, 45% of capelin eggs while the corresponding loss of lump sucker eggs amounted for 8.4%.

The minimum estimated mortality due to egg cannibalism in capelin accounted for 1-2% of the total egg production in the year of study, while consumption estimates of capelin eggs in red king crab accounted for 0.04% and 2.23% in the years of study. Large variability in number of eggs per predator indicates that individual specialization in feeding behaviour occurs in red king crab. Consumption of lump sucker eggs by the red king crab was equivalent to one-third of the commercial catches in the same area in the year of study. The uncertainty in stomach data generated most of the uncertainty in consumption estimates of the red king crab feeding on both capelin and lump sucker eggs.

This study has established new knowledge about the occurrence and magnitude of predation on capelin and lump sucker eggs by the invasive red king crab and in capelin also by egg cannibalism. Mortality in capelin eggs caused by cannibalism and egg consumption and damage of eggs by the red king crab may influence mortality of eggs, but is not considered to hamper capelin recruitment. Recruitment of lump sucker on the other hand, may be hampered by the red king crab chasing away the egg guarding male, damaging and feeding on their eggs.

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1. List of papers

- I. Egg cannibalism in relation to a narrow spawning distribution.
- II. Invasive red king crab affects lumpsucker recruitment by egg consumption
- III. Invasive red king crab feed on capelin and their eggs

Understanding causes of recruitment variability is a desirable goal, “solving the problem” may be an unrealistic goal

E.D. Houde 2008

2. Introduction

2.1 Recruitment variability in marine fish stocks

Marine fish populations experience high variability in recruitment, which is considered to be a major driving force in stock fluctuations (Jakobsen et al. 2009). Fluctuations in year-class strength and the following recruitment in marine fish have long been impetus for fisheries investigations and were given the attention of fishermen, managers and fishery scientist already in the late 19th century (Hjort 1914). Understanding what mechanisms are responsible for recruitment variability of marine fish populations is and has been one of the most important issues in fisheries ecology (Brunel & Boucher 2006). No standard definition of recruitment is accepted by all fish ecologists, but all agree that recruitment is the number of fish at some age or stage, but the choice of age or stage vary (Myers 2004). Recruitment variability has major biological and economic implications for the management of commercial fisheries (Leggett & Deblois 1994). In the Barents Sea capelin *Mallotus villosus*, the age at recruitment is one year (Gjørseter et al. 2002).

The generally high mortality rates in early life stages of teleost fish are believed to determine year-class strength (Bailey & Houde 1989, Houde 2002) and the survival is controlled by both abiotic and biotic factors. In short-lived species, like capelin, recruitment failure of one year-class has significant impact on stock abundance, while long-lived species like cod *Gadus morhua* and Atlantic herring *Clupea harengus*, which spawn many times throughout their life cycle are not as affected when the production of one year class fail. Several hypotheses explaining what mechanisms are responsible for recruitment variability in marine fish have been suggested.

One of the first hypotheses which have been widely investigated is referred to as the “Critical Period hypothesis” (Hjort 1914), where the critical period refers to the first feeding stage of larvae. Another hypothesis, which is an extension of Hjorts hypothesis is commonly called the “Match mismatch” hypothesis (Cushing 1975), and has been supported by evidence in field (Cowan & Shaw 2002). Several other explanations of recruitment variability have been presented, many of them connected to environmental variability (Fogarty et al. 2001, Corten 2013), but other causal factors such as poor nutrition and disease must also be taken into account (Bailey & Houde 1989, Wotton 1998). Some important environmental factors that

may affect survival in marine fish egg are; spawning substrate characteristics (Soulsby et al. 2001), water quality (Houde 2002), temperature (Jobling 1995) and pollution (Short et al. 2003).

Since the late 1970s, predation has been considered as a major source of mortality in the early life stages by many scientists (Hamre 1994, Leggett & Deblois 1994, Houde 2002). Early life mortality caused by predation has been identified as the major cause of recruitment variability in flatfish (Bailey 1994), capelin (Gjørseter et al. 2002), and Baltic cod (Köster & Möllmann 2000 a). The collapses in the Barents Sea capelin stock, which is a major forage fish in the Barents Sea ecosystem, have been linked to recruitment failure (Gjørseter et al. 2002, Gjørseter et al. 2009) and it has been suggested that this recruitment failure was caused by predation by the juvenile herring on capelin larvae also referred to as the “Hamre hypothesis”. Hamre suggested that when strong year classes of Norwegian spring spawning herring were present in the Barents Sea, they preyed on capelin larvae to such an extent that the capelin recruitment was hampered (Hamre 1994).

In light of Hamres hypothesis, Gjørseter and Bogstad (1998) attempted to investigate the possible effects from herring on capelin recruitment in the Barents Sea by analysing the stock – recruitment relationship. They concluded that an inclusion of young herring biomass parameter in the recruitment function improved the fit of the recruitment function, which is a modified Beverton and Holt recruitment function. In a follow up to this work, the inclusion of effects of temperature and 0-group cod was investigated, but these factors were not found significant in explaining the variability in capelin recruitment (Mikkelsen & Pedersen 2004).

2.2 Reproductive strategies in fish

Knowledge about the reproductive strategy, spawning dynamics and causes of early life mortality is essential for a broad understanding of the population dynamics in all fish (Hilborn & Walters 1992). Reproductive strategy in fish affects mortality of their offspring (Dahlberg 1979). Most marine fish species of commercial importance have pelagic eggs and are iteroparous, i.e., spawns more than once during their lifetime, but some commercial important fish species are semelparous as they spawn once and then they die (Murua & Saborido-Rey 2003). The Barents Sea capelin and Pacific salmonids *Oncorhynchus* sp. are

semelparous fish (Crespi & Teo 2002, Christiansen et al. 2008), while Atlantic cod, Atlantic herring and American plaice *Hippoglossoides platessoides* are iteroparous (Jennings & Beverton 1991, Trippel 1998, Rickman et al. 2000). A low ratio of juvenile to adult mortality leads to semelparity, while a high ratio will favour iteroparity (Schaffer 1974, Cole 1954). Semelparity in fish may be enhanced by the high cost of spawning migrations and concomitant low adult survival from one breeding episode to the next (Schaffer & Elson 1975). The Barents Sea capelin undertake an extensive spawning migration during winter and early spring from the central parts of the Barents Sea south of the ice edge to the coast of northern Norway (Troms and Finnmark counties) and Russia (Kola county) (Gjørseter 1998).

The majority of marine fish species have external fertilization (Wotton 1998), and may release their eggs in a single episode (total spawners), or in several batches throughout the spawning season, a strategy applied by most of the commercially important fish in the Atlantic (Murua & Motos 2006). Highly fecund fish may be limited to batch spawning due to the expanding of body cavity caused by increasing volume of eggs during the hydration phase in oocytes (Fordham & Trippel 1999). Batch spawners, like autumn spawned herring, prolong the spawning season and this reproductive strategy may increase survival probability of some offspring by releasing their eggs over a long period of time (Lambert & Ware 1984). Total spawners may increase the survival of offspring by reducing their risk of being eaten by predators, which may be swamped (Ims 1990), even though they can be aggregated at spawning site (Bogetveit et al. 2008). Simultaneous hatch is also an advantage when hatching time matches high peaks of food supply, which increase growth rates in larvae so they may pass through the vulnerable larval stage faster.

Most marine fish species have pelagic eggs (Pavlov et al. 2009), but some species have demersal eggs which adhere to substrate or are buried, exemplified by the commercially important capelin, herring and lumpsucker *Cyclopterus lumpus* L (Lønning et al. 1988, Murua & Saborido-Rey 2003) and the unexploited species of shorthorn sculpin *Myoxocephalus scorpius* (Luksenburg et al. 2004). Demersal spawners usually tend to produce few large eggs (Christiansen et al. 1998), when compared to pelagic spawners who release smaller but many eggs (Duarte & Alcaraz 1989). By maximizing the number of eggs, most pelagic spawners should increase the number of eggs hatching in suitable locations in the patchy pelagic environment and thus increase their reproductive success (op. cit.). Demersal spawners may improve survival of offspring when the fish find suitable spawning sites with stable

environmental conditions. Survival of demersal eggs of marine fish stocks, e.g., the Barents Sea capelin, Atlantic herring and Pacific herring *Clupea pallasii*, is generally considered to be high when predation mortality is omitted (Dragesund & Nakken 1973, Gjørseter et al. 1974, Bunn et al. 2000, Nakashima & Wheeler 2002), whereas survival of pelagic eggs is reported to be low (Dahlberg 1979).

Egg guarding species are more frequently found in freshwater species than in marine (Dahlberg 1979). Some marine species which provide parental care are the lumpsucker (Zhitenev 1970), shorthorn sculpin *Myoxocephalus scorpius* (Luksenburg et al. 2004) and Atlantic wolffish *Anarhichas lupus* (Keats et al. 1985). Guarding of eggs may enhance survival, but may also promote egg cannibalism by the guarding male (FitzGerald & Whoriskey 1992). Egg guarding behaviour of demersal spawners can include protection of eggs from predators, ventilation of eggs to provide oxygenated water while also clearing away any accumulation of silt and the removal of dead eggs (Wotton 1998). The parental care giving lumpsucker has been observed to remove invertebrate predators such as sea urchins *Strongylocentrotus droebachiensis* and periwinkles *Littorina* spp. (Goulet et al. 1986).

Lumpsucker is an iteroparous, demersal batch spawner with high fecundity compared to other demersal spawners. Females spawn several batches with intervals of 8 to 15 days and may mate with several males (Zhitenev 1970, Collins 1976, Goulet et al. 1986) in shallow water and sub-littoral areas on rocky bottom among beds of *Fucus* spp. and *Laminaria* spp. macroalgae (Zhitenev 1970, Mochek 1973). Males may mate with several females that can release their eggs in existing nest already guarded by the male who stay behind to protect the eggs after spawning (Davenport 1985). Egg weight in females can constitute up to one-third of the total fish weight (op. cit.), and each batch may contain from 15 to 100 thousands egg (Mochek 1973). As the fish spawn several batches, the total fecundity may range from 10 000 to 400 000 eggs per female (Andrijašev 1954, Davenport & Lønning 1983). In comparison, the mean number of eggs spawned by another marine demersal spawner; the Barents Sea capelin, amounts to 11 500 eggs per female (Huse & Gjørseter 1997). Capelin also differs from lumpsucker by releasing all their eggs in one episode and is not guarding eggs after spawning. However, during spawning, the male is rapidly digging his abdomen into the gravel to bury the eggs in the substrate (Fridgeirsson 1976), potentially preventing predation by some bottom feeding animals.

2.3 Mortality in the early life stages of marine fish

The natural mortality rates of marine fish are highest in early life stages and gradually declines during larval and juvenile stages (Houde 2002). For many typical marine teleosts, mortality exceeds 99% during egg and larval stages (Trippel et al. 1997). Estimating the abundance of eggs and larvae is difficult due to both patchy distribution and changing environment of most marine species, concurrent the estimation of loss of eggs is also challenging. There are both logistic and technical difficulties involved in systematic studies on survival of demersal eggs (Frank & Leggett 1981).

Mortality can be given in percentage surviving offspring or by instantaneous daily mortality rates (Z). Z is calculated by monitoring the abundance of the surviving individuals of a cohort over time producing a survival curve (Frank & Leggett 1981, Shackell et al. 1994, Wootton 1998). In marine fish eggs, Z is most commonly below 1.0 d^{-1} (Bunn et al. 2000) and pelagic eggs usually have higher mortality rates than demersal eggs (Dahlberg 1979). Mortality rates of pelagic eggs have been estimated for several species; e.g., Atlantic mackerel *Scomber scombrus* in Gulf of St. Lawrence $Z = 0.44 \text{ d}^{-1}$, Northern anchovy *Engraulis mordax* in California $Z = 0.13 \text{ d}^{-1}$ and for Atlantic cod in Lofoten, Norway $Z = 0.10 \text{ d}^{-1}$ (Based on Table 1, Bunn et al. 2000). A much lower Z has been estimated for the demersal eggs of the Atlantic herring $Z = 0.05 \text{ d}^{-1}$ (op. cit.), corresponding to ca. 5% mortality per day.

An indirect method for estimating predation mortality is to calculate it as the difference between total mortality and starvation mortality, assuming that other causes of mortality are insignificant (Bailey & Houde 1989). Egg predation mortality can be estimated indirectly from egg production estimates and modelled survival rates of eggs from predation (Richardson et al. 2011). Predation mortality rates can be directly estimated from consumption models based on stomach content analysis and digestion rates of predators (Bajkov 1935, Olson & Boggs 1986, Hallfredsson & Pedersen 2009). Another direct method to study and estimate predation mortality is by mesocosm experiments (Cowan et al. 1992, Houde et al. 1994).

2.4 Intraspecific predation; the case of egg cannibalism

Intraspecific predation is the process of killing and eating an individual of the same species, typically referred to as cannibalism (Polis 1981). Mortality due to cannibalistic behaviour is common in nature among fishes (Dominey & Blumer 1984) and is particularly well represented in piscivorous and parental care-giving species (Smith & Reay 1991). The extreme high fecundity, external fertilization and production of small offspring amongst many fish species promote cannibalism (Dominey & Blumer 1984). Several species with pelagic eggs have been identified as egg cannibals; Anchovy *Engraulis capensis* (Valdes et al. 1987), Anchovy *Engraulis mordax* (Hunter & Kimbrell 1980) and Baltic sprat *Sprattus sprattus* (Köster & Mollmann 2000 a). Demersal spawners with no parental care have also been observed to display cannibalistic behaviour by feeding on their eggs. The Atlantic herring (Skaret et al. 2002) and the osmeriformes Ayu *Plecoglossus altivelis* (Iguchi & Tsukamoto 2001) and capelin (Templeman 1948, Sætre & Gjørseter 1975, Huse et al. 1996) are demersal spawners that have been observed to feed on their own eggs.

The majority of identified cases of egg cannibalism by fishes are non-kin intercohort cannibalism (Dominey & Blumer 1984, Smith & Reay 1991). However, filial egg cannibalism, where parents are eating their own offspring, also occurs frequently in fish that provide paternal care during egg stage (Manica 2002, Karino & Arai 2006). Benefits and cost of cannibalistic behaviour have been described by several authors (Hrdy 1979, Smith & Reay 1991). Most obviously, benefits should exceed the costs of such behaviour by reduction in number of offspring in order to be an evolutionary stable strategy. Cannibalism may lead to nutritional benefits to normal diet (FitzGerald & Whoriskey 1992). Iteroparous fish would profit from this high energy food, as exemplified by Atlantic herring feeding on their eggs resulting in a higher condition factor for cannibals than for non-cannibals (Skaret et al. 2002).

High density of either prey or predator promotes cannibalism through increased predator-prey encounter and has been identified as one important factor controlling the intensity of cannibalism in a number of studies (Smith & Reay 1991). Cannibalism has also been observed to occur more frequently with increasing population density (Valdes et al. 1987, Elgar & Crepsi 1992). Therefore, cannibalism can be important for its potential regulatory effects on population abundance and for its overall contribution to natural mortality (Smith & Reay 1991). Effects of cannibalism as density dependent regulation of recruitment can be

studied by spawning stock recruitment functions. The stock recruitment model of Ricker (1954) takes into account density dependent mortality when it calculates the potential number of recruits by a certain spawning stock biomass and the density dependent mechanism is arising largely through cannibalism (Ricker 1954).

Cannibalism by fish in field can be studied by both field and experimental work. In field, information about the occurrence and the extent of such behaviour can be obtained by stomach analysis from field samples (Acha et al. 2002, Skurdal et al. 1985, Skaret et al. 2002). Through experimental work, the declining abundance of eggs due to predation can be monitored and mortality calculated (Lindstrom & Sargent 1997, Sandkam & Fuller 2011). As cannibalistic behaviour has been recorded in capelin both in the Barents Sea (Sætre & Gjøsæter 1975, Huse & Toresen 1996) and in Newfoundland (Templeman 1948), the importance for its overall contribution to natural mortality and regulatory effects on population abundance cannibalism should be investigated.

2.5 Predation and predator feeding dynamics

Predators may detect their prey by mechanoreceptors, vision, chemoreceptors or a combination of these (Wotton 1998) and depending on type of prey in addition to predator morphology, fish use different feeding strategies. Many fish rely on vision for detection of its prey and are constrained by light regime (Eggers 1977, Aksnes & Giske 1993), while crustaceans are often directed to potential food resources by chemotaxis, i.e., by tracking chemical cues (Zhou & Shirley 1997, Stiansen et. al 2010). The red king crab is attracted to prey by odour plume (Zhou & Shirley 1997), while the capelin may visually detect larger prey in addition to filter feeding of smaller prey.

Many pelagic fishes are switching between filter-feeding and raptorial feeding strategies (Bailey & Houde 1989). Capelin display both filter-feeding strategy (Templeman 1948) and feeding by picking single particles of prey, also from substrate (Huse & Toresen 1996, Godiksen et al. 2006, Hallfredsson & Pedersen 2009). Their major prey types are copepods, krill and amphipods (Gjøsæter 1998). However, findings of small stones and capelin eggs in immature capelin have verified that bottom feeding on the demersal eggs occurs, where capelin must be picking up prey from substrate. Most carnivore fish swallow their prey whole, while most crustaceans crush and tear apart their prey before they ingest it. The red king crab

are grasping and tearing apart larger prey or they are scooping sediment by lesser chela and sieving it through the third maxillipeds, making identification of prey by stomach analysis difficult (McLaughlin & Hebard 1961, Jørgensen 2005).

Predators can be classified according to how many prey types they are feeding on. A generalist feeding predator feed on several types of prey, while a specialist consumes a single or few types of prey (Begon et al. 1996). Specialist feeding behaviour has been identified in coral feeding fish *Cheatoodon trifascialis* (Graham 2007), however, most predators have a relatively broad diet. The red king crab is commonly known to display a generalist feeding behaviour (Britayev et al. 2010), often feeding on the most abundant prey available (Jewett & Feder 1982, Cunningham 1969) and on sessile or slow moving benthos (Falk Petersen 2011 and references therein). The generalist feeding behaviour of the red king crab is supported by the different feeding strategies it displays.

Some predators have significant shifts in diet when prey like fish eggs are available in high densities for a short period of time. The species of Atlantic cod, haddock *Melanogrammus aeglefinus*, Pollack *Pollachius pollachius* and saithe *Pollachius virens* all had a significant shift in diet during Atlantic herring spawning season on the coast of Western Norway where they all fed on herring eggs (Høines & Bergstad 1999). Haddock is a demersal fish which have been found to feed extensively on the demersal fish eggs of both Atlantic herring and capelin (Toresen 1991, Sætre & Gjøsæter 1975). Some other identified predators of capelin eggs in the Barents Sea are the seabirds *Somateria mollissima*, *Somateria spectabilis* and *Clangula hyenalis* (Sætre & Gjøsæter 1975) and the invasive red king crab (Anisimova et al. 2005).

The number of prey consumed by predators over a defined period of time can be determined by the functional or numerical response by the predator (Wotton 1998). Numerical response is the change in predator abundance as a result of increased prey density (Holling 1959). Eggs of demersal spawners that exhibit no parental care, such as the Barents Sea capelin, often occur in dense aggregations and are known to attract high densities of fishes (e.g., haddock) and other predatory animals such as seabirds (Dragesund & Nakken 1973, Sætre & Gjøsæter 1975, Bunn et al. 2000). Such a response was also observed in the winter flounder *Pseudopleuronectes americanus* feeding on capelin eggs at Newfoundland (Frank & Leggett 1984). Another response by the predator to prey density is the increase in number of prey

consumed per predator, as prey density rise, termed functional response (Holling 1959). A functional response was identified at Newfoundland when the amphipod *Calliopius laeviusculus* fed on eggs from the beach spawning capelin (DeBlois & Leggett 1993). The availability of alternative prey may influence both the functional (Chesson 1989, Tschanz et al. 2007) and numerical response by the predator (Holling 1973).

2.6 Red king crab: The new benthic top predator in the Barents Sea

The red king crab was introduced to the Barents Sea (Murmansk Fjord, Russia) by Russian scientists through several releases during the 1960s with the intention of establishing a new fishery (Orlov & Karpevich 1965, Orlov & Ivanov 1978). The crab stock acclimated fast and established in Murmansk area in the late 1970s and since then, it has become invasive and spread widely (Britayev et al. 2010). The crab is now abundant throughout the southern Barents Sea, from coastal waters near Kolguyev Island (69°01'N, 49°22'E) in the east and along the coast of northern Norway to Sørøya (70°35'N, 22°44'E) in the west, also invading fjords at the coastline. In spring, the adult crab in Norwegian waters migrates to shallow water to moult and spawn at the coast of Finnmark, northern Norway (Sundet & Hjelseth 2010) and thereby enters important spawning areas for the Barents Sea capelin and lumpsucker (Fig. 1). At present, the crab distribution area does not overlap the spawning areas of the Norwegian spring spawning herring. The red king crab has been observed to feed on eggs from both capelin and lumpsucker (Sokolov & Milyutin 2006) and it has also been suggested that the invasive red king crab may displace the lumpsucker from its spawning sites when the adult crab enters shallow water to moult and spawn in spring (Kudryavtseva & Karamushko 2002).

In feeding studies of red king crab in Varangerfjord, the first invaded fjord in Norway, the most frequent prey found in crab stomachs was polychaetes, in addition to algae, gastropods, several classes of echinoderms and some fish were also frequently observed (Sundet et al. 2000, Haugan 2004). In a study of impacts of the red king crab in Varanger Fjord, there has been found clear indications that soft-bottom epifauna and infauna has become markedly reduced (Oug et al. 2010).

Despite of the increased focus on invasive species in common, very few attempts have been made to assess the impact of the invasive red king crab on native fish populations in

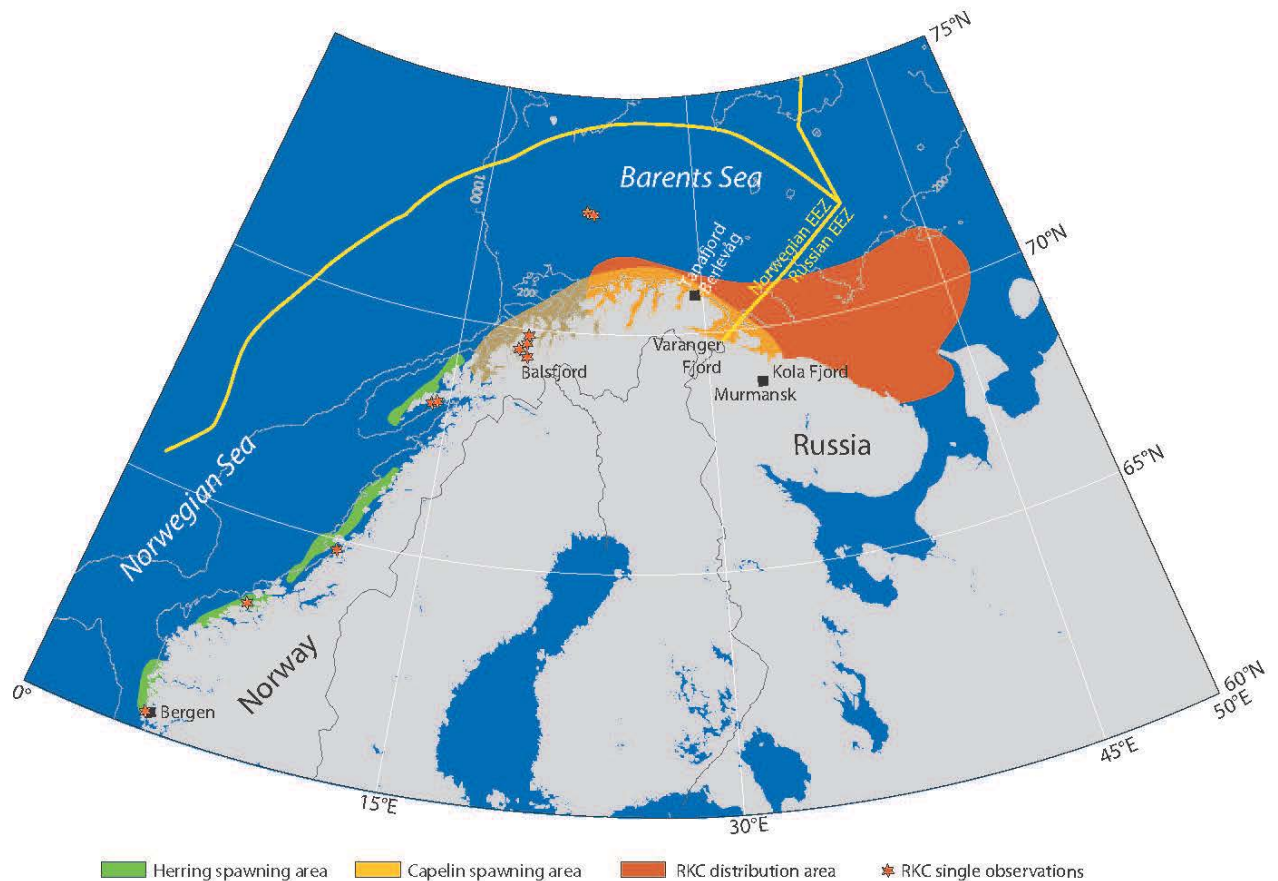


Fig. 1. Spawning areas of capelin and herring, distribution area of red king crab (RKC) in 2012 RKC (based on Bakkteteig et al. (2013)) and single observations of RKC.

Norwegian waters. Knowledge about impact by the crab on fish species that dispose their eggs at the bottom is sparse. Future management of both crab and commercial fish species should take into account consumption by red king crab on fish eggs and if this consumption contributes significantly to mortality in early life stages.

Predator behaviour can be studied in field by remotely operated vehicle (ROV) (Penton et al. 2012), drop camera and video recordings by divers (Bennett & Bellwood 2011). The occurrence of prey and extent of predation in field is commonly studied by stomach analysis of predators. Diet preferences may be investigated by experiments, where predators feed on a single prey or a group of prey to detect preference in diet. Since the diet composition often change with the seasons, it may be necessary to sample stomachs in field throughout the year.

2.7 Stomach evacuation rates and consumption estimates in decapods

Quantitative studies on food consumption by marine organisms are important to understand the ecological role of species in marine communities (Maynou & Cartes 1998) and several approaches have been applied to study consumption (Heroux & Magnan 1998). Some studies have focused on energy requirement for the predator for maintenance, growth and reproduction (Wotton 1998), while others have estimated prey consumption by combining data from stomach analysis from field samples and gastric evacuation rates from experiments (Bunn et al. 2000). Enclosures have also been applied to estimate consumption by in situ experiments abundance of predator and prey close to natural abundance levels (op. cit.).

To estimate consumption over a period of time (month, season or annual), daily ration models which require gastric evacuation rates are often used. Many feeding models assume that the gastric evacuation follows an exponential decay function, while Olson & Boggs (1986) used an alternative approach, as their evacuation data on yellowfin tuna *Thunnus albacares* fitted the exponential function poorly. They applied a method that is appropriate for a wide range of evacuation functions (Olson & Mullen 1986), using data on average stomach content and the integral of the gastric evacuation function.

Time needed to evacuate stomach content is species-specific and vary with size of predator (Jobling 1981, Britayev et al. 2010), prey type (Sarda & Valladares 1990, Waddington 2008) prey size (Bromley 1994), temperature (dos Santos & Jobling 1991, Włodarczyk et al. 1992), and meal size (Bromley 1994). The gastric evacuation rates can be obtained by studies in field if the species under study has a distinct diurnal cycle of food intake (Jones 1978, Heroux & Magnan 1996, Cristo 2001). When the food intake of predators does not have a pronounced diurnal cycle, gastric evacuation rates can be obtained by experimental work (Jones 1978, Cristo 2001, Sarda & Valladres 1990).

In gastric experiments, markers in food and X-Ray (Palsson et al. 1992, McGaw & Reiber 2000) and radioactive isotopes (Storebakken et al. 1981) have been used. However, the experiments are usually performed by feeding predators with prey weights which are proportional to predator weight or size (Toresen 1991), thereafter stomach content is sampled at specific time intervals and the proportion of prey left in the stomach at a given time can be calculated (Hill 1976, Waddington 2008). Stomach content is usually sampled by killing the

predators and dissecting stomachs, but stomach content may also be retrieved by gastric lavage (Bromely 1994).

Several mathematical models have been used to describe gastric evacuation of prey in fish (most frequently; linear, exponential, square root) and an exponential decay model was also applied to haddock feeding on herring eggs (Toresen 1991). The exponential decay models are most frequently applied to crustaceans (Hill 1976, Sarda & Valladares 1990, Cristo 2001). However, when estimating the consumption of prey in red king crab, Pavlova (2009) used Bajkov's feeding model (Bajkov 1935), assuming a linear gastric evacuation function. So far, gastric evacuation rates of fish eggs in decapod crustaceans have not been available, and studies of consumption in field by decapod crustaceans are scarce, compared to studies on marine fish. An exception is the study of daily rations in deep-water decapod crustaceans of the North Western Mediterranean (Maynou & Cartes 1998). Consumption of fish egg by the red king crab has been observed in several studies (Sundet et al. 2000, Anisimova et al. 2005, Sokolov & Milyutin 2006), but there has been little effort to quantify the consumption. However, Anisimova et al. (2005) provided a rough estimate on crab consumption on Barents Sea capelin eggs in Russian part of the eastern Barents Sea in 2001 to account for 0.03% of egg mass available.

Prey consumption estimates are influenced by the uncertainty in input data (e.g., predator abundance, stomach content, digestion rates, and availability of prey). The occurrence of different prey in the diets of generalist feeding predators may be highly variable adding uncertainty to estimates of mean number of specific prey in stomach content. The uncertainty in digestion rates obtained in experimental studies might be affected by individual levels of stress in experimental animals and meal size of prey (% of predator weight) actually eaten in experiments. When estimating consumption of eggs, the incubation time of eggs may vary within and between years adding uncertainty to the number of days eggs are available for consumption.

It is important to determine which input data and variables that contribute most to the uncertainty in consumption estimates. When estimating the consumption of fish by harp seals *Phoca groenlandica*, the uncertainty in input data was quantified by Monte Carlo simulations to guide in future research (Shelton et al. 1997). Monte Carlo simulations can be used to provide confidence limits on consumption estimates and to examine the uncertainty in such

estimates by randomly selecting values for input data from distributions considered to describe the uncertainty in the inputs (Shelton et al. 1997, Overholtz & Link 2007).

3. Objectives

The overall objective of this study was to investigate predation mortality impact by the red king crab on lumpfish and capelin eggs, and egg cannibalism in capelin. Both prey species have demersal fish eggs, but differ with regard to reproductive strategies. Capelin are small pelagic fish who are total spawners, display semelparity and each female spawn in average 11 000 eggs per year. Lumpfish are iteroparous batch spawners with high annual fecundity from 10 to 400 thousand eggs and the male guard their eggs by removing predators and aerating their eggs.

The specific objectives were to;

- i. Investigate egg cannibalism of the Barents Sea capelin (Paper I)
- ii. Investigate if the egg guarding lumpfish is able to protect his eggs against the red king crab (Paper II)
- iii. Investigate the occurrence of predation on demersal eggs and capelin as alternative prey by the red king crab (Paper II and Paper III)
- iv. Examine if the red king crab show functional or numerical response to capelin egg density (Paper III)
- v. Estimate stomach evacuation rates of fish eggs in red king crab by experimental work (Paper II and Paper III)
- vi. Estimate consumption estimates with uncertainty of demersal fish eggs by the red king crab (Paper II and III)

4. Approach

In this study, the occurrence and magnitude of capelin egg cannibalism was quantified from stomach analysis of capelin caught at capelin spawning sites throughout the spawning season. The occurrence of lumpsucker and capelin eggs in crab stomachs from field was analysed and quantified, while the occurrence of adult capelin as alternative prey was explored by occurrence in crab stomachs. The ability of the lumpsucker male to guard his eggs against predation from the red king crab was investigated by video recordings from a remotely operated vehicle and by divers.

Study areas at capelin spawning sites were stratified and egg density was estimated from random grab sampling in strata, while crab abundance was estimated from swept trawl area. These data were used to investigate if the red king crabs display a functional and/ or numerical response to capelin egg density.

Stomach evacuation rates of capelin and lumpsucker eggs in red king crab were investigated by experimental work, where the proportions of eggs left in stomach at a given time were fitted to mathematical models for stomach evacuation. The estimated average times for the lumpsucker and capelin eggs to evacuate from crab stomachs were used in egg consumption models.

Monte Carlo simulations were used to estimate consumption of fish eggs with 95% confidence intervals by the percentile method. To investigate the effects of uncertainty in input data on capelin egg consumption estimates, values for input data to egg consumption models were randomly selected from distributions considered to adequately describe the uncertainty in the data.

5. Results

5.1 Mortality caused by egg cannibalism in capelin (Paper I)

Both the occurrence of egg cannibalism and the degree of cannibalism increased with stage of maturity, being highest in spent fish, and higher in males than in females. However, at similar stomach fullness, females had consumed more eggs than males. Males had a higher content of sand in the stomachs than females. In the full stomachs, the mean consumption in females and males was 623 and 334 eggs respectively. When only whole eggs were counted, the minimum estimates (mean \pm 95% confidence intervals) of egg consumption in spent females and males were 75.4 ± 6.9 and 58.4 ± 12.0 eggs respectively.

Using minimum estimates on consumption calculated by sex and stomach fullness, the estimated mortality caused by cannibalism constituted of 1-2% of the total egg production the year of study, given a mean fecundity of 11 500 eggs per female.

5.2 Red king crab predation on lumpsucker eggs (Paper II)

Field studies showed that the red king crab was able to chase away the egg guarding male lumpsucker and feed on his eggs by pushing him aside with his leg (http://www.int-res.com/articles/suppl/m469p087_supp/). Five crabs were observed feeding on clumps of lumpsucker eggs that had been removed from the original egg clutch. These observed egg feeding crabs were spilling a substantial proportion of eggs while feeding.

Lumpsucker eggs occurred in 7.9% of all crab stomachs analysed and the occurrence was not affected by crab sex or sampling areas in Varanger Fjord, northern Norway. Nevertheless, the average number of eggs found in crab stomachs was highly variable, reaching from one to 1640 eggs per stomach with a mean number of eggs per crab stomach estimated to 20 (95% CI: 1, 52)

The stomach evacuation rate of lumpsucker eggs at 6⁰C was estimated to approximately 9.97 hours in an experiment where crabs consumed in average 0.26% of their body weight within 20 minutes and spilled in average 8.4% of the amount of eggs fed. The estimated initial loss of

eggs during feeding was 17.3% of the eggs eaten. The ogive stomach evacuation model fitted the data well and the adjusted r^2 was 0.84, while the residuals were not significantly correlated (Pearson coefficient of correlation) to crab weight ($r = 0.45$, $p = 0.07$), digestion time ($r = -0.08$, $p = 0.76$) or meal size ($r = 0.36$, $p = 0.15$).

The total annual consumption of lump sucker eggs by the red king crab in Varanger Fjord 2003 was estimated to 30.7 tons (95% CI: 0.74, 89.3) and was equivalent to approximately one-third of the commercial catch of roe the same year. Monte Carlo model input for average number of eggs in stomach was highly correlated to consumption estimates ($r_s = 0.93$), showing that stomach input data were the main source of uncertainty in consumption estimates.

5.3 Red king crab feeding on capelin eggs and capelin (Paper III)

Red king crab was feeding on both capelin eggs and capelin in field. Capelin was found more frequently in crab stomachs than capelin eggs both years, with the highest occurrence by year in 2005 at 82%, while in 2006 capelin occurred in 22% of all analysed crab stomachs. Capelin eggs occurred in 23% of all analysed crabs in 2005 and 10% in 2006. The average number of capelin eggs found in crab stomachs per station was highly variable ranging from 0 to 2283 eggs. When stomach data for all stations were pooled by year, the average number of eggs in crab stomachs was higher in 2006 (Mean \pm SD: 171.7 ± 217.1) than in 2005 (Mean \pm SD; 9.0 ± 8.6), while the estimated abundance of crab (ind. km²) in the study area in 2005 was 2.6 times higher than the study area selected in 2006.

Occurrence of capelin eggs in red king crab stomachs increased with increasing egg density in the logistic regression analysis, while the effects of distance from centre of spawning area and crab size were not significant. The likelihood ratio test indicated that the model was highly significant (chi-squared test, $\chi^2 = 26.21$, $df = 1$, $p < 0.01$).

Red king crab did not display functional response, as the correlations between number of eggs in crab stomach with egg and egg density were not significant (2005: $r_s = -0.04$, $p > 0.05$, $n = 29$, 2006: $r_s = 0.49$, $p > 0.05$, $n = 6$). Nor was the correlation between red king crab abundance and egg density significant in any of the two investigated years (r_s 2005 = -0.26 , $p > 0.05$, $n =$

14, $r_{s2006} = -0.16$, $p > 0.05$, $n = 25$). This lack of correlation suggests that the red king crab show no numerical response to capelin egg density. The abundance of crabs was not significantly correlated to distance from centre of spawning area either (Kruskal – Wallis tests: 2005; $\chi^2 = 7.25$, $df = 3$, $p = 0.06$, 2006: $\chi^2 = 3.63$, $df = 3$, $p = 0.31$).

Red king crabs showed individual feeding behaviour when feeding on capelin eggs in a stomach evacuation experiment. The capelin eggs were evacuated from red king crab stomachs after 5.38 hours at a temperature of 2.9°C and the exponential decay model fitted the data well with an adjusted r^2 at 0.78. Eighteen crabs successfully completed experiment and consumed in average 0.53% of their body weight, spilling 45% of the capelin eggs offered by weight. After 14 h no capelin eggs could be detected in crab stomachs.

Consumption of capelin eggs by year was estimated using Monte Carlo (MC) methods and the mean consumption was estimated to 3.06×10^8 in 2005 and 4.14×10^8 in 2006. The estimated consumption in 2006 (Mean: 171.7, 95% CI: 0, 744.9) was higher than in 2005 (Mean: 9.0, 95% CI: 0.3, 24.6) due to a much higher estimate for average number of eggs per crab stomach.

Consumption estimates from MC were highly correlated to the input values for number of eggs per stomach which contributed to most of the uncertainty in the consumption estimates ($r_{s2005} = 0.99$, $r_{s2006} = 0.80$). The uncertainty in number of red king crab in the study areas also added uncertainty to consumption estimates ($r_{s2005} = 0.22$, $r_{s2006} = 0.20$), while digestion time ($r_{s2005} = -0.15$, $r_{s2006} = -0.11$) and time eggs are available had less influence ($r_{s2005} = 0.07$, $r_{s2006} = -0.01$).

The highest proportion of total number of capelin eggs present in spawning area, were found in 2006 at the stratum where the centre of spawning area was located. When compared by year 2.23% of the total egg number in the stratified area was consumed by crab in 2006 while in 2005 the red king crabs consumed 0.03% of all eggs available.

6. Discussion

6.1 Egg cannibalism in the Barents Sea capelin

Males were more frequently found to exercise cannibalistic behaviour than females in the Barents Sea capelin (Paper I), which can be explained by spawning activity where they are more in contact with bottom substrate than females and they normally remain at the spawning sites for a longer period of time than females (Gjørseter et al. 1974). This might also explain why both the occurrence and the magnitude of egg cannibalism were highest in spent fish. Egg cannibalism in species with no parental care have been reported to be biased towards males in spawning capelin at Newfoundland (Templeman 1948), in another osmeroid; the Ayu *Plecoglossus altivelis* (Iguchi & Tsukamoto 2001) and in Atlantic herring *Clupea harengus* in southern Norway (Skaret et al. 2002).

The magnitude of egg cannibalism in capelin was higher in females than in males and this discrepancy between occurrence and degree (number of eggs in stomach) of cannibalism between males and females could be influenced by digestion (Paper I), as the male stomachs contained more slime possibly from digested eggs, than females. Improved physical condition could be a benefit of cannibalism by post spawn capelin if they eat sufficient amounts of eggs. However, the Barents Sea capelin is commonly considered to exhibit absolute semelparity (Christiansen et al. 2008), although it has been suggested that females may follow an iteroparous reproductive strategy (Huse 1998). If females are more likely to survive, they may gain more by consuming eggs than males (Paper I). Iteroparity in capelin has been identified in demersal spawning capelin off Iceland (Vilhjalmsson 2002) and at demersal spawning sites off Newfoundland (Shackell et al. 1994), but it has never been demonstrated in the Barents Sea capelin. In an experimental study of post-spawn survival of Barents Sea capelin, all individuals died within two months (Christiansen et al. 2008). Cannibalistic behaviour in the Barents Sea capelin is therefore not likely to be a behaviour exerted for enhanced condition by postspawners.

The cannibalistic behaviour of spawning capelin can be either active or passive, happening by chance while ventilating during spawning activity (Templeman 1948). However, the relative large amount of eggs found in some cannibals our study (Paper I), makes the explanation of passive feeding questionable. Active egg cannibalism was also suggested for some individuals

in another demersal spawner, the Atlantic herring, where mass feeding of eggs occurred (Skaret et al. 2002). Active cannibalism in Barents Sea capelin is supported by an experimental study, where males were observed swimming behind the actively spawning individuals and fed upon their eggs before they adhered to substrate (J. S. Christiansen, University of Tromsø, Pers. Comm.).

A potential benefit of non – kin cannibalism is an increased contribution of genes by the egg cannibals in the next generation by decreasing the survival and reproductive success other individuals (Wotton 1998). Nevertheless, egg cannibalism by males does also occur on eggs which are adhered to sand grains and therefore not newly spawned. This feature was observed in some capelin egg predators where some capelin eggs found in stomachs were adhered to sand grains and were identified to be in a stage close to hatching (N. Mikkelsen, unpublished data). These findings are supported by the higher proportion of sand grains in male stomachs, which can be explained by males feeding actively on eggs which are attached to substrate, or by swallowing sand grains incidentally during spawning activity. Unless the predator is able to recognize and avoid eating their own offspring when feeding on eggs, the chance of filial cannibalism increase when capelin feed on eggs from substrate, and the cost of cannibalism can be decreased contribution of own genes in the next generation.

High density of either cannibal or prey promotes cannibalism through increased encounter rate between the two (Smith & Reay 1991) and as the spawning distribution of capelin was narrow in 2002 this could have enhanced cannibalistic behaviour (Paper I). However, the total stock of the capelin was at a fairly low level at the time, and it is doubtful that cannibalism acted as a strong density dependent factor this year. These findings are supported by a previous study where time series of spawning stock and recruitment of the Barents Sea capelin were fitted to two spawning stock – recruitment models; the Beverton & Holt and the Ricker models (Mikkelsen & Pedersen 2004). The fit of the Beverton & Holt model was superior the fit of the Ricker model which takes into account density dependent mortality due to cannibalism. This implies that egg cannibalism, which in 2002 accounted for 1 – 2% of the total eggs production, does not act as an important density dependent regulatory mechanism in the Barents Sea capelin.

6.2 Paternal care in lumpsucker fail in protecting eggs against the red king crab

That the egg guarding lumpsucker was not able to protect his eggs from the red king crab was documented by video recordings from both divers and ROV (Paper II). This could lead to total loss of egg mass due to predation by the crab and other egg feeding predators, once the guarding male is chased away by the crab. Guarding lumpsucker males in Newfoundland were observed to leave their eggs to be eaten when groups of cunners *Tautoglabrus adspersus* attacked their nests and they were ineffective in preventing destruction of their eggs (Goulet 1986). Although such attacks resulting in total loss of eggs in some nests were reported in Newfoundland in the 1980s, the decline in lumpfish stocks at Newfoundland has been explained by overexploitation over a period of time (Hoenig & Hewitt 2005), and the lumpsucker and cunners are coexisting in this environment although the egg predation may have an impact on recruitment.

A few red king crabs were observed to feed on egg clumps that had been removed from the original egg clutch (Paper II), suggesting partial loss of eggs from the egg clump to predation. Such partial removal of eggs from the egg clutch might also lead to damage of the eggs remaining in the original egg clutch, enhancing egg mortality as the guarding male may have left their nest and is not providing parental care by removing dead and sick eggs. Damage and spillage of prey not eaten has also been observed in experimental studies of red king crab (Jørgensen 2005, Pavlova 2009, Michelsen 2011, Paper I, Paper II) and in Chinese mitten crabs *Eriocheir sinensis* (Culver 2005).

Two other egg guarding species which may experience confrontations with the egg feeding red king crab in Norwegian waters are the Atlantic wolffish *Anarhichas lupus* and the shorthorn sculpin *Myoxocephalus scorpius*. The guarding wolffish is larger than lumpsucker male, and is known to show aggressive behaviour against competitors during feeding (Godø et al. 1997). These features may improve the success of egg guarding by wolffish against the red king crab. In contrast, the egg guarding males of shorthorn sculpin in Norwegian waters is much smaller than lumpsucker males (Luksenburg & Pedersen 2002) and may be even more inefficient egg guards than lumpsuckers, thus experiencing an even higher loss of eggs due to predation by the red king crab than lumpsucker.

The non-guarded, non-buried demersal eggs of the Norwegian spring spawning herring contribute significantly to annual prey consumption by several coastal species of fish at the coast of Norway (Høines et al. 1995). This Atlantic herring stock spawns in areas south of 69°N (sjekk, Fig. Kart) not yet invaded by the red king crab, but if the crab continues to expand its distribution in at south and westwards direction, it will eventually reaches these spawning grounds. However, a local population of herring established in Balsfjord approx. 69°18'N 19°22'E (Fig.1, Jørstad et al. 1994) may be exposed to egg predation by the crab in near future. This shallow water spawning herring stock has been termed an outpost of the outpost of the Pacific herring *Clupea pallasii* (Laakkonen et al. 2013). Red king crab have been caught at the entrance and inside Balsfjord on several occasions since 2007 with the last identified individual being a large mature male (~3.5 kg) caught at the entrance of Balsfjord (69°31'02" N 18°59'05"E) in May 2013 (N. Mikkelsen, unpublished data).

6.3 Occurrence of predation on demersal eggs by the red king crab

At the coast of Finnmark, northern Norway, the invasive red king crab was feeding on fish eggs of both capelin (Paper III) and lumpsucker (Paper II). The frequency of occurrence of capelin eggs in crab stomachs (FO₂₀₀₅: 23%, FO₂₀₀₆: 10%) was similar to the occurrence of capelin eggs in another study in the Russian part of the Barents Sea in 2001, where 19% of the analysed crabs had been feeding on capelin eggs (Anisimova et al. 2005). Other capelin egg predators which have been found to feed much more frequently on capelin eggs are; haddock (FO: 70%) (Sætre & Gjørseter 1975), diving ducks *Somateria spectabilis*, *S. mollissima*, *Clangula hyemalis* (FO: 95%) (Gjørseter & Sætre 1975) and winter flounder *Pseudopleuronoectes americanus* (FO: 46%) (Frank & Leggett 1984) and possible causes for these differences in occurrences this will be discussed in the following.

The occurrence of capelin eggs found in crab stomachs vary between years (Anisimova et al. 2005, Paper III) and can be explained by; capelin changing spawning sites between years, variable egg density, temperature effects on stomach evacuation rates and egg incubation time and the availability of alternative prey for the red king crab at the time of sampling. In previous field studies, the crab has been observed to feed on the most abundant prey available (Jewett & Feder 1982) and such a feeding behaviour can explain why capelin occurred more frequently in crab stomachs than capelin eggs (Paper III). As capelin die after spawning, the

amount of post spawn capelin available as prey for the crab is most likely much larger than the amount of capelin eggs, as the gonadosomatic index for female capelin is estimated to about 27% just before spawning (Christiansen et al. 1998). Hence, if crabs dispose an opportunistic feeding behaviour, this can explain the higher occurrence of capelin rather than capelin eggs in crab stomachs (Paper III).

Logistic regression models predicting the occurrence of capelin eggs in crab stomachs showed that the occurrence of capelin eggs increase with increasing capelin egg density (Paper III). If the crabs ingest capelin eggs incidentally when feeding on other prey that eggs are adhered to or they are ingested by chance when whirled up by crab during feeding activity, the occurrence of capelin eggs in crab stomachs is expected to increase by increasing egg density as well as with active feeding on eggs. The crab may also be “testing” many different prey taxa as it invades new areas. Such “testing and tasting” of potential prey may result in an increased proportion of crabs consuming capelin eggs with increased egg density, although the amount of egg ingested may not necessarily increase.

Capelin eggs occurred more frequently in red king crab stomachs than lumpsucker eggs in current investigations, but for lumpsucker eggs, the occurrence may be underestimated because crabs were collected for stomach analysis at lumpsucker spawning sites early in spawning season. Also, the methods used to collect crabs were different for the two species, where scuba divers collected crabs at lumpsucker spawning grounds while crabs were caught by trawl at capelin spawning grounds. Collection of red king crabs by diving might have been biased towards calm animals which were more easily captured, as some crabs which were feeding actively on clumps of lumpsucker egg were very aggressive and hard to handle. It is likely that the lumpsucker egg density is higher in the middle of the spawning season as the lumpsucker release its eggs in several batches (Davenport 1985). As juvenile red king crabs are also observed to feed on lumpsucker eggs (Sokolov & Milyutin 2006), the occurrence of lumpsucker egg in all size groups of crabs may be higher than found in this study and the consumption of lumpsucker eggs by red king crab may be underestimated.

The juvenile red king crabs are present in shallow waters all year round at or nearby lumpsucker spawning sites, but they were not included in the study in Varanger Fjord in 2003. Aggregations of juvenile red king crabs may seriously damage both their food resources and those of fish in benthic communities (Pavlova 2008). However, the egg guarding lumpsucker

male may be able to protect his eggs from small crabs and the juveniles themselves must consider the risk of being eaten themselves by cannibalistic crabs (Long et al. 2012) as they need to move out of their shelter to feed on lumpsucker eggs.

As the juvenile red king crabs most commonly are distributed in shallower and more sheltered areas (Pavlova 2008, Jørgensen & Nilssen 2011) than those used as spawning sites for the Barents Sea capelin (Gjørseter 1998), the predation on capelin eggs by juvenile red king crab is probably less important for capelin than for lumpsucker. When fitting the logistic regression model with the aim to predict the occurrence of capelin eggs in red king crab stomachs, the effect of crab size was insignificant (Paper III). The lack of a crab size effect may be explained by the relatively narrow size composition of the crab sample, as most crabs caught were large crabs with a carapace length > 110 mm.

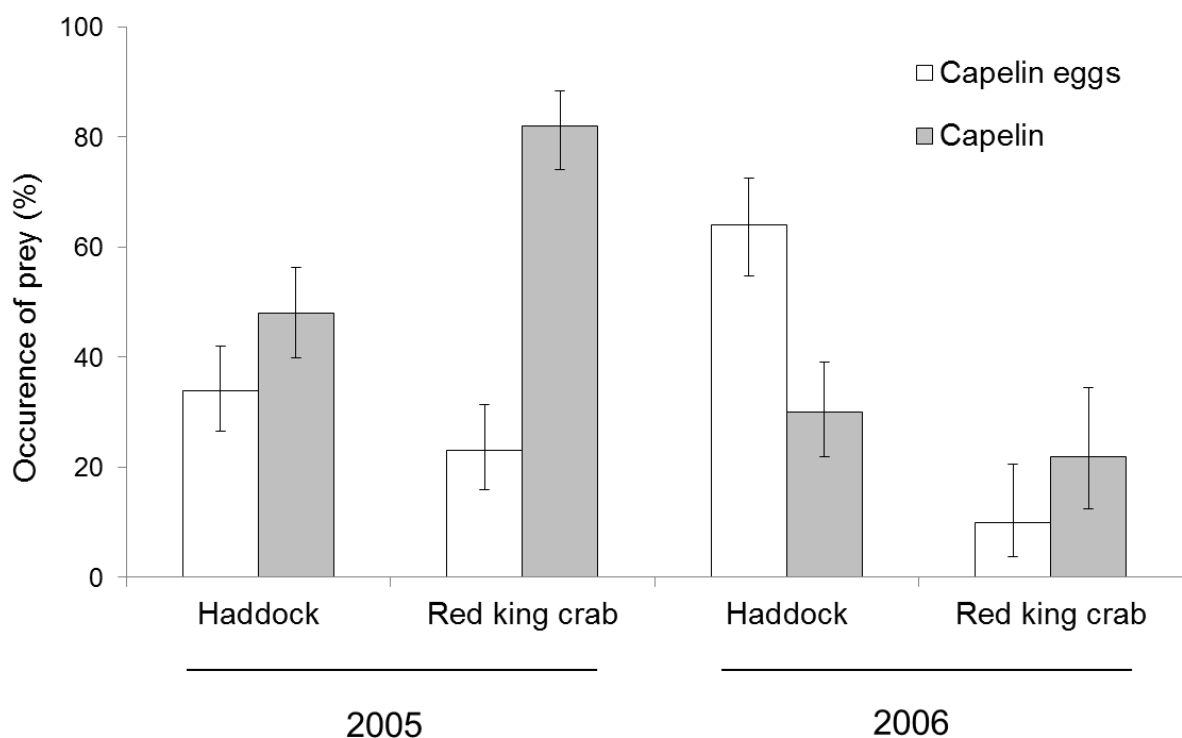


Fig.2. Occurrence (%) of capelin eggs (black bars) and capelin (white bars) found in haddock and red king crabs in 2005 and 2006. Haddock were sampled at and nearby the same spawning sites and at the same as the sampled red king crabs both years (Haddock; $n_{2005} = 152$, $n_{2006} = 120$, Red king crab; $n_{2005} = 125$, $n_{2006} = 60$).

Haddock has also been identified as a very important predator on herring eggs from several stocks (Toresen 1991, Richardson et al. 2011). A population model for herring at Georges Bank, USA, which incorporates egg predation by haddock in addition to fishing mortality, explains the major population trends of herring over four decades (Richardson et al. 2011). In haddock caught nearby the capelin spawning sites, capelin eggs occurred more frequently in 2005 (34%) and 2006 (64%) than in red king crab (Fig. 2) (N. Mikkelsen, unpublished data). The occurrence of capelin eggs in haddock stomachs increased significantly from 2005 to 2006 while the occurrence of capelin decreased, indicating that haddock may have switched from actively feeding on capelin in 2005 to capelin eggs in 2006. This could be an effect of capelin as alternative prey already being eaten up at the time of sampling in 2006 by haddock and other predators such as the red king crab. This is supported by the decrease in occurrence of capelin in red king crabs from 2005 to 2006. However, the occurrence of capelin eggs also decreased in crabs at the same time. These findings imply that haddock is likely to be a more efficient capelin egg feeder than the red king crab. Nevertheless, as capelin and capelin eggs are important prey for haddock during spring season (Dolgov 2002, Bogetveit et al. 2008); the invasive crab may enhance haddock to switch from capelin to capelin eggs as prey.

6.4 Numerical and functional response of Red king crab to capelin egg density

That the number of capelin eggs found in egg feeding crabs was highly variable and did not increase with increasing egg density, indicates no strong functional response by the crab to capelin egg density (Paper III). Functional response by predators to prey density is commonly classified as; Type I (number of prey consumed per predator is assumed to be directly proportional to prey density), type II (the number of prey eaten per predator increases very rapidly with initial increase in prey density and thereafter increase more slowly approaching a certain fixed level) or type III (the risk of being preyed upon is small at low prey densities, but increases to a certain point as prey density increases (Holling 1959, Juanes et al. 2004). The relationship between beach spawned capelin egg density and egg consumption by the amphipode *Calliopius laeviusculus* at Newfoundland was found to be sigmoid (Deblois & Leggett 1991), classified as at Type III functional response. A type II response was found in an experimental work where juvenile red king crab exhibited cannibalistic behaviour to 0-group crabs (Long et al. 2012). The type II response can lead to local extinction of prey

species (Hassell et al. 1977), as the risk of being eaten is high at low prey densities (Juanes et al. 2004).

The apparent lack of functional response in red king crab to capelin egg density in this study can be a consequence of the patchy egg distribution and the difficulties in measuring egg density in field. Patches of high or low egg densities could have been missed in between grabbing stations. Also, as the estimate of egg density representing each trawl haul was restricted to one station at the middle of each crab trawl hauls track, that in average were approximately 2.1 km long, this one station may not be fully representative for the whole area covered by trawl hauls.

Predator response to prey density is dependent on prey characteristics, the density and quality of alternate foods and predator characteristics (Holling 1959). An increased abundance of capelin as an alternative prey would then dampen the predation pressure on capelin eggs. The life history strategy of the Barents Sea capelin by displaying semelparity may contribute to the low predation pressure on their eggs by predator swamping. Predators may be swamped if very high abundance of prey saturates the predators (Ims 1990). The demersal spawners, wolffish, shorthorn sculpin and the herring may experience egg predation by the invasive red king crab already or in the future as the crab expands its distribution area southwards. They are all iteroparous species which does not have the advantage of “swamping” the predator by dying after spawning.

The high number of both capelin and lump sucker eggs found in some crabs suggest active egg feeding by at least some crabs that specialise in feeding on fish eggs (Paper II and III). Some crabs were also able to find and feed on substantial amounts of capelin eggs at low egg density in a distance up to 6 km from the centre of the spawning area. Even though the red king crab is commonly described to be a generalist feeding crustacean (Britayev et al. 2010), this study suggests that individual specialisation in feeding behaviour occurs in red king crabs and such individual specialisation in invasive species may affect prey populations (Bolnick et al. 2007).

A numerical response to capelin abundance has been identified in gadoid predators following capelin migration and spawning dynamics (Bogetveit et al. 2008), but the red king crab showed no numerical response to capelin egg density (Paper III) implying that they were not

attracted to areas with high capelin egg density. Nevertheless, as there was a tendency, although not significant, towards higher abundance of crabs 2 - 4 km from the centre of spawning area, the crabs could be attracted towards capelin as an alternative prey outside the centre of capelin spawning area. Although no capelin was found in grab or crab trawl samples in this study, this has been observed in other studies where large masses of dead capelin have been found at the sea floor nearby spawning sites (Gjørseter 1998). Red king crabs are attracted to bait by olfactory stimuli (Zhou & Shirley 1997), and if dead post-spawned capelin release more odour than capelin eggs, this may explain the higher occurrence of capelin than capelin eggs in crab stomachs (Paper III).

6.5 Stomach evacuation rates of fish eggs in red king crab

The estimated average stomach evacuation time for lumpsucker eggs (9.97 h^{-1}) in red king crab was higher than for capelin eggs (5.38 h^{-1}) (Paper II and Paper III), even though the estimates for lumpsucker eggs was based on experimental work at a higher temperature than for capelin eggs, and it is known that higher temperatures increases digestion rates. However, as the evacuation time is dependent on size of prey (Jobling 1987, Loya-Javellana et al. 1995), this result is plausible because lumpsucker eggs are approximately twice the size of capelin eggs, when egg diameter is used as the parameter (Lønning et al. 1988). Also, egg chorion of lumpsucker egg (ca. $60 \mu\text{m}$) is thicker than in capelin eggs (ca. $15 \mu\text{m}$), and the hardness of lumpsucker eggs, measured as egg resistance to mechanical pressure, is much higher in lumpsucker eggs (ca. 2000 g) than in capelin eggs (ca. 250 g) (op. cit). These features most likely make the eggs of lumpsucker more resistant to digestion than capelin eggs and thereby increase the stomach evacuation time when compared to capelin eggs. The average stomach evacuation time of lumpsucker eggs in red king crab ($\sim 10 \text{ h}$) (Paper III) is similar to earlier findings in an experimental study conducted at the same temperature where other prey eaten by smaller crabs 70 to 90 mm CL (Pavlova 2009).

No capelin eggs were found in crab stomachs 14 h after ingestion, and the concurrent time for lumpsucker eggs was 17 h. As the crabs were spilling a substantial amount of capelin eggs in storage tanks before the experiment started, the size of meal was increased in order to fulfil the assumption that experimental animals had to eat a minimum of 0.20% of their body weight. Even though the crabs on average spilled 45% of capelin eggs during feeding activity

in experiment, their ingested meal of capelin eggs was twice the size of the meal ingested by crabs feeding on lump sucker eggs in laboratory study. As meal size may affect the relative stomach evacuation times (McGaw & Curtis 2013), and the general trend in crustaceans is that larger meals move faster through the gut system (Murtaugh 1984, Haddon & Wear 1987), the size of the ingested meal size may have affected stomach evacuation time of capelin eggs when compared to lump sucker eggs.

When haddock fed on herring eggs, which are similar to capelin eggs when compared by egg diameter, the time for complete gastric emptying was 96 h in an experiment where the temperature was in the range from 5 to 6 °C (Toresen 1991). This implies that the stomach evacuation rate in red king crab is relatively high compared to haddock (Paper II and Paper III) supporting the finding in a previous study (Pavlova 2009). The exponential decay model was applied when estimating consumption of herring eggs by haddock (Toresen 1991) and was also used in this study (Paper III). This model described the relationship between the proportions of capelin eggs left in stomach at a given time well and was used to estimate the average stomach evacuation rate of capelin eggs in red king crab (Paper III). Exponential decay models are commonly considered appropriate to estimate digestion of relatively easily digested particles from fish stomachs (Jobling 1986).

As the experimental data on stomach evacuation rate of lump sucker eggs fitted the exponential decay model poorly, an alternative ogive model was fitted to the experimental data (Paper II). The proportion of lump sucker eggs left in stomach at a given time was well described by the ogive model, which can be explained by the process of lump sucker egg digestion; the thick chorion resists digestion for a certain time, but once the egg chorion cracks and gastric fluids enter the eggs, egg contents are rapidly evacuated from the stomach. The ogive stomach evacuation model also included a variable for initial loss of prey as percentage of the offered meal (Paper II). Initial loss of prey has been observed in other studies of crustaceans (Hill 1976, Cristo 2001), and was observed in our experiment as some eggs were punctured, leading to loss of egg contents and a broken chorion (Paper II).

6.6 Consumption of demersal fish eggs by the red king crab

The estimated consumption of capelin eggs at the spawning sites investigated in 2005 and 2006 by the red king crab accounted for less than 2.5% of the eggs available (Paper III). These estimates are similar to the estimates of capelin egg consumption of the Barents Sea capelin stock by diving ducks throughout the spawning season which accounted for 2 – 3% of the total egg production (Gjøsæter & Sætre 1975). Another capelin egg predator, the amphipode *Calliopius laevisculus* caused predation mortality from 15 - 30% of the total egg deposition at spawning beds of capelin at Newfoundland (DeBlois & Leggett 1993). In comparison to egg predation mortality, the daily larval mortality of capelin caused by predation from juvenile herring was estimated to account for 7.3% and 9.9% of the capelin larvae standing stock in the Barents Sea in 2001 and 2003 respectively (Hallfredsson & Pedersen 2009).

Consumption of lumpsucker eggs in Varanger Fjord in 2003 was equivalent to approximately 33% the commercial catches of roe in the same area and year (Paper II). The lack of estimates of the spawning stock of lumpsucker in Varanger Fjord makes it difficult to evaluate the effects of this consumption and damage of eggs by the red king crab. There have not been any previous studies to quantify predation mortality on lumpsucker eggs by other predators either. Nevertheless, as the decline in the Norwegian lumpsucker stock from the 1990s has been associated with overexploitation (Albert et al. 2002) and the consumption of roe by the red king crabs was equivalent to one-third of the catches in 2003, this consumption may hamper the recruitment of lumpsucker in Varanger Fjord. Consumption by juvenile red king crabs on lumpsucker eggs was not estimated in this study because of the lack of abundance estimates for the juvenile crabs. Since the juveniles are present in shallow waters year round they may consume high amounts of lumpsucker eggs if they are not hindered by the egg guarding male.

Uncertainty in consumption estimates was mostly due to the uncertainty in input data for stomach content of the red king crab. In all three years studied, the correlation between input data for stomach content and the consumption estimates were above 0.80 (Paper II, Paper III). These findings stress the importance of increased effort in stomach analysis in future work, to improve the precision of estimates of red king crab consumption of fish eggs.

Food consumption estimates may be biased due to sampling intervals, diel feeding rhythm and stomach evacuation rates in predators. The stomach evacuation rate of fish eggs in red king crab are high (Paper II, Paper III) and may lead to bias in frequency of occurrence in field samples because sampling intervals may be too long. Sampling of crabs by divers at some spawning sites for lump sucker was restricted due to the high speed of current, as it was only possible to dive at high tide, potentially causing underestimate in stomach content. However, the wide range in number of eggs found in crab stomach at all sampling hours supports the previous findings that crab in Norwegian waters display no diurnal rhythm in feeding activity during polar summer, when light levels are relatively high at night (Jørgensen et al 2007). Previous studies in fish show that sampling intervals as large as 12 h gave reasonable estimates of food consumption (1-20% error) when temperature was $< 10^{\circ}\text{C}$ (Finstad 2005). Assuming the same tendency in red king crab, bias due to long sampling intervals is not likely in studies on egg predation on fish eggs by the red king crab, since the measured temperature in field ranged from 2.9 to 3.4°C (Paper II, Paper III).

That red king crabs were observed to damage and spill a substantial amount of fish eggs both in field and laboratory studies (Paper II, Paper III) will lead to a higher egg mortality caused by the crab, than can be estimated from stomach data (Paper I, Paper II, http://www.int-res.com/articles/suppl/m469p087_supp/). As decapod crustaceans are messy feeders that tear apart their prey before ingestion (Ahvenharju and Ruohonen, 2005), the spilling and damage of prey can be expected in red king crab during feeding activity and such spilling has been observed in other studies where crabs fed on different prey (Jørgensen 2005, Britayev et al. 2010). In another experimental study where red king crabs were fed lump sucker eggs, the crabs were observed to tear off clumps of egg from the original egg clutch, causing some damage to eggs not eaten and a substantial spilling of eggs during feeding activity (Michelsen 2011). Crabs spilled more capelin eggs than lump sucker eggs during feeding in laboratory experiments (Paper II, Paper III). This can be explained by the crab being a more efficient feeder of lump sucker eggs which are larger and also are glued together harder than capelin eggs. Capelin eggs are small and difficult for crabs to pick if they were lost to bottom of the experimental tanks.

Ecosystem approach to management of fisheries implies consideration and assessment of high degree of trophic interaction between species. Estimates of prey consumption and the uncertainty in such estimates are therefore important in management of both commercial and

non-commercial species. My studies show that for the invasive red king crab, the highest amount of uncertainty in consumption estimates are generated by the uncertainty in stomach content data from field which imply that more effort is needed in order to reduce this uncertainty. Assessing the potential impact by juvenile red king crab consumption on demersal fish eggs is demanding, as the abundance estimates for the juvenile crab are missing and sampling of red king crab at spawning sites can be a challenging. If the red king crab enters spawning areas of the Norwegian spring spawning herring, it is likely that crabs will consume the non-guarded and non-buried demersal eggs of herring and potentially they may have an impact on recruitment of this important commercial species. In addition to consumption, it is also important to take into account the increased mortality due to killing or damage of prey not eaten by the red king crab.

7. Conclusions and future perspectives

This project has provided new knowledge about the predation mortality of the demersal fish eggs for capelin and lumpsucker at the coast of northern Norway. The ecological impact of the invasive red king crab on demersal fish eggs was found to be more important for lumpsucker than for capelin and may hamper the recruitment of lumpsucker in areas invaded by the red king crab. The total loss of eggs due to red king crab feeding is likely to be higher than the estimated consumption rates for both capelin and lumpsucker egg due to damage and loss of eggs during feeding activities. As a follow up on my studies, the occurrence of fish eggs in red king crab stomachs should be compared to other prey items, in order to reveal its importance in red king crab diet during spring. Also, the potential impact by juvenile red king crab consumption on demersal fish eggs should be assessed as they are present in shallow water year round. Field studies applying video analysis may be an applicable approach to study the predation by juvenile red king crabs.

The consumption of capelin eggs by red king crab and by egg cannibalism was considered to be too low to significantly regulate capelin recruitment. The red king crab did not show functional or numerical response to capelin egg density in field. It is suggested that as a consequence of the semelparous life history of capelin, the red king crab may be swamped by post-spawn capelin as alternative prey, reducing the predation pressure by crabs on capelin eggs. Some other fish species that may experience increased egg mortality due to egg

predation by the red king crabs are the wolffish *Anarhichas lupus*, shorthorn sculpin *Myoxocephalus scorpius* and the Norwegian Spring Spawning herring *Clupea harengus*. All of these species are iteroparous, not having the advantage of potentially swamping the crab as predator when dying and serving as alternative prey for the crab. The first red king crabs are at present invading Balsfjord and the local “Pacific” herring *Clupea pallasii* stock there may be the first herring stock experiencing egg predation from the crab. It should be considered to estimate the stock abundance of this local herring population before the red king crab establish in Balsfjord, so that the potential impact on herring recruitment by the egg feeding red king crab can be assessed in future investigations.

Stomach evacuation data of capelin eggs in red king crab stomach fitted the exponential model well, while the lump sucker eggs in crab stomach fitted an ogive model taking into account initial loss of prey. Stomach evacuation rates were successfully included in consumption models taking into account the uncertainty in input data using Monte Carlo simulation. The uncertainty in stomach data was highly correlated to consumption estimates in all years studied. In future investigation on prey consumption of the invasive red king crab, more effort should be applied to stomach analysis to potentially reduce the uncertainty in input data for stomach content in consumption models and thereby get more precise estimates of consumption.

As capelin is a short-lived species that is important both ecologically and commercially in the Barents Sea ecosystem, it is important to follow up on potential impacts of the invasive red king crab on the capelin stock. Also, the potential prey competition between the crab and the native species which feed on capelin is important to investigate. One of these native species that feed on capelin eggs and capelin is the Northeast Arctic haddock. If the haddock experience increased competition on post-spawned capelin by the crab, it may compensate by feeding more heavily on capelin eggs. It is important to investigate the consumption of capelin egg and capelin by haddock. At present, the haddock stock is at high levels causing a heavy predation pressure on the capelin stock. Although the haddock stock size is expected to decrease the following years, due to lower year-classes entering the spawning stock, it is expected that the haddock stock will remain at relatively high stock levels in the coming years (ICES 2013).

Another invasive decapod crustacean in the Barents Sea, the snow crab *Chionoecetes opilio*, is rapidly increasing in abundance and distribution range. Only a few specimens have been recorded close to the coast in the Norwegian part of the Barents Sea so far, but the abundance is expected to increase and snow crab will probably be distributed more northerly than the already established red king crab (ICES 2012). Snow crab has been observed to feed on capelin in Newfoundland waters (Squires & Dawe 2003) and may represent an additional competitor to native species who feed on the post-spawn capelin and should therefore be monitored carefully.

8. References

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9. Paper I

10. Paper II

11. Paper III



ISBN xxx-xx-xxxx-xxx-x