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Female life-history parameters in the introduced red king crab (*Paralithodes camtschaticus*, Tilesius 1815) in the Barents Sea:

A study of temporal and spatial variation in three Norwegian fjords

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Good friends are important and you all mean a lot to me!
To My Dearest Magnus, Elise and Sigri,
You Are Filling My Days With
Love and Happiness!

Tromsø May 2012 Ann Merete Hjelset

Summary

The red king crab (*Paralithodes camtschaticus*) was deliberately introduced to the Barents Sea by Russian scientists during the 1960s, with the purpose to improve coastal fishery and thus improve the local economy. Since the red king crab was caught for the first time in the Varangerfjorden area, the stock has increased in abundance and expanded westward inhabiting coastal areas along the coast of Finnmark from the Russian border in east to the area around Hammerfest in west. Today the population of red king crab supports a valuable fishery in the Barents Sea, representing an ex-vessel value of 150 million NOK in 2011.

Several challenges are related to management of the red king crab, since it is an introduced species. The Norwegian management regime today has two goals, one is to keep a long term harvest within a geographical limited area and the second is to limit further spread of the crab. Basic knowledge is needed to meet both objectives, particularly knowledge on life-history traits.

The main study area in this thesis has been three large fjords in Finnmark in northern Norway. There is a historical westward spread of the crab along the Norwegian coast, and it has been present in Varangerfjorden, Tanafjorden and Laksefjorden for about 35, 25 and 15 years respectively. Crabs have been sampled annually during scientific autumn cruises from 1994 until 2011.

Size at maturity is a key life-history parameter in fishery management and should be monitored routinely. For female red king crabs this means the recording of presence or absence of eggs. In paper I the size at maturity was estimated in female crabs from each of the three fjords which constitute the main study area in this thesis. No temporal differences were seen and the size at maturity varied from 108 to 111 mm carapace length in the three fjords and was found to be generally higher than in native areas.

Knowledge about the species individual fecundity gives information on size and number of offspring produced. Fecundity is closely related to life-history traits such as size at maturity, life-span and egg size. In this study both spatial and temporal patterns in fecundity and a reduction in individual egg weight was found. A main finding in paper II was a reduction in the individual fecundity during a part of the study period. An average female produced about 30 % less eggs in 2007 compared to 2002. Fecundity is the life-history

parameters that respond most rapidly to changes in environment or other factors, such as fishery.

The abundance estimates of red king crab females have increased in our area during the study period, but in the last two years, a decrease was observed in Tanafjorden and Laksefjorden. The stock size composition and the individual fecundity parameters established in paper II has been used in paper III to obtain a reproductive potential of the crab stock for the period 1995 to 2011. The male-only fishery and introduction of a female quota has had influence on the size composition and fecundity, and thus on the potential egg production in the stock. The study also showed that an observed reduction in size of large males was correlated to a size reduction of large females with a one year lag.

List of publications and manuscript

This thesis is based on three papers referred to in the text by their roman numerals.

Paper I:

Hjelset, A.M., Sundet, J.H., Nilssen, E.M., 2009. Size at sexual maturity in the female red king crab (*Paralithodes camtschaticus*) in a newly settled population in the Barents Sea, Norway. J Northw Atl Fish Sci. 41:173-182

Paper II:

Hjelset, A.M., Nilssen, E.M., Sundet, J.H., 2012. Reduced size composition and fecundity related to fishery and invasion history in the introduced red king crab (*Paralithodes camtschaticus*) in Norwegian waters. Fish Res. 121ï 122:73-80

Paper III:

Hjelset, A.M., (manuscript). Red king crab (*Paralithodes camtschaticus*) recruitment potential in Norwegian fjords.

1. Introduction

The primary aims of all species are to survive and to reproduce. How an organism reproduces profoundly affects how it contributes to future generations (Stearns, 1976), and thereby the future survival of the species. Life-history theory explains the broad features of a life cycle; how fast the organism will grow in size and numbers, when it will mature, how long it will live, how many times it will give birth, and how many offspring it will have through a life span (Stearns, 1992). Important life-history parameters in a life cycle include size at birth, individual growth pattern, both the mean and the variance in age or size at maturity, number, size and sex ratio of offspring, age- and size-specific reproductive investments, age- and size-specific mortality schedules and length of life (Stearns, 1992). The traits are always bound together by numerous trade-offs which may include current reproduction and survival rates, current reproduction and future reproduction rates, number, size, and sex of offspring (Stearns, 1992). A given combination of these traits is a life-history tactic characteristic of the species, and which is crucial for survival and future reproduction (Stearns, 1976). Environmental variables such as food, temperature, breeding sites, refugia, competitors, and predators are also important for a speciesô life-history tactics (Stearns, 1976). Some aspects of reproductive biology such as reproductive strategy are characteristics of the species and are fixed (e.g. batch vs. total spawners, determinate vs. indeterminate spawners) (Morgan, 2008). Other life-history traits are highly plastic (e.g. size or age at maturity, sex ratio, fecundity and spawning and hatching time and duration) and these traits can vary between populations (Morgan, 2008). Species may be classified by the life-history characteristics which control population size, where *r*-selected species have the ability to increase rapidly in number and take advantage of temporarily favourable environments, often by producing many small off-spring. The *K*-selected species inhabit stable environments, in which the ability to compete with rival species is more important, and their off-spring are fewer and larger (Pianka, 1970).

Non-native species that become invasive can reach high to exceptionally high densities in their range of introduction, threatening both biodiversity and ecosystem function (Tibbets et al., 2010). The ability of the introduced species to cope with changing conditions during the establishment phase may determine its success as an invader. One important question is whether life-history traits predict the fate of introduced species, and which parameters are important in this respect (Rosecchi et al., 2001). Starting with a small population, establishment in a new environment can be studied under density-independent and density dependent conditions. In the early stages of the process, the density will be low and no intraspecific competition need to be expected; later, as the density increases intraspecific competition can be expected to intensify, which can result in a density-dependent reaction norm[1] of life-history traits. The ability of the species to display plasticity in terms of growth and fecundity is vital. Plastic responses and selection for relevant traits can soon modify phenotypes[2] of the introduced species in periods of rapid population growth (Reznick et al., 1997). Long time series covering the complete invasion and establishment process may be used to estimate the time needed before the invadersô plastic life-history stabilises in the new environment. Expected life-history characteristics typical for invasive marine species may include high fecundity, planktonic dispersal, a wide range of habitat and food preferences, tolerance to a wide range of environmental conditions, longevity and large size (Brockerhoff and McLay, 2011). Of all species introduced, only one out of every ten will become invasive (Williamson and Fitter, 1996; Allendorf and Luikart, 2007). Life-history traits are fundamental to population dynamics and thus of importance to evolutionary ecologists and fishery managers (Stearns, 1992).

Fisheries for a particular species or stock are initiated for several reasons. Growing global demand for food and improved technology has simplified capture, processing, distribution and sales. Uncontrolled fishing for a species is seen as undesirable and natural fishing resources are now regarded as a common property (King, 2007). Fishery management has numerous objectives, which may be grouped into four general areas; biological, economic, recreational and social (Hillborn and Walters, 1996), and management is intended to maximise certain (biological, social or economic) benefits of the fishery (Jennings et al., 2001). Political objectives may also play an important role in management regulations. The most important task of fisheries science is to provide advice to managers that make it possible to meet the chosen set of management objectives (Jennings et al., 2001). The main objective of a biological management regime is to produce the maximum sustainable yield, and higher catches are better (Hilborn and Walters, 1996). The economic objective is to maximise the net profit from the fishery. Many of the worldôs fisheries are important for recreation, and these also need to be managed (Hilborn and Walters, 1996). The social objective of management is that fisheries should generate benefits for the local society by creating employment.

[1] In ecology and genetics, a norm of reaction describes the pattern of phenotypic expression of a single genotype across a range of environments.
[2] A phenotypic trait is an obvious and observable trait.

Management very often aims to fulfil two or more of these objectives (Hilborn and Walters, 1996).

Understanding the life-cycle and distribution of a targeted species is central to understanding how they are affected by the fishery and the environment (Hilborn and Walters, 1996). An understanding of how the species reproduces, its reproductive strategies and potential, and the links with other life-history traits such as growth, fecundity and age or size at maturity are fundamental to population management. The effect of fishing on life-history traits is also important for success in long-term management (Kuparinen and Merilä, 2007).

The red king crab (*Paralithodes camtschaticus* Tilesius 1815) is a highly valuable resource in the northern part of the Pacific Ocean, and Russian authorities therefore introduced the species into the Barents Sea between 1961 and 1969. A total of 1,655 egg-bearing females and 954 large males were released into the sea close to Murmansk (Orlov and Ivanov, 1978). A further 10,000 juveniles aged 1 to 3 years, together with about 1.5 million stage I zoeas, were also released in the same area as the adults (Orlov and Ivanov, 1978). In 1974 the first red king crab was caught in the release area, Kolsky Bay (near Murman), and in 1977 the first crabs were caught by local fishermen as bycatch in Varangerfjorden (Orlov and Ivanov, 1978), 250 km from the release area. In accordance with an agreement between the Russian and Norwegian governments, all king crabs caught were to be released back into the sea (Anon., 1978). For 17 years fishing for this species was banned, in order to enable the crab stock to grow and spread through both Norwegian and Russian waters, to become a fishery resource. Since 1994, the estimated stock in Norwegian waters has risen from 62,000 to 3.3 million in 2011. The stock estimates actually peaked in 2008 at 5 million individuals. The quota has been raised in accordance with the rise in the total stock of legal males from 11,000 in 1994 to 545,000 (1,200 tonnes) in 2011. The exploitation rate peaked at 95% in 2009. The management of the red king crab in Norway is based on a White Paper adopted by the Norwegian Parliament in 2008 (Anon., 2007). The fishery is regulated by quotas within a limited area off eastern Finnmark (Fig. 1). Outside the regulated fishing areas the main management aim is to keep the king crab stock at a minimum level, as it is an introduced species and could have impact on the marine ecosystem. There is therefore a free fishery for red king crab outside the regulated area (Anon., 2007). Several alien crab species support locally important fisheries, but the red king crab is the only crab that has become a profitable fishery, and is managed for sustainability (Brockerhoff and McLay, 2011).

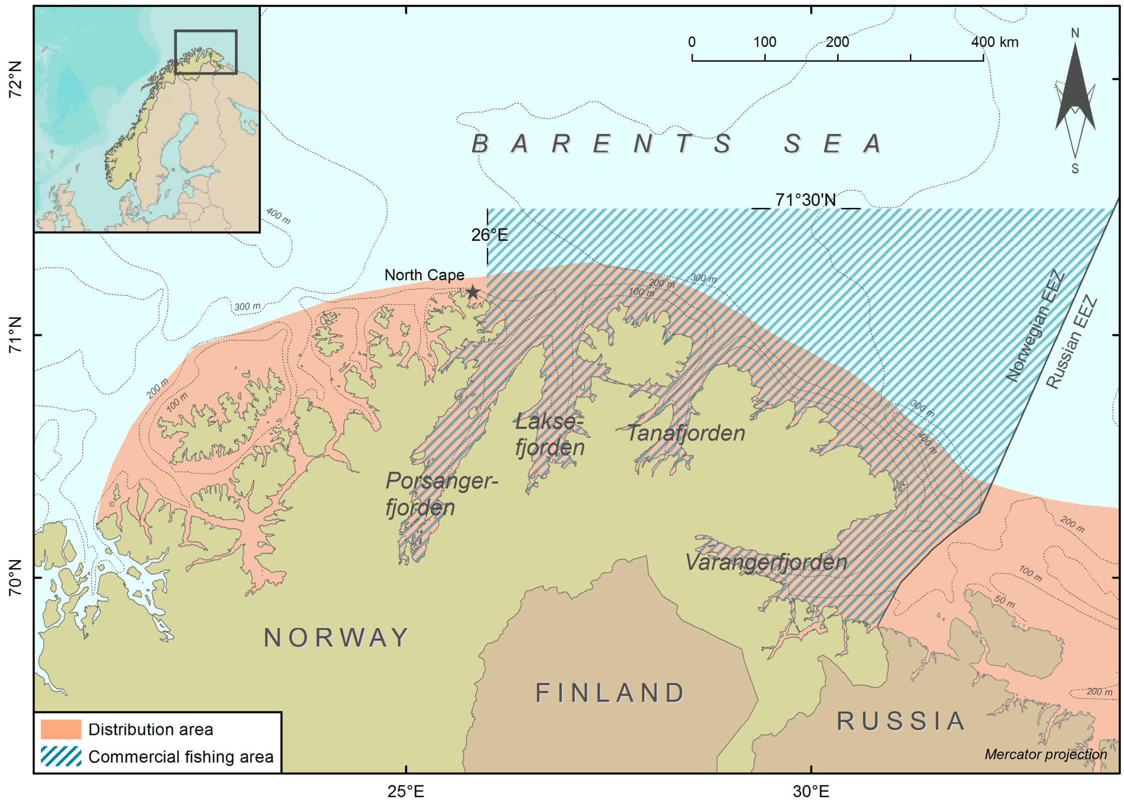


Figure. 1. The study area off the county of Finnmark in northern Norway. The grey area shows the current distribution of red king crab in Norwegian waters. The current area for commercial fishing is the hatched area.

Adult red king crabs in their native areas of the Pacific migrate seasonally between deep and shallow waters, governed by their mating, moulting and feeding habits (Marukawa, 1933; Stone et al., 1992), and the same migration pattern is seen in Varangerfjorden (Sundet and Hjelset, 2010). Life-history characteristics can be classified according to their parameters as either *r*- or *K*-selected strategies (Hammer et al., 2010). In the literature, the red king crab is categorised as a *K*-selected species, in that it attains a large maximum size and displays a fairly sophisticated reproductive behaviour. However, natural mortality rates and maximum age are intermediate between *r*- and *K*-selection traits, but are closer to *K*-selection (Powell and Nickerson, 1965; Kruse, 1993).

2. Main objectives

2.1 Background

The red king crab is an intentionally introduced species as well as a commercial fishery resource in the Barents Sea. Today, some 550 boats participate in the fishery and the ex-vessel value of the fishery is about 150 million NOK (Fig. 2). It is therefore important to have a fundamental understanding of the reproductive biology of the species if we wish to understand its population biology. This is a necessary basis for management advice, whether the crab is regarded as a fishery resource (e.g. Hillborn and Walters, 1992) or an undesirable species (e.g. Weis, 2010). In the case of the red king crab, the management goals are to have a sustainable fishery within a geographically limited area and to stop further spread of the species. Reproductive biology, together with survival and individual growth, largely determines productivity and therefore the resilience of a population to exploitation or perturbation by human activities (Jennings, et al., 2001). This PhD project aimed to reveal the major features of important life-history parameters related to the reproductive biology of the female red king crab, in order to provide basic knowledge for management advice.

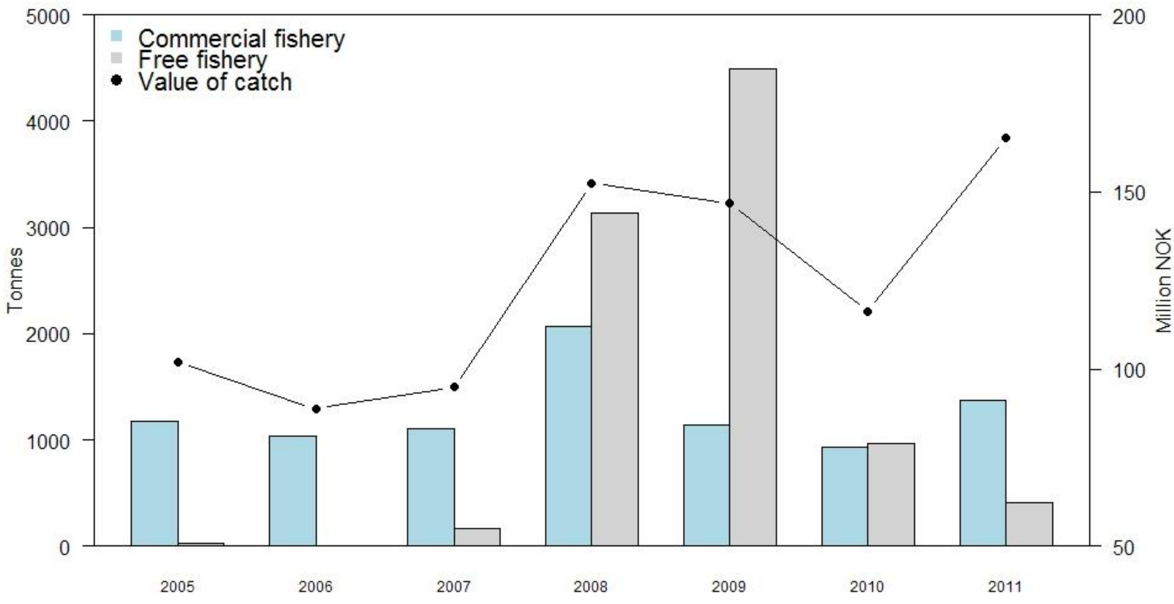


Figure. 2. Norwegian landings of red king crab (*Paralithodes camtschaticus*) in tonnes in the period 2005 to 2011 and ex-vessel value in million NOK.

2.2. Specific objectives

Size at maturity is a key life-history parameter in fishery management since it is highly plastic and can therefore be easily affected by the fishery (Stearns, 1992; Watters and Hobday, 1998; Poos et al. 2011). It is recommended that data on this parameter should be collected routinely, and especially during the early stages of exploitation of a new fishery (Watters and Hobday, 1998). The aim of paper I was to find the size at sexual maturity, which was defined as the size at which the female produces her first batch of eggs. I wanted to determine whether spatial and/or temporal patterns were present in size at maturity and to compare our findings with data from native areas.

Individual fecundity is also a key life-history parameter that can differ between populations. This parameter is typically even more sensitive to changes in both biotic and abiotic factors than size at maturity. Selective pressure exerted by the fishery can also change fecundity through the removal of larger individuals, which have higher individual fecundity. The aim of paper II was to study temporal and spatial patterns in fecundity at individual level, and to chart individual egg weight and size structure among ovigerous females. We also compared our findings with similar data from native areas.

By quantifying the reproductive potential of the red king crab stock, paper III aimed to increase our understanding of variations in reproductive potential in this species in Norwegian waters. In paper III the reproductive potential of the red king crab stock is presented in terms of number of eggs, and both spatial and temporal patterns were studied. The impact on the reproductive egg potential of the current pattern of exploitation and the recently introduced female quota are also discussed in this paper.

3. Presentation of main findings in the papers:

The main study area in this thesis has been three large fjords in Finnmark in northern Norway (Fig. 1). They represent different stages in the development of the red king crab stock, and have different crab densities. Given that the expansion has been westwards along the Norwegian coast, the crab has been present in Varangerfjorden, Tanafjorden and Laksefjorden for about 35, 25 and 15 years respectively. Crabs have been sampled annually during scientific autumn cruises from 1994 until 2011. The results presented here are mainly based on female data, but data on male crabs have also been included in paper III.

3.1. Paper I: Size at sexual maturity in the female red king crab in a newly settled population in the Barents Sea, Norway.

Sexual maturity is defined as the size at which a female produces her first batch of eggs. The ovigerous carapace length, at which 50% of the red king crabs bear eggs (OL_{50}), is the most common parameter defining size at maturity in a crustacean species. The study showed that the females in Laksefjorden had a significantly higher OL_{50} value than the OL_{50} values in Varangerfjorden and Tanafjorden, which may be because this area has been invaded more recently, and densities were still low. The study also showed that the OL_{50} value in Varangerfjorden had not changed according to changes in fishing regime or in crab density from 1994 to 2007. The large annual variation meant that pooling of data was necessary. In other studies from native areas, the size at maturity ranged from 71 to 102 mm carapace length (CL), which is 38 to 7 mm CL smaller than the average size at maturity in our study. We believe that the large size at maturity is a result of relatively low crab density, good access to food and low exploitation rates.

3.2. Paper II: Reduced size composition and individual fecundity related to fishery and invasion history in the introduced red king crab in Norwegian waters.

Fecundity was defined as the total number of eggs attached to the female at the time of sampling. It was found that individual fecundity ranged from 18,000 to 560,000 eggs. We found both temporal and spatial variations in fecundity in the three fjords. Fecundity in a standard sized female (CL=125 mm) showed a clear reduction in individual fecundity in all three fjords in the course of the sampling period. The individual egg weights also displayed a falling trend in the course of the sampling period in Varangerfjorden and Tanafjorden. The upper size range of ovigerous crabs fell in the period from 1995 to 2010, and it is believed that both higher densities and increased harvesting of males have changed the size composition of the crabs in these fjords.

3.3. Paper III: Red king crab recruitment potential in Norwegian fjords.

The indices of abundance for ovigerous females generally increased during the sampling period, with a falling trend in Tanafjorden and Laksefjorden being seen only from 2009 to 2011. The estimated abundance indices seen in Varangerfjorden show no trend, even during the last years. There was a positive relationship between potential egg production (PEP) and abundance estimates of ovigerous females in the period studied. During the time of sampling, the contribution of eggs to the stock was dominated by smaller females compared with the early sampling period, and today 80% of the eggs are produced by ovigerous females of less than 137 mm CL (minimum legal size until 2011). In order to elucidate the importance of size composition among females and males, a 95^{th} percentile CL value was calculated for both sexes and the analysis showed that the 95^{th} percentile value fell from 1995 to 2011. PEP is dependent on the size composition of ovigerous females in the stock, and a reduction in the legal size of males and females, due to a high harvest rate, appears to have influenced potential egg production in the stock.

4. General discussion

In this study I have shown that female red king crabs in Norwegian waters grow large before they reach size at maturity and have eggs (paper I). I have also registered that individual fecundity fell during the eight-year study period (paper II). I further demonstrated a remarkable reduction in the range of sizes of ovigerous females in the population (papers I, II and III), and also of large males (paper III). Estimated indices of abundance for the ovigerous female stock rose until 2009 with a subsequent decrease, and there is a positive relationship between estimated stock size and the number of eggs (paper III). The increased harvest rate for large males and the introduction of a quota on females have presumably affected female size range and changed their size composition, which may have caused a decrease in potential egg production in the stock (paper III) and thereby also the potential recruitment.

The red king crab is the largest, most abundant and most widespread king crab species in the northeast Pacific Ocean and the Bering Sea. The native populations extend from the Sea of Japan (40ºN) in the northwestern Pacific to British Columbia in the northeastern Pacific, and through the Bering Sea into the Chukchi Sea (70ºN) (fig. 3) (Grant et al., 2011).

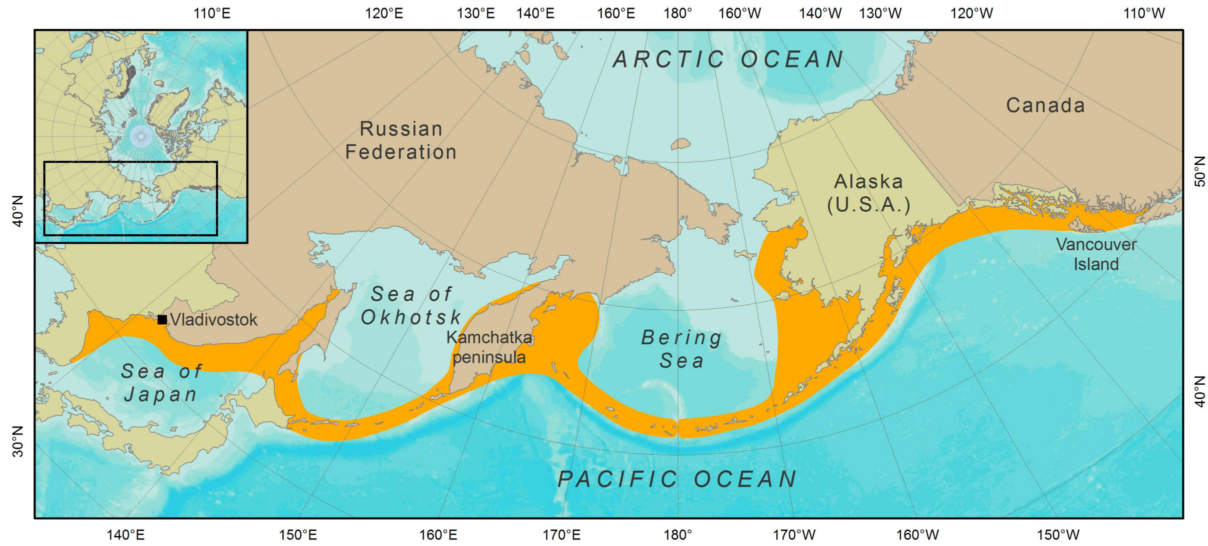


Figure. 3. Native distribution area for red king crab (*Paralithodes camtschaticus*) in the Pacific Ocean, ranging from 130ºE to 130ºW.

The Barents Sea population of red king crab is unique since it has developed and expanded into large areas with only limited exploitation until recent years, and no initiative aimed at checking further spreading of the crab has been taken until quite recently. The rise in total stock estimates indicates that the crab is well adapted to its new environment. This gives us an opportunity to study the development of a king crab stock from its introduction through its build-up, and from being virtually unexploited to being a relatively large and valuable fishery resource.

To investigate the processes that influence general population dynamics, we need to focus on the biology of the larval, juvenile and adult stages (Anger, 2006). The life cycle of the red king crab includes both pelagic (larval) and benthic (juvenile-adult) phases. There are inherent ecological difference between the two, and the larval stage is very often the most critical phase. After hatching, the survival of the larval is mainly determined by prey availability and the activity of predators (Jennings et al., 2001). According to Anger (2006), king crabs have an advantage as an introduced species because their larvae are pre-adapted to tolerate both low temperatures and planktonic food limitations. For the study and monitoring of stock development, however, data are only collected from the adult part of the stock. Juvenile crabs are difficult to find during their first years of life (Stevens, 2012), and not until they are about 25 mm CL do they begin to form pods that contain hundreds of crabs of both sexes (Powell and Nickerson, 1965; Dew, 1990). This behaviour makes it difficult to measure recruitment on juvenile stadiums, so therefore potential recruitment in red king crab measure in terms of eggs rather than larvae, juveniles or recruits to the fishery.

The biology of the red king crab in its native areas is well documented (e.g. Wallace et al., 1949; Powell et al., 1973; Stone et al., 1992; Stevens, 2012). The temporal and geographical fluctuations in size at sexual maturity of female red king crabs documented in paper I could be due to variations in year-class strength through the period of study. The large size at maturity of ovigerous females in the Norwegian fjords might also be due to good growth conditions for the crab in the study period. Large size at first maturation tends to benefit a high reproductive potential (Stearns, 1992). Thanks to low exploitation rates and good availability of food, the Barents Sea crabs can delay size at first maturity and achieve higher individual fecundity at first spawning. Another benefit of maturing late is lower instantaneous juvenile mortality rates through the production of off-spring of higher quality (Stearns, 1992).

Individual fecundity is also an important life history parameter in determining the success and population recruitment potential of a newly established population. Even though there is a higher size at maturity in the Barents Sea compared to native areas, there are spatial and temporal variations in individual fecundity within the study area. This (paper II) may be due to differences in first size at maturity (OL_{50}) among the three fjords, with the largest crabs being found in the fjord with shortest residence time. Limited availability of food may have led to the decrease in fecundity observed in the course of the study period. The responses of life-history traits to temperature and food availability are more flexible than the response to long-term climate changes, which are seen on a longer timescale. Fecundity, sexual maturity and embryonic development are important for reproductive success, because they are important for population survival (Viegas et al., 2012). Compared with all the studies in native areas, the onset of maturity and egg production started at a much larger size in the three fjords in our study.

The absolute stock reproductive potential changed little during the period studied, which may be due to a wide distribution of sizes and differences in year-class strength among ovigerous females. However, a reduction in potential egg production was observed during the last two years of the study. We can thus see that the total production of eggs in the population over time fell relative to population size. A combination of a higher number of small female crabs producing fewer eggs towards the end of the study period, and the gradual disappearance of large females, may be the cause of the reduction in potential egg production relative to stock size. A reduction in the range of male sizes could be observed during the seventeen years of data-gathering (1995-2011), and this could also have indirectly influenced the reproductive potential of the stock. The status today is that we are in a period with low potential recruitment and fewer eggs per female, with the added effect of lower investment per egg and generally smaller females, which may have influenced the potential recruitment to the stock.

During the introduction and establishment phase of a species, available genotypes in the invaded range will be determined (Anger, 2006), since only well-adapted individuals will survive. If there are multiple introductions, a hybrid population with heightened genetic diversity is more likely to be the starting point (Sakai et al., 2001; Anger, 2006), as was the case with the red king crabs in the Barents Sea. The loss of genetic variation (founder effect) that occurs when a new population is established by a very small number of individuals from a larger population is thus avoided. There may therefore be reason to believe that the introduction programme implemented over a period of ten years succeeded in establishing a genetically robust starting population in the Barents Sea (Jørstad et al., 2007; Zelenina et al., 2008).

It is quite certain that the red king crab has been highly successful in the establishment phase and has become a self-sustaining population that has spread widely in the course of the years. The complex of life-history traits, such as large size at maturity (OL_{50}), high individual fecundity, high maternal investment in eggs and a wide range of sizes in both females and males, in addition to their introduction into an ecosystem that is both rich in prey (Oug et al., 2010) and that offers optimal environmental conditions, helps to explain the success. Furthermore, they have probably been exposed to few predators in their new environment (Rosecchi et al., 2001; Sakai et al., 2001; Weis, 2010; Amundsen et al., 2012; Chapple et al., 2012), and there was no harvest of crabs for several years after the introduction (Anon., 1978). Life-history parameters in introduced species are often different from those of their native relatives (e. g. Amundsen et al., 2012). The populations of red king crab in Alaska have fluctuated greatly in the course of the past three decades. These fluctuations are probably a result of variable recruitment, but there are alternative theories regarding the ultimate cause of recruitment variability. Egg predation has been suggested by Kuris et al. (1991), while diseases and overfishing (Orensanz et al., 1998), bycatch (Dew and McConnaughey, 2005), and climate changes (Zheng and Kruse, 2000) are among the hypotheses that have been advanced. Change in spatial distribution associated with climate variability may be a primary cause of population fluctuations (Loher and Armstrong, 2005), but the link between environmental change and population abundance is not yet fully understood. A highly fluctuating and occasionally heavy fishing pressure is probably another important cause of stock declines. The Alaskan red king crab fishery has historically supported one of the most valuable fisheries in the United States (Stevens, 2012; Swiney et al., 2012). The populations in Alaskan waters have declined and never recovered their peak level in 1980. Since the decline of the Alaskan stocks, the main focus, beside traditional management for sustainable fishery, has been on trying to rebuild the stocks and using stock enhancement to achieve this goal (Swiney et al., 2012). As a stock enhancement measure, juvenile crabs were reared in captivity before being released into the sea. The main challenge in enhancement is the elimination of cannibalism (Swiney et al., 2012), but several technical challenges also exist, and these will have to be solved if a large-scale enhancement programme is put into effect (Stevens, 2006; 2012). Better knowledge of the same fundamental reproductive parameters will be essential, whether the goal is rebuilding a stock or management, whether for a fishery or eradication.

It is well understood that fishing is a dominant selective agent in evolution (Jørgensen et al., 2007). Fishing can lead to mortality rates that are several times higher than natural mortality, so the overall evolutionary response in a harvested species may be strong (Enberg et al., 2012). Fishing is therefore likely to influence the course of evolution. Which traits will evolve, and in which direction and how quickly evolution will proceed is not obvious. The importance of fishing relative to other forces causing phenotypic changes is also difficult to assess (Enberg et al., 2012). Change in size at maturity may be governed by several biotic and abiotic factors. Reduced population abundance (density) can make more food available for individual fish, leading to an increase in growth rate and thus to maturation at a younger age. Higher temperature can also influence growth rate and cause maturation at younger age and smaller sizes. Different mortality rates can select for variation in size of maturity, and if maturation takes place at a higher age, a high mortality rate will reduce survival to reproductive age. Change in size at maturity is a long-term process and was not expected to be observable during the period of this study.

There has been a reduction in number of spawning events in the female red king crab in Norwegian fjords. In 1994 the mean CL for a female was 135 mm, equivalent to five spawning seasons after the onset of maturation. In 2011, however, the mean length for an ovigerous female was 117 mm, which is equivalent to only 1.6 spawning events on average. This means that there has been a major reduction in the number of spawning events for an average female in the course of only 18 years, representing about 3.5 generations.

The observed reduction in size range of females during the study period took place before the onset of fishing for females, and fell further when the quota for females was implemented. The reduction of large sized males, due to size-selective fishing, seems to have had an impact on the survival of the females. It is therefore necessary to examine the interdependence of male and females when discussing reductions in the number of large female crabs. Availability of males is important for females since the female crab requires the presence of a male during the mating event (Powell and Nickerson, 1965; Kruse, 1993). This is different from the reproductive biology of brachyuran crabs (Botsford, 1991), where the females are less dependent on the presence of a male since they can store sperm. It has been shown that the ratio of males to females in the stock is of less significance for the red king crab, since it is assumed that one male can mate with several females within the same mating season (e.g. Powell et al., 1974). However, the presence of males is also important during the female moulting prior to spawning (paper III). A lack of males may therefore lead to increased female mortality. Two studies by Powell and Nickerson (1965) and Powell et al. (1974) have shown that in the wild, the average CL of mating males was 32-42 mm larger than that of their female partners, which indicate that the relative size of males is of significance for mating success. The physiological and morphological size at maturity of male crabs is shown to be 20-15 mm smaller than that of functional maturity (Powell and Nickerson, 1965; Powell et al., 1974; Schmidt and Pengilly, 1990). This may help to protect newly moulted females from being preyed on. A reduction in the abundance of large females may also have a major impact on the reproductive potential of the stock.

5. Concluding remarks

This PhD study has provided new knowledge about size at maturity in female red king crabs and on the status on individual fecundity and the reproductive potential of the stock. Size at maturity has been stable throughout the period studied and the large size is probably due to good growth conditions and is not influenced by change in the level of exploitation. The significant reduction in individual fecundity and the change in the female size range probably have an impact on potential recruitment in the stock. An east to west size gradient was seen among the three fjords studied, and may be related to dispersal direction. Given the life-history traits described for the red king crab in Norwegian waters, with large size at maturity and large body size, and the relatively low minimum legal size, this will make the red king crab more vulnerable to harvesting pressure than species with faster life-history traits. It is vital to continue observation of the development in the life-history parameters of the red king crab stock, both because it is an introduced species and its status as a fishery resource. Any change in these parameters can be seen as early warning signs of decline for the stock.

The fishery for crabs contributes very little to global landings of marine recourses but can be a very valuable fishery (Jennings et al., 2001; King, 2007). This also applies to the red king crab fishery in Norwegian waters. Red king crab landings in 2011 had ex-vessel value of 150 million NOK. At present, there is a high exploitation rate of males and probably also of females, since the legal size for both sexes is as low as 130 mm CL. Size at maturity has remained stable during the period of this study and will probably not influence the recruitment, since the size at maturity for females is about 20 mm lower than the legal size. But the size at maturity given, will contribute to a further potential dispersal of both larvae and adults out of the commercial area. The observed reduction in individual fecundity is probably due to a high harvest rate of large males. However, todayôs minimum legal size (130 mm CL) and high harvest rate may involve a risk for future recruitment failure in the commercial area. On the other hand, it may also help to reduce further spread of the crab. The reduced individual fecundity, together with the reduction in size range among large ovigerous females, leads to reduced reproductive potential for the stock. This is probably due to both a high harvest rate on males combined with a low minimum legal size (130 mm CL) and the harvest at females. This may influence future recruitment and thereby jeopardise the aim of maintaining a stable long-term fishery. However, reduced potential recruitment would contribute significantly to further spread of the crab.

The focus on further spread of the crab was first included in the monitoring programme 31 years after the first catch of red king crab in Norwegian waters. The two goals today are *a*) a long-term predictable fishery and *b*) prevention of further spread of the crab. On one hand it is necessary with a high abundance of crabs to maintain a fishery, whilst an abundant stock of crabs increase the possibility for further spread, especially in the border areas. The knowledge gained through this study therefore appears to be fundamental, regardless of goals. Knowledge on reproductive parameters is essential for management, and shows how challenging it is to combine the two goals set in the Norwegian management regime.

6. References

Anon., 1978. Det Kgl. Utenriksdepartement, Overenskomster med fremmede stater 1978; Oslo 1978, "Avtale mellom Norge og Sovjetunionen om en midlertidig praktisk ordning for fisket i et tilstøtende område i Barentshavet. (In Norwegian).

Anon., 2007. Stortingsmelding nr 40 (2006-2007) Management of red king crab. Whitepaper from the Ministry of Fisheries and Coastal Affairs Det kongelige fiskeri-og kystdepartement:144 pp.

Allendorf, F.W., Luikart, G., 2007. Invasive species. Conservation and the genetics of populations Blackwell Publishing Ltd.

Amundsen, P.-A., Salonen, E., Niva, T., Gjelland, K., Præbel, K., Sandlund, O., Knudsen, R., Bøhn, T., 2012. Invader population speeds up life history during colonization. Biol Invasions:1-13.

Anger, K., 2006. Contributions of larval biology to crustacean research: a review. Invertebr. Reprod. Dev. 49:175-205.

Botsford, L.W., 1991. Crustacean egg production and fisheries management. In: Abele, L.G. (Ed.), The Biology of Crustacea. Academic Press, pp. 379-394.

Brockerhoff, A., McLay, C., 2011. Human-mediated spread of alien crabs. In: Galil B.S., Clark P.F., Carlton J.T., (Eds.) In the Wrong Place - Alien Marine Crustaceans: Distribution, Biology and Impacts. Invading Nature - Springer Series in Invasion Ecology 6, DOI 10.1007/978-94-007-0591-3.2

Chapple, D.G., Simmonds, S.M., Wong, B.B.M., 2012. Can behavioral and personality traits influence the success of unintentional species introductions? Trends Ecol Evol. 27:57-64.

Dew, C.B., 1990. Behavioral ecology of podding red king crab, *Paralithodes camtschatica*. Can J Fish Aquat Sci. 47:1944-1958.

Dew, C.B., McConnaughey, R.A., 2005. Did trawling on the brood stock contribute to the collapse of Alaska's king crab? Ecol. Appl. 15, 919-941.

Enberg, K., Jørgensen, C., Dunlop, E.S., Varpe, Ø., Boukal, D.S., Baulier, L., Eliassen, S., Heino, M., 2012. Fishing-induced evolution of growth: concepts, mechanisms and the empirical evidence. Mar Ecol. 33:1-25.

Grant, W.S., Merkouris, S.E., Kruse, G.H., Seeb, L.W., 2011. Low allozyme heterozygosity in North Pacific and Bering Sea populations of red king crab (*Paralithodes camtschaticus*): adaptive specialization, population bottleneck, or metapopulation structure? ICES J Mar Sci. 68:499-506.

Hammer, C., von Dorrien, C., Hopkins, C.C.E., Koster, F.W., Nilssen, E.M., St John, M., Wilson, D.C., 2010. Framework of stock-recovery strategies: analyses of factors affecting success and failure. ICES J Mar Sci. 67:1849-1855.

Hilborn, R., Walters, C., J., 1992. Quantitative Fisheries Stock Assessment: Chapman and Hall. p 570.

Jennings, S., Kaiser, M.J., Reynolds, J.D., 2001. Marine Fisheries Ecology. Blackwell Publishing, p. 417.

Jørgensen, C., Enberg, K., Dunlop, E.S., Arlinghaus, R., Boukal, D.S., Brander, K., Ernande, B., Gardmark, A., Johnston, F., Matsumura, S., Pardoe, H., Raab, K., Silva, A., Vainikka, A., Dieckmann, U., Heino, M., Rijnsdorp, A.D., 2007. Ecology - Managing evolving fish stocks. Science. 318:1247-1248.

Jørstad, K.E., Smith, C., Grauvogel, Z., Seeb, L., 2007. The genetic variability of the red king crab, *Paralithodes camtschatica* (Tilesius, 1815) (Anomura, Lithodidae) introduced into the Barents Sea compared with samples from the Bering Sea and Kamchatka region using eleven microsatellite loci. Hydrobiologia. 590:115-121.

King, M., 2007. Fisheries Biology, Assessment and Management. Blackwell Publishing, p 382.

Kruse, G.H, 1993. Biological perspectives on crab management in Alaska. In: Kruse, G.H., Eggers, D.M., Marasco, R.J., Pautzke, C., Quinn II, T.J. (Eds.), Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations. University of Alaska Sea Grant Rep. 02-01, pp. 305-321.

Kuparinen, A., Merilä, J., 2007. Detecting and managing fisheries-induced evolution. Trends Ecol Evol. 22:652-659.

Kuris, A.M., 1991. A review of patterns and causes of crustacean brood mortality. In: Wenner, A., Kuris, A.s (Eds.), Crustacean egg production, pp. 117-141.

Loher, T., Armstrong, D.A., 2005. Historical changes in the abundance and distribution of ovigerous red king crabs (*Paralithodes camtschaticus*) in Bristol Bay (Alaska), and potential relationship with bottom temperature. Fish Oceanogr. 14:292-306

Marukawa, H., 1933. Biological and fishery research on Japanese king crab *Paralithodes camtschatica* (Tilesius). J. Imp. Fish., Exp. Sta. 4, 123-152.

Morgan, M.J., 2008. Integrating reproductive biology into scientific advice for fisheries management. J Northwest Atl Fish Sci. 41:37-51.

Orensanz, J.M.L., Armstrong, J., Armstrong, D., Hilborn, R., 1998. Crustacean resources are vulnerable to serial depletion - the multifaceted decline of crab and shrimp fisheries in the Greater Gulf of Alaska. Rev Fish Biol Fish. 8:117-176.

Orlov, Y.I., Ivanov, B.G., 1978. On the introduction of kamchatka king crab *Paralithodes camtschatica* (Decapoda: Anomura: Lithodidae) into Barents Sea. Mar. Biol. 48, 373-375.

Oug, E., Cochrane, S.K.J., Sundet, J.H., Norling, K., Nilsson, H.C., 2010. Effects of the invasive red king crab (*Paralithodes camtschaticus*) on soft-bottom fauna in Varangerfjorden, northern Norway. Marine Biodiversity, 1-13.

Pianka, E.R., 1970. On *r*-selection and *K*-selection. Am Nat. 104:592-597.

Poos, J.J., Brannstrom, A., Dieckmann, U., 2011. Harvest-induced maturation evolution under different life-history trade-offs and harvesting regimes. J Theor Biol. 279:102-112

Powell, G.C., Nickerson, R.B., 1965. Reproduction of king crabs, *Paralithodes camtschatica* (Tilesius). J. Fish. Res. Board Can. 22, 101-111.

Powell, G.C., Shafford, B., Jones, M., 1973. Reproductive biology of young adult king crabs *Paralithodes camtschatica* (Tilesius) at Kodiak, Alaska. Proc Natl. Shellfish. Assoc 63, 77-87.

Powell, G.C., James, K.E., Hurd, C.L., 1974. Ability of male king crab, *Paralithodes camtschatica*, to mate repeatedly, Kodiak, Alaska, 1973. Fish. Bull. 72, 171-179.

Reznick, D.N.; Shaw, F.H.; Rodd, F.H.; Shaw, R.G., 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). Science. 275:1934-1937.

Rosecchi, E., Thomas, F., Crivelli, A.J., 2001. Can life-history traits predict the fate of introduced species? A case study on two cyprinid fish in southern France. Freshwat Biol. 46:845-853

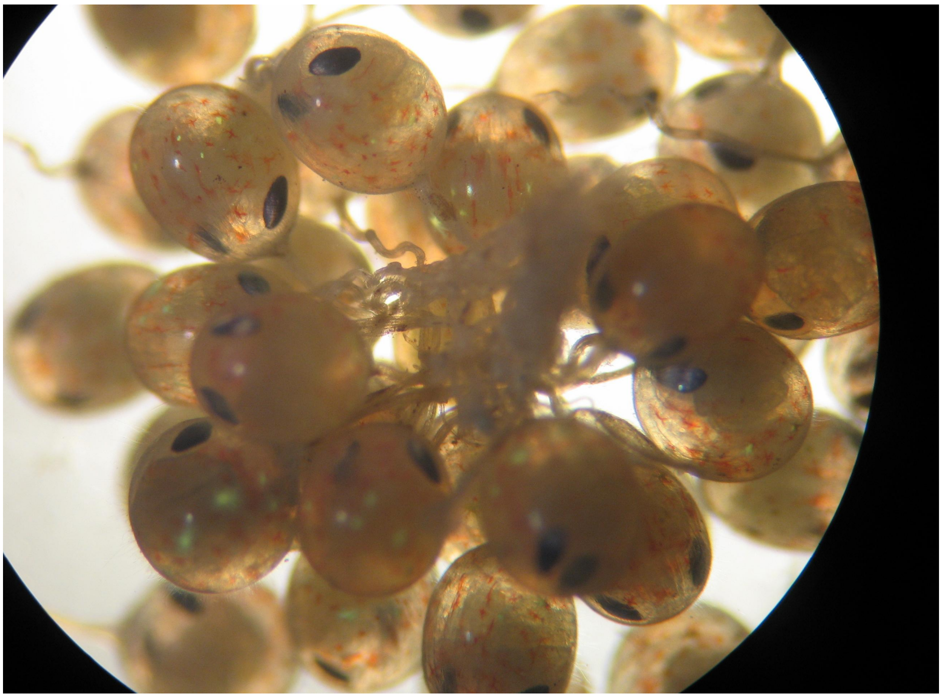
Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M., Thompson, J.N., Weller, S.G., 2001. The population biology of invasive species. Annu Rev Ecol Syst. 32:305-332

Schmidt, D., Pengilly, D., 1990. Alternative red king crab fishery management practice: modelling the effects of varying size-sex restrictions and harvest rates. In: Proceedings

of the International King and Tanner Crab Symposium, University of Alaska Fairbanks. Alaska Sea Grant College Program Rep. 90-04, pp. 551-565.
Stearns, S.C., 1976. Life-history tactics - review of ideas. Q Rev Biol. 51:3-47.
Stearns, S.C., 1992. The Evolution of life histories. Oxford University Press, Oxford, 249 pp.
Stevens, B.G., 2006. Is it possible to enhance king crab populations in Alaska? In: Steven, B.G. (Ed.), Alaska crab stock enhancement and rehabilitation. Alaska Sea Grant College Program, Fairbanks, pp. 79-89.
Stevens, B.G., 2012. Growth of juvenile red king crabs, *Paralithodes camtschaticus*, through sequential molts in the laboratory. J Crust Biol. 32:215-222.
Stone, R.P., OôClair, C.E., Shirley, T.C., 1992. Seasonal migration and distribution of female red king crabs in a Southeast Alaskan Estuary. J. Crust. Biol. 12, 546-560.
Sundet, J.H., Hjelset, A.M., 2010. Seasonal depth distribution of the red king crab (*Paralithodes camtschaticus*) in Varangerfjorden. In: Kruse, G.H., Eckert, G.L., Foy, R.J., Lipicus, R.N., Sainte-Marie, B., Stram, D.L., Woodby, D. (Eds), Biology and management of exploited crab populations under climate change. Alaska Sea Grant, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.20, pp. 403-412.
Swiney, K.M., Long, W.C., Persselin, S.L., 2012. The effects of holding space on juvenile red king crab, *Paralithodes camtschaticus* (Tilesius, 1815), growth and survival. Aquacult Res:1-10
Tibbets, T.M., Krist, A.C., Hall, R.O., Riley, L.A., 2010. Phosphorus-mediated changes in life history traits of the invasive New Zealand mudsnail (*Potamopyrgus antipodarum*). Oecologia 163, 549-559.
Tilesius, W.C., 1815. De Cancris Camtschaticis, Oniscis, Entomostracis et Cancellus marinis microscopicis noctilucentibus cum tabulis IV: Aenaeis et appendice adnexo de Acaris et Ricinis Camtschaticis. Auctore Tilesio. Mémoires de lôAcadémie Impériale de Sciences de St Pétersbourg. 5:75, pl. 75ï 78
Viegas, I., Marques, S.C., Bessa, F., Primo, A.L., Martinho, F., Azeiteiro, U.M., Pardal, M.A., 2012. Life history strategy of a southern European population of brown shrimp (*Crangon crangon* L.): evidence for latitudinal changes in growth phenology and population dynamics. Mar Biol. 159:33-43
Wallace, M.M., Pertuit, C.J., Hvatum, A.R., 1949. Contribution to the biology of the king crab (*Paralithodes camtschatica* Tilesius). US Dept. Interior, Fish Wildl. Serv. Fish. Leaflet 340, 50.
Watters, G., Hobday, A.J., 1998. A new method for estimating the morphometric size at maturity of crabs. Can J Fish Aquat Sci. 55:704-714
Weis, J.S., 2010. The role of behavior in the success of invasive crustaceans. Mar Freshwat Behav Physiol. 43:83-98
Williamson, M., Fitter, A., 1996. The Varying Success of Invaders. Ecology. 77:1661-1666
Zelenina, D.A., Mugue, N.S., Volkov, A.A., Sokolov, V.I., 2008. Red king crab (Paralithodes camtschaticus) in the Barents Sea: A comparative study of introduced and native populations. Russ J Genet. 44:859-866
Zheng, J., Kruse, G.H., 2000. Recruitment patterns of Alaskan crabs in relation to decadal shifts in climate and physical oceanography. ICES J Mar Sci. 57:438-451

Paper I

Paper II



Paper III

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