FACULTY OF BIOSCIENCES, FISHERIES AND ECONOMICS
DEPARTMENT OF ARCTIC AND MARINE ECOLOGY

The invasive red king crab (*Paralithodes camtschaticus*):

Mortality, individual growth and dispersal in Norwegian waters

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Cover illustration

Carina Andreassen

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Kristin Windsland
Tromsø, June 2014

"The only true wisdom is in knowing you know nothing"
Socrates

Summary

With the aim of creating a new coastal fishery resource and improving local economies, the red king crab (*Paralithodes camtschaticus*) was introduced to the Barents Sea by Soviet scientists in the 1960s. The species adapted well to the new environment and in the course of the following decades, the growing population expanded into Norwegian waters, gradually invading new areas along the coast of northern Norway. The estimates of total stock abundance (>70 mm carapace length) have increased from 62,000 in 1994 to 3.8 million individuals in 2013, peaking in 2008 at 5.2 million individuals: the stock now supports a coastal fishery with recent annual landings in excess of 2000 tonnes.

The red king crab has become a valuable marine resource, but as an introduced species, it is also a potential threat to the ecosystem. The Norwegian government has chosen a two-pronged policy for dealing with the red king crab: in the quota-regulated area, the aim is to maintain a stock capable of supporting a commercial fishery. Outside of this area, the aim is to get as close to eradication as possible in order to reduce further spread. To meet these goals, more knowledge about the growth, mortality and dispersal of the species is essential. This thesis includes three papers providing this knowledge.

In paper I, we developed Bayesian hierarchical models to estimate growth parameters of the von Bertalanffy growth function using tag-recapture data. We showed that the inclusion of individual variability in these models was important and led to more realistic values for the growth parameters and improved accuracy of length estimates. The models successfully estimated red king crab lengths at intervals where data were sufficient. However, the length-at-relative age of small males were overestimated, while those of small females were not. This is believed to be due to differences in growth patterns after maturity.

In paper II, we explored the dispersal behaviour and extent of dispersal of red king crab in Norwegian waters. The results indicated that the range expansion of this species is a result of both the existence of long-distance dispersers and time-dependent slow migration by short distance-dispersers and that there is a substantial dispersal of crabs out of the quota-regulated area.

In paper III, estimates of annual total mortality (Z) were calculated using length-converted catch curves in three time-periods that represented different levels of exploitation. Natural mortality was estimated using a linear regression of total mortality and exploitation rate and by using indirect methods based on life-history parameters. There was a steady increase in total mortality rates (Z) from period I to period III, which for males were

consistent with the increase in exploitation rate. The increase in female mortality was not consistent with exploitation history but is rather believed to be a result of the deficit of large males. Male red king crab protects females from predation during and directly after moulting. With a deficit of large males, large females are more vulnerable to predation. The estimates of natural mortality ranged from 0.23-0.44 year^{-1}; the larger values are probably an overestimate due to unaccounted bycatch mortality while the lower ones are consistent with life-expectancy.

The open fishery and decimation fishery outside the quota-regulated area most likely contributed to the reduction in the rate of range expansion. In order to reduce spread in the future it is essential to continue these efforts. It is equally important to keep the stock of red king crab at a low level. However, care must be taken to ensure that the stock does not fall to a level where it is unable to support the commercial fishery. Without the commercial fishery, the stock would be able to increase in both number and range, posing a future threat to the native ecosystem.

List of publications and manuscripts

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

Paper I:

Evaluation of von Bertalanffy growth curves for the introduced red king crab (*Paralithodes camtschaticus*) in Norwegian waters.Windsland, K., Hvingel, C., Nilssen, E. M., Sundet, J. H., 2013. Fisheries Research 145: 15-21.

Paper II:

Dispersal of the introduced red king crab (*Paralithodes camtschaticus*) in Norwegian waters: a tag-recapture study. Windsland, K., Hvingel, C., Nilssen, E. M., Sundet, J. H. 2014. ICES J. Mar. Sci. doi: 10.1093/icesjms/fst241

Paper III:

Total and natural mortality of red king crab (*Paralithodes camtschaticus*) in Norwegian waters: Catch curve analysis and indirect estimation methods. Windsland, K., submitted to ICES Journal of Marine Science.

1 Introduction

The red king crab (*Paralithodes camtschaticus*) is native to the North Pacific Ocean and the Bering, Japan and Okhotsk Seas (Orlov and Karpevich, 1965; Pedersen *et al.*, 2006). In the Bering Sea and Gulf of Alaska it has been one of the most economically important species for decades. With the intention to create a new fishery resource and improve local economies, Soviet authorities initiated a program to transport and release red king crab adults and larvae into the Barents Sea between 1961 and 1969. A total of 1,655 egg-bearing females, 954 large males, 10,000 juveniles (age 1-3) and 1.5 million stage I zoeas were released mainly in the Kol'skij Zaliv region close to Murmansk (Orlov and Ivanov, 1978). The species adapted well to the Barents Sea environment, and during the following decades the growing population expanded into Norwegian waters (Anisimova *et al.*, 2005). The first red king crab in Norwegian waters was caught in Varangerfjorden in 1977 as bycatch in fisheries directed at other species (Orlov and Ivanov, 1978). As the population grew in the following years, bycatches in traditional fisheries increased proportionally. In the 1990s, bycatch of red king crab had become a serious problem for the gillnet and longline fisheries, causing damage to gear, reducing gear efficiency and increasing the work load of fishermen (Sundet and Hjelset, 2002). The total stock estimates (> 70 mm carapace length) in Norwegian waters rose from 62,000 in 1994 to 3.8 million in 2013, peaking in 2008 at 5.2 million individuals (Hjelset, 2014) and the stock now supports a coastal fishery with recent annual landings in excess of 2000 tonnes (Hvingel *et al.*, 2012). The annual catch quotas are set as a percentage of the overall survey biomass estimate (Hvingel *et al.*, 2012). A directed fishery for red king crab started as a research fishery in 1994 (Anon., 2007). The commercial fishery started in 2002 and exploitation rate (catch/stock size) increased along with the stock estimates; from 13 % in 2002 to 75 % in 2013 with a peak in 2009 at 95 % (Anon., 2013).

The paradigm of r-selected and K-selected species is used to describe the amount of parental investment and the quantity and quality of offspring. While r-selected species maximize their reproductive potential, K-selected species has evolved toward the most efficient use of their environment (Pianka, 1970). K-selected traits like slow growth and delayed reproduction (Hjelset *et al.*, 2009) make the red king crab vulnerable to recruitment overfishing (Loher *et al.,* 1995). In order to prevent this, the red king crab stock has been subjected to male-selective harvesting in both native (Zheng *et al.*, 1997) and invaded areas (Anon, 2007). Until recently, a "3S" regime (size, sex and season) was used as a management tool. Only males (until 2008) with a carapace length greater than 137 mm (reduced to 130 in

2011) could be legally harvested during a limited fishing season. However, Otto *et al.* (1990) showed that an imbalance in sex ratio may place constraints on the reproductive success of the species; see also Hjelset (2013). The red king crab may therefore be vulnerable to recruitment overfishing in spite of low exploitation of females.

Since its introduction to Murmansk waters in the 1960s, the red king crab has spread to Norwegian waters (Fig 1). In the early 90s, Varangerfjorden, to the west of the Russian border, was the first area to be colonized by the red king crab. From there it continued to spread west, reaching Tanafjorden in the mid 90s, while Laksefjorden, Porsangerfjorden and areas west of North Cape followed in the late 90s.
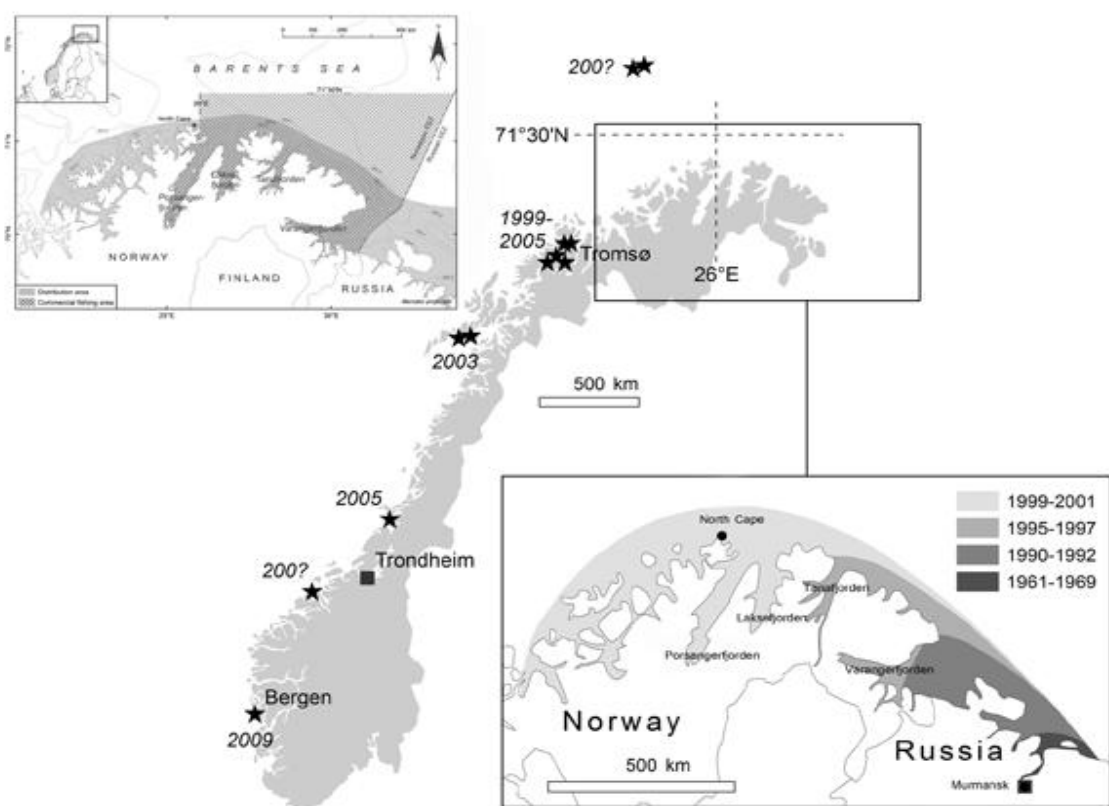

Fig. 1: Map of current distribution area (grey area), quota-regulated area (crosshatched area) and range expansion of red king crab (*Paralithodes camtschaticus*) from its introduction in the 1960's. Star indicates observations that may be result of human-mediated dispersal. "?" indicates that the exact year of observation is uncertain.

A study on advection of red king crab larvae along the coast of northern Norway revealed a net transport in the eastward direction, carried by the eastbound Norwegian Atlantic and Norwegian Coastal Current (Pedersen *et al.*, 2006). There is also a dispersion of

larvae in westbound direction but this is small compared to the eastbound dispersion. In native areas, juvenile red king crabs (24-69 mm carapace length) are found all year round in shallow waters, forming pods with crabs of similar size (Powell and Nickerson, 1965). Both males and females are found in the same pod. When they reach maturity, they begin an annual cycle of movements (Powel and Reynolds, 1965). Mature males begin their shoreward movements in November and moult en route to the mating grounds in shallow waters (Powell, 1964). Females follow in early spring and moult at the mating grounds after paring up with males (Bright, 1967; Marukawa, 1933; Powell and Nickerson, 1965b; Stone *et al*., 1992; Wallace *et al*., 1949). Moulting is followed by mating, after which the crabs return to the feeding grounds in deeper waters. During the feeding migrations, males and females are again separated and remain so until the next mating season (Wallace *et al*., 1949). The same pattern is observed in Norwegian waters (Sundet and Hjelset, 2010). Mature males are found in deeper areas from June through September, while females are observed in deeper waters from June to November.

According to Williamson and Fitter (1996), only 10 % of all introduced species succeed in the establishment of a new populations. Propagule pressure, the number of individuals released into a region to which they are not native, is a key element to understand why some species succeed in establishment whereas other fail (Lockwood *et al*., 2005). The programme for transplanting king crab to the Barents Sea began in the 1960s, and was a continuation of a process started more than 30 years earlier. But while all previous attempts had failed, new long-distance transportation facilities led to increased survival during transport, and thereby greater propagule pressure (Kuzmin *et al*., 1996). Furthermore, the red king crab possesses many of the qualities of a successful invader (Ehrlich, 1986). It is capable of surviving in a wide range of physical conditions (Jewett and Onuf, 1988) and it has a high level of genetic variability (Jørstad *et al*., 2007), suggesting a high potential for adapting to new environments. Its reproductive potential is also high (Otto *et al*., 1990; Hjelset *et al*., 2012). The successful invasion and subsequent range expansion of red king crab should therefore come as no surprise.

The red king crab has become a valuable marine resource but as an introduced species, it also poses a potential threat to the ecosystem (Jørgensen and Primicerio, 2007; Oug *et al*., 2011). The effect of red king crab on the epifauna and infauna of Varangerfjorden was evaluated by Oug *et al*. (2011) who found a reduction in abundance of soft-bottom epifauna and infauna. In addition, the sediment habitat quality was degraded due to hypoxic conditions and low biological activity below the surface layers. The results suggest that the red king crab

reduces the functional diversity of the resident species assemblages by removing organisms that perform important functions such as bio-irrigation and sediment reworking. Due to its negative ecological effect on native communities, eradication of the species has been considered. However, this is not a feasible option due to the size and range of the stock off the coasts of Northern Norway and Russia. Instead, the Norwegian government has chosen a two-pronged policy for dealing with the red king crab: in the quota-regulated region (Fig 1), the aim is to maintain a stock capable of supporting a commercial fishery. Outside this region the aim is to keep this part of the stock as low as possible in order to reduce further spread.

2 Main objectives and approach

2.1 Objectives

In stock assessment, two alternative approaches are used, depending on the availability of data. While synthetic methods use the theoretical relationship between the level of fishing intensity and the total catch, analytical methods rely on the relation between recruitment, growth and mortality (Garcia and Cochrane, 2005). For a more complete assessment the following biological information is needed: the age structure of the stock, age-at-maturity, fecundity (average number of eggs each animal can produce), sex ratio, natural mortality rate (M), fishing mortality rate (F), growth rate, spawning behaviour, habitats of larvae, juveniles and adults, migratory habits, food preferences and an estimate of the total number or weight of individuals in the stock (Wallace and Fletcher, 2001). Studies in recent years have shed some light on the parameters of red king crab reproduction (Hjelset, 2013; Hjelset *et al*., 2009; Hjelset *et al*., 2012), and a study by Nilssen and Sundet (2006) provided growth increment and moulting probabilities. However, our knowledge of dispersal (emigration and immigration), mortality (both fishing and natural) and individual growth curves including growth parameters is still either meagre or completely lacking. Filling this knowledge gap would be a great step towards an optimal management of the red king crab as they are important regulating factors of stock size (Fig. 2). The biomass of a population of any given species is affected by several factors. Factors that increase the biomass include recruitment, individual growth and immigration while emigration, fishing mortality and natural mortality reduce it.

In this thesis, I present three papers which give new knowledge about dispersal, individual growth and mortality using data from annual scientific cruises along the coast of Northern Norway (Fig. 1) from 1994-2013. I hope that the result of this work will be useful tools for maintaining adequate management of the red king crab stock.
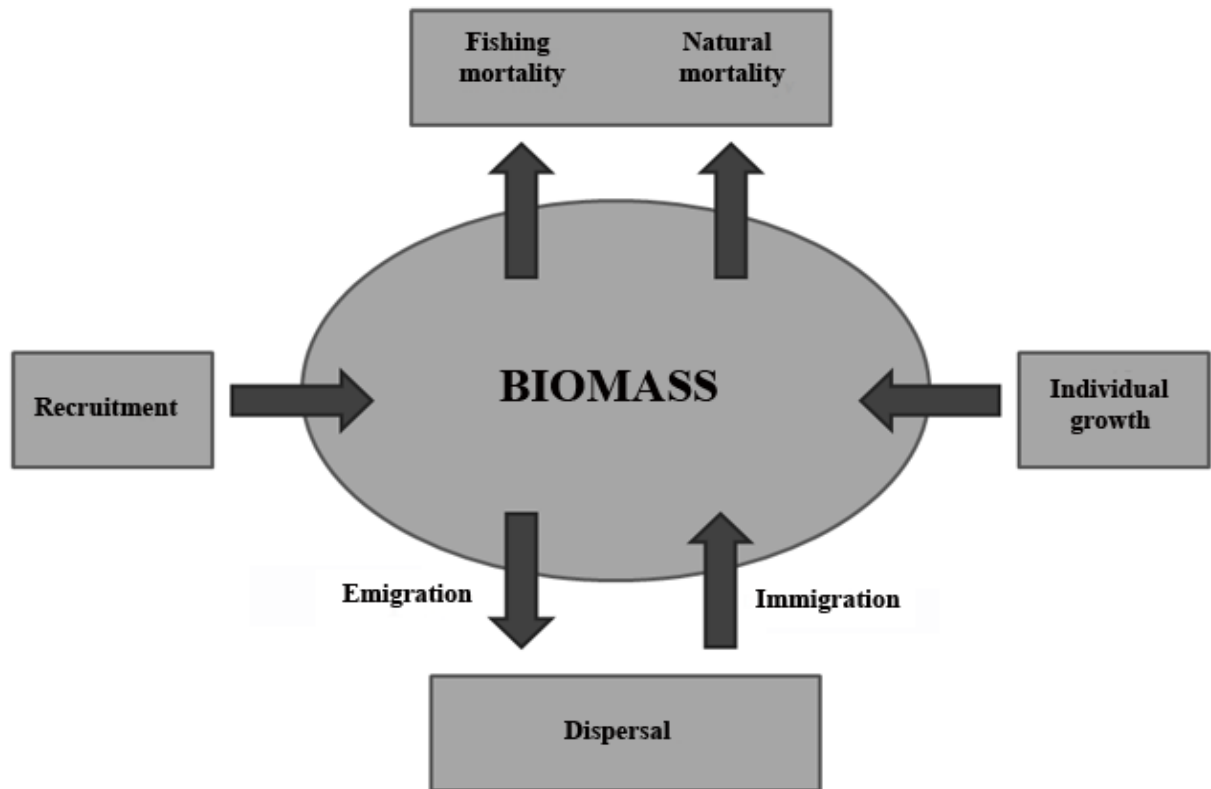
Fig. 2: Factors regulating the biomass of a population in a given area.

2.2 Approach

In paper I, we developed Bayesian hierarchical models to estimate growth parameters, L_∞ (asymptotic length) and k (von Bertalanffy growth coefficient) of the von Bertalanffy growth function using tag-recapture data. We constructed separate growth curves for males and females. Since the parameter t_0 cannot be estimated from tagging data alone when age is unknown (Wang, 1998; Zhang *et al*., 2009) we had to assume that $t_0 = 0$. The growth curves therefore provide length at relative ages. Substantial bias in the estimates of L_∞ and k may appear when individual variability is ignored (Wang and Ellis, 1998; Chang *et al*., 2012). We therefore explored the effect of individual variability on the estimation of growth parameters.

In paper II, we explored the effect of sex, size, region and density on the dispersal rate of red king crab in Norwegian waters using a logistic regression analysis. Tag-recapture data corrected for fishing effort enabled us to estimate dispersal rates from four main regions along the Norwegian coast; Varangerfjorden, Tanafjorden, Laksefjorden and Porsangerfjorden. We further compare our results with dispersal in native areas.

In paper III, annual total mortality (Z) was estimated using length-converted catch curves in three time periods representing different levels of exploitation. Separate analyses were run on trap and trawl data as well as on original and CPUE-corrected data. Natural mortality (M) was estimated using a linear regression of total mortality and exploitation rate and by using indirect methods based on life-history parameters. Fishing mortality was estimated by subtracting M from Z.

3 Summary of results

3.1 Paper I: Individual growth

The importance of including individual variability was confirmed: Variability in L_∞ for individuals was high compared to population variability in L_∞. The model that incorporated individual variation produced values for the growth parameters that were more in tune with observed values and increased the precision of length estimates compared to the model that estimates a common L_∞. The models successfully estimated red king crab lengths at intervals where data were sufficient. However, the lengths of small males were overestimated, whereas the lengths of small females were correctly estimated.

3.2 Paper II: Dispersal

The probability of dispersal was independent of sex and size, but both the logistic regression and the evaluation of corrected tag-recapture data revealed differences in dispersal between regions and with increasing duration. The recapture data indicated a relationship between population density and dispersal within study regions, but not between population density and dispersal between study regions. There are large individual differences in dispersal ability and the range expansion of red king crab is a result of both the presence of long-distance dispersers and time-dependent slow migration by short distance-dispersers. There appears to be less dispersal in Norwegian waters than in native waters, which might be caused by differences in geographical complexity. Recaptures of animals tagged in later years show a substantial dispersal of crabs out of the quota-regulated region. This movement of animals between two areas with very different management regimes and goals offers a challenge to managers, as abundance in one area is not independent of abundance in the other.

3.3 Paper III: Mortality

Total mortality (Z) was estimated for three different time periods: 1995-2001, 2002-2007 and 2008-2012. Analyses of trap and trawl data using both uncorrected data and data corrected for CPUE revealed a steady increase in Z with period. In males, the increase coincided with the increase in exploitation level. The increase in female Z, which was not explained by exploitation level, is probably an effect of the increase in male mortality. The estimated M using linear regression of Z as a function of exploitation rate was 0.37 and 0.44 (for trap and trawl data, respectively) which is probably an overestimate. The indirect

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estimates of natural mortality (M) for both males and females averaged at 0.23 year^{-1}, which is consistent with life expectancy. Subtracting estimates of M from estimates of Z resulted in estimates of fishing mortality (F) in the range of 0.62-0.84 year^{-1} in period III. There has been a steady decline in stock of legal males (> 137 mm carapace length) since 2004, which appears to coincide with the increase in exploitation level (% of legal male abundance harvested).

4 General discussion

In paper I, we constructed von Bertalanffy growth curves for male and female red king crab in the Barents Sea that provides length at relative ages. Literature describing native areas states that males and females grow at the same rate until they reach sexual maturity (Dew, 1990; Loher *et al.*, 2001). Assuming that this is true in the Barents Sea also, male red king crab should reach morphological maturity at 110 mm, same as Barents Sea females (Hjelset *et al.*, 2009). According to the estimated growth curves (paper I), this corresponds to relative ages of 40 and 60 months for males and females, respectively. In other words, according to the growth curves, juvenile males grow faster than females, which is not consistent with literature (Powell, 1967; McCaughran and Powell, 1977; Loher *et al.*, 2001). However, the size-at-relative age of small males were overestimated by the growth curve while the growth curve for females fitted the data well. The difference in fit may be a result of different growth patterns after maturity: mature females moult every year with an increment of 5 mm while males have an increment of 15 mm per moult but start skipping moults as they grow larger (Nilssen and Sundet, 2006).

McCaughran and Powell (1977) constructed stochastic growth curves for red king crab in the Kodiak Island region in the Pacific Ocean by combining two sub-models: (1) growth increment as a function of premoult length and moulting history and (2) a probabilistic model of frequency of moulting by age, premoult length, and moulting history. This resulted in carapace length-at-age for male and female red king crab. The growth curves constructed in paper I present size at a <u>relative</u> age, instead of actual age, by assuming that $t_0 = 0$. Shifting the growth curves 1 and 2 years for females and males, respectively, allows the growth curves from the two areas to be compared. Both the female growth curves and the growth curves of adult males were very similar in Norway and the Pacific (Fig. 3). However, the overestimation of length-at-age of smaller males in my material becomes evident; the slope of the beginning of the curve is considerably steeper than both male and female curves from the Bering Sea (McCaughran and Powell, 1977) and the female curve from the Barents Sea. The close fit between the growth curves from the two areas is consistent with literature that shows that the growth rate of Barents Sea red king crab is comparable to that of Bering Sea red king crab, although there were indications that growth of immature crabs might be slightly less than in native areas (Rafter *et al*. ,1996; Nilssen and Sundet, 2006).

Size and age-at-maturity around Kodiak Island in the Pacific Ocean is approximately 100 mm and 5 years (Powell and Nickerson, 1965b; McCaughran and Powell, 1997, Pengilly *et al.*, 2002; Powell *et al.*, 2002), while Bristol Bay red king crab mature at 89-105 mm and 6-7 years (Wallace *et al.*, 1949; Otto *et al.*, 1990; Zheng *et al.*, 1995; Loher *et al.*, 2001). Thus, females in the Barents Sea mature at a larger size (110 mm) than in native areas, which could be due to differences in crab density, food availability and exploitation rates (Hjelset *et al.*, 2009). This attempt to convert the relative ages of the growth curves to absolute ages indicates that Barents Sea red king crab reach maturity at 5-6 years.
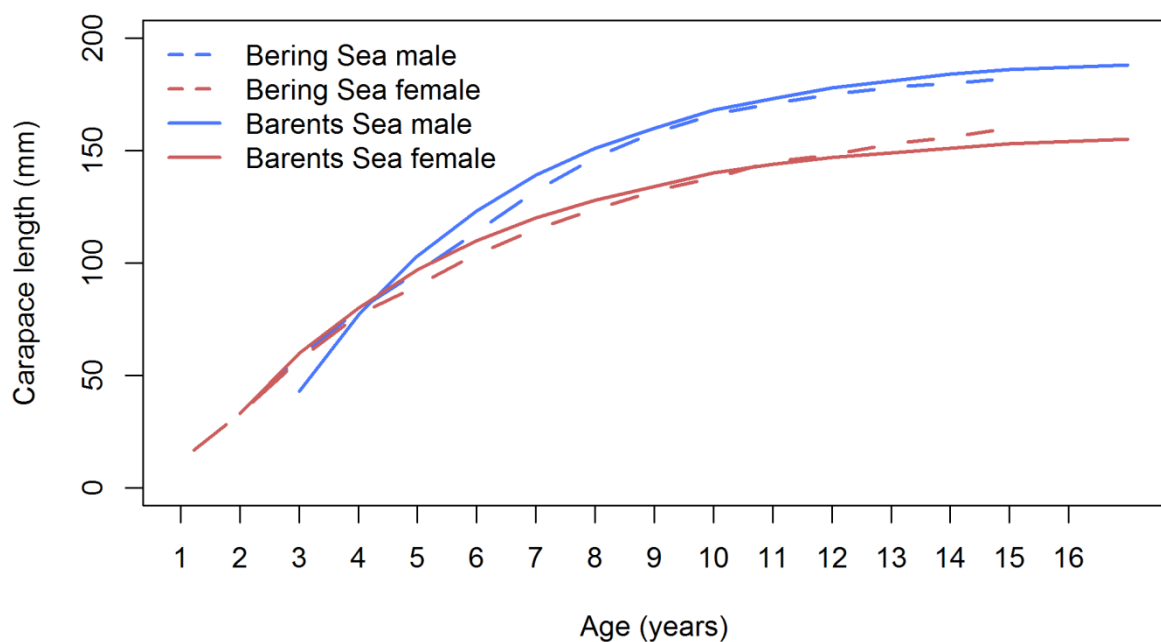

Fig. 3: Length-at-absolute age of male (blue lines) and female (red lines) red king crab in the Bering Sea (broken lines) (McCaughran and Powell, 1977) and length-at-relative age (+1 and 2 years for females and males, respectively) of male and female red king crab in the Barents Sea (solid lines) (paper I).

Assuming that Barents Sea males mature at 110 mm carapace length, they reach maturity at a relative age of 40 months (paper I). Until 2011 they were targeted in the fishery from 137 mm, which corresponds to 59 months. From 2011 the lower size limit was reduced to 130 mm, corresponding to 53 months. This means that they reach maturity less than two years before entering the commercial fishery. Furthermore, studies in the Bering Sea suggest that males do not mate until they reach 120-130 mm (Powell and Nickerson, 1965b; Pengilly and Schmidt, 1995) as male crabs in mating pairs need to be larger than their female partners.

This means that male red king crab will barely reach functional maturity before they enter the fishery. Furthermore, only 50% of mature males are believed to mate in any given as they do not mate and moult within the same year (Fujita *et al.*, 1973, Dew and McConnaughey, 2005). The general consensus in the native areas has been that an imbalance in sex ratio places no constraints on reproductive success (Otto, 1985 in Dew and McConnaughey, 2005). However, Wada *et al*. (2000) showed that a male to female ratio of 0.17 inhibited reproduction of spiny king crab (*Paralithodes brevipes*). In Bristol Bay in 1982, when the male to female ratio of red king crab was 0.16 (Dew and McConnaughey, 2005), a substantial proportion of mature females, large females in particular, failed to reproduce *(*Otto *et al.*, 1990).

The current management of red king crab thus faces major challenges. The initial minimum legal size ensured that each male crab could participate in two mating seasons before being targeted by the fishery (Anon., 2007). With the reduced minimum legal size and the fact that male crabs do not mate and moult in the same year, some males may not get to participate in mating at all before being targeted by the fishery. A deficit of males in the population could mean that not all females are able to reproduce, which in combination with the observed reduction in individual fecundity of females in Norwegian waters (Hjelset *et al*., 2012), could impede recruitment.

According to Williamson (1996), there are three phases to an invasion: 1) arrival and establishment; 2) spread; and 3) equilibrium. In phase one, the species arrives and establishes a viable and permanent population in which little dispersal from the introduction site occurs (the lag effect, Crooks and Soulé, 2001). In phase two, the species spreads and expand its range. During a biological invasion, the expanding front will be dominated by individuals with better dispersal abilities, which in course of several generations will lead to a selection of traits that increase dispersal rates (Alford *et al*., 2009; Travis *et al*., 2009). In phase three, there is a deceleration of range expansion caused by either geographical limits or environmental and biotic constraints on growth, reproduction or dispersal as the habitat becomes saturated (Williamson, 1996; Shigesada and Kawasaki, 1997; 2002, Lyons and Scheibling, 2009). In the equilibrium/saturation phase the population ceases to increase in numbers and range (Williamson, 1996). The relationship of rate of range expansion and time can thus be explained by a sigmoid curve (Fig. 4), which is well documented for aquatic species (Kelly *et al*., 2014).
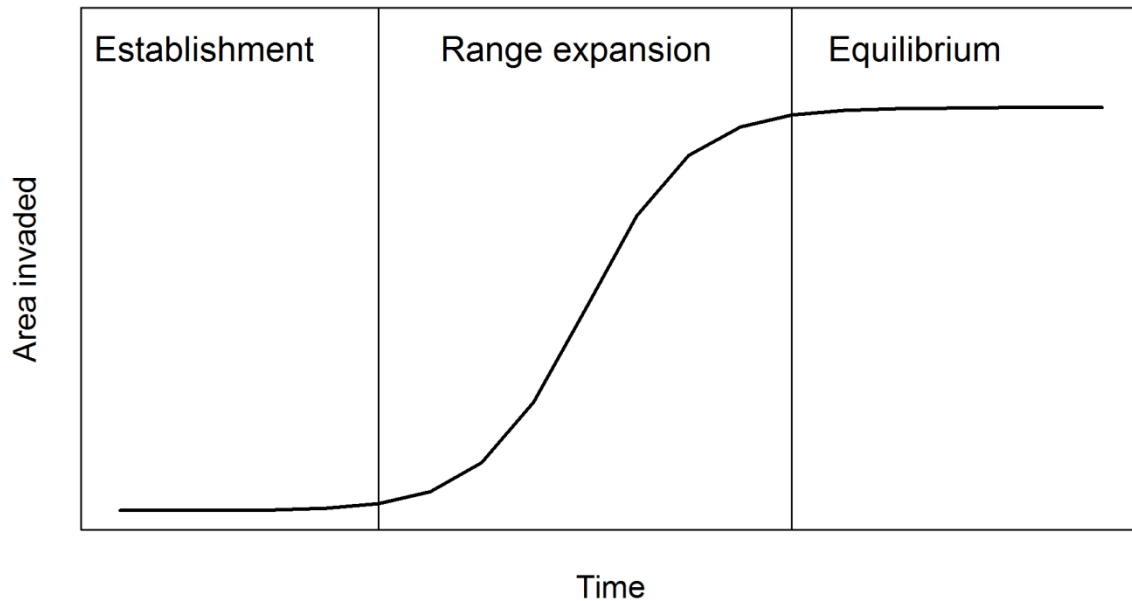
Fig. 4: Three phases to an invasion: 1) arrival and establishment; 2) spread and range expansion; and 3) equilibrium.

The history of range expansion of red king crab is a perfect match to dispersal theory. After its introduction to the Murmansk area in the 1960s, the red king crab was in the establishment phase: it took 20 years before it became common in Varangerfjord (Fig. 1). Then there was an acceleration in dispersal rates; after five years it was common in Tanafjord and a few years later the population had spread to Laksefjorden and Porsangerfjorden. There were also occasional observations west of the North Cape. Then there was a sudden reduction in the rate of expansion (equilibrium phase). Since 2002, the rate of range expansion has been less than in earlier periods, and the distribution of red king crab has not increased since 2009 (Hjelset, 2014). Such a reduction has several possible causes. The red king crab has not met any geographical boundaries, and with its wide temperature and salinity tolerances (Jewett and Onuf, 1988), it should not be restricted by the physical environment. Saturation dispersal occurs when a population reaches a threshold density determined by, for example, limited food supply (Stenseth and Lidicker, 1992). Commercial exploitation of a species may reduce the population to a point at which competition for food is low enough to avoid dispersal. The commercial fishery started in 2002, and from 2004 onwards, there was a reduction in the population of adult males (Fig. 5). There was a correlation between dispersal rate and population density of red king crab in Varangerfjord (paper III) which suggests that increased food availability could be part of the explanation.

Another possible explanation is the effort of the open fishery and decimation fishery outside the quota-regulated area. The open fishery started in 2004 and has been responsible for the large removal of individuals, of both sexes of all sizes, and fishing is permitted throughout the year. The decimation fishery started in 2010 and fishermen are paid to fish in areas where abundances are too small to make a profit.
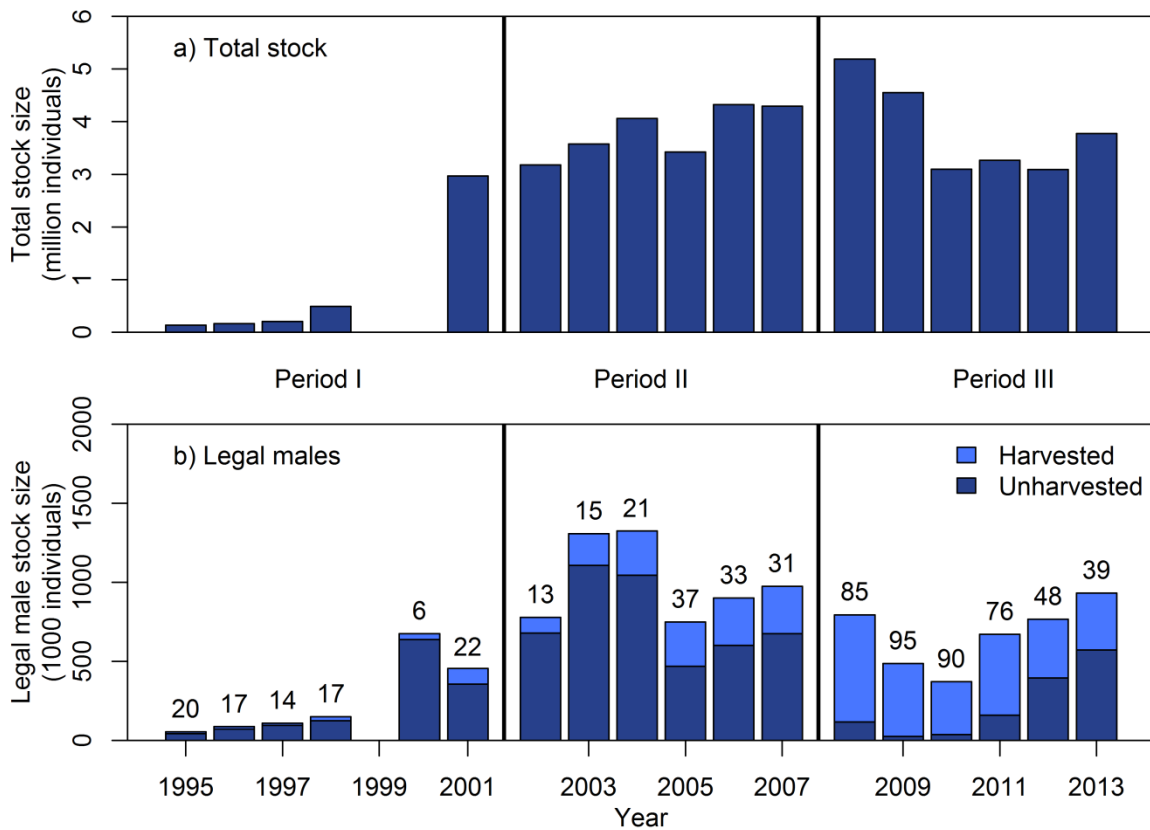

Fig. 5: a) Total stock size of red king crab (> 70 mm carapace length) in Norwegian waters in three time periods of different exploitation levels and b) harvested and unharvested parts of the legal male population (> 137 carapace length in 1995-2010; 130 from 20011) in the Norwegian red king crab fishery in the quota-regulated area. Numbers above bars represents exploitation rate (% of legal male abundance harvested).

Study of the dispersal of red king crab (paper II) may shed some light on as to why the range expansion halted. Empirical data on dispersal are often leptokurtic (with more propagules near the centre and in the tails than in a normal distribution of comparable mean and variance) (Kot *et al*., 1996). This distribution, which is seen in many decapods species (Hines *et al*., 1995; Freire and Gonzalez-Gurriaran, 1998; Taggart *et al*., 2008), has also been

observed in the dispersal distances of red king crab; while most animals disperse only short distances within a year, some individuals move long distances within a relatively short period of time (paper II). It is natural to assume that these long-distance dispersers are responsible for the range expansion of red king crab. However, in a logistic regression, the time between tagging and recapture was found to have a significant effect on dispersal probability, and of all animals that were recaptured more than three years after tagging, 56 % had left their tagging region. The conclusion of the study was that the range expansion of red king crab is caused by both the presence of individual crabs with great migratory abilities and a general "slow migration" that is time-dependent. In the period after the start of the commercial fishery (period II), the total instantaneous mortality (Z) of both males and females was estimated at 0.6 year^{-1} (paper III). This is equivalent to an annual mortality of 45 %, meaning that almost half of the animals are removed either by fishery or by natural causes every year. The time between physiological maturity, starting the migratory behaviour of red king crab, and entering the fishery is less than two years (probably even less due to the delay in functional maturity) (paper I). The contribution of the slow-migrating portion of the population is cut short due to high mortality. Males are removed directly by the commercial fishery whereas female, who depend on the protection of males during their moulting period to avoid the risk of predation (Kruse *et al*., 2000; Hjelset, 2013) are believed to experience increased mortality due to deficit of males. The removal of animals, both males and females, before they have the time needed to disperse, is a plausible explanation of the reduced range expansion of the species.

The red king crab used to provide a lucrative fishery in the Bering Sea and Gulf of Alaska. In the late 1970s, annual catches reached 70,000 tonnes in the Bering Sea alone. The subsequent collapse in the early 1980s resulted in a complete closure of fishery in 1983 (Blau, 1986). Various theories have been put forward as to what caused the collapse, including both overharvesting and natural events like meteorological regime shifts, increased groundfish predation and epizootic diseases (Dew and McConnaughey, 2005). Despite a low exploitation rate since the collapse, the population has not been rebuilt (Loher *et al*., 1995), indicating that the presence of other factors, such as bycatch and discard mortality, are holding the population down (Reeves, 1993). The changes in the total stock abundance of red king crab in Norwegian waters (Fig. 5) are concurrent with the changes in exploitation history; quotas were dramatically increased after 2008 (Fig. 5, Table 1).

Table 1: Estimated total mortality (Z) (paper III, trap data*), estimated fishing mortality (F) (unpublished data), estimated natural mortality (M) and exploitation rate (% of legal male abundance harvested) of red king crab in 1995-2012.

Year	Z	F	M	Exploitation rate (%)
1995	0.350	0.024	0.326	20
1996	0.280	0.032	0.249	17
1997	0.380	0.026	0.354	14
1998	0.300	0.041	0.259	17
1999	0.260	0.060	0.200	NA
2000	0.690	0.053	0.637	6
2001	0.550	0.139	0.411	22
2002	0.670	0.102	0.568	13
2003	0.510	0.154	0.356	15
2004	0.660	0.230	0.430	21
2005	0.630	0.265	0.365	37
2006	0.600	0.219	0.381	33
2007	0.600	0.228	0.372	31
2008	0.910	0.782	0.128	85
2009	1.110	0.420	0.690	95
2010	1.090	0.333	0.757	90
2011	1.210	0.508	0.702	76
2012	0.930	0.418	0.512	48

*annual estimates were not presented, only estimates of the three time periods.

Annual fishing mortality (F) was estimated using a surplus production model of stock dynamics and Bayesian inference (Hvingel *et al.*, in prep). When these estimates of F are subtracted from the annual estimates of Z (Table 1), the average M are 0.348, 0.412 and 0.558 years^{-1} in periods I, II and III, respectively. The estimates of M for period I and II are close to the estimated M from linear regression of Z and exploitation rate, while the estimate from Period III is considerably higher. The estimates of M, 0.37 and 0.44 year^{-1}, based on trap and trawl data respectively (paper III), are therefore probably good estimates of mortality due to other causes than the directed fishery. However, bycatch of red king crab has been a serious problem since the 1990s (Jensen and Sundet, 2008), but has not been explicitly taken into

account in this analysis. In 1999, over 121,000 individuals were taken as bycatch, and due to rough handling by the fishermen, the mortality rate of by-caught individuals is believed to have been close to 100% during that period (Sundet, 2000). In recent years, fishermen have learned how to avoid the red king crab and the numbers taken are somewhat lower, but unaccounted mortality due to bycatch is still believed to be substantial (Jensen and Sundet, 2008). Furthermore, the red king crab, with its potential lifespan of 20 years (Matsuura and Takeshita, 1990), had not entered parts of the study area 20 years ago. This means that the proportion of older individuals is lower that what would be expected in an older population. This can lead to an overestimate of Z. These factors make it difficult to estimate M, but considering the life-expectancy, an M of closer to 0.2 year^{-1}, which was estimated by indirect methods (paper III) is more plausible than one closer to 0.4 year^{-1}.

With the estimates of L_∞ and k (paper I) and M (paper III), I am able to run two additional analysis that can tell us something about the effect of the exploitation of red king crab stock. The first additional analysis is a "relative yield-per-recruit" analysis (Y'/R) that is based on the Beverton and Holt (1966) Y/R model, and can be used when the absolute values of Y/R are not important. This Y'/R model is defined by:

$$\frac{Y'}{R} = E * U^{M/K}\{1 - \left(\frac{3U}{1+m}\right) + \left(\frac{3U^2}{1+2m}\right) - \left(\frac{U^3}{1+3m}\right)\}$$

where

E = F/Z ratio (from 0.05 to 0.95),

U = 1-(L_c/ L_∞) (L_c = 137 mm, L_∞ = 192 mm),

M = natural mortality rate (0.2 year^{-1} and 0.4 year^{-1}),

K = 0.2556 year^{-1},

m = (1-E) / (M/K)

and the relative biomass per recruit (B'/R) can be calculated using the following equation:
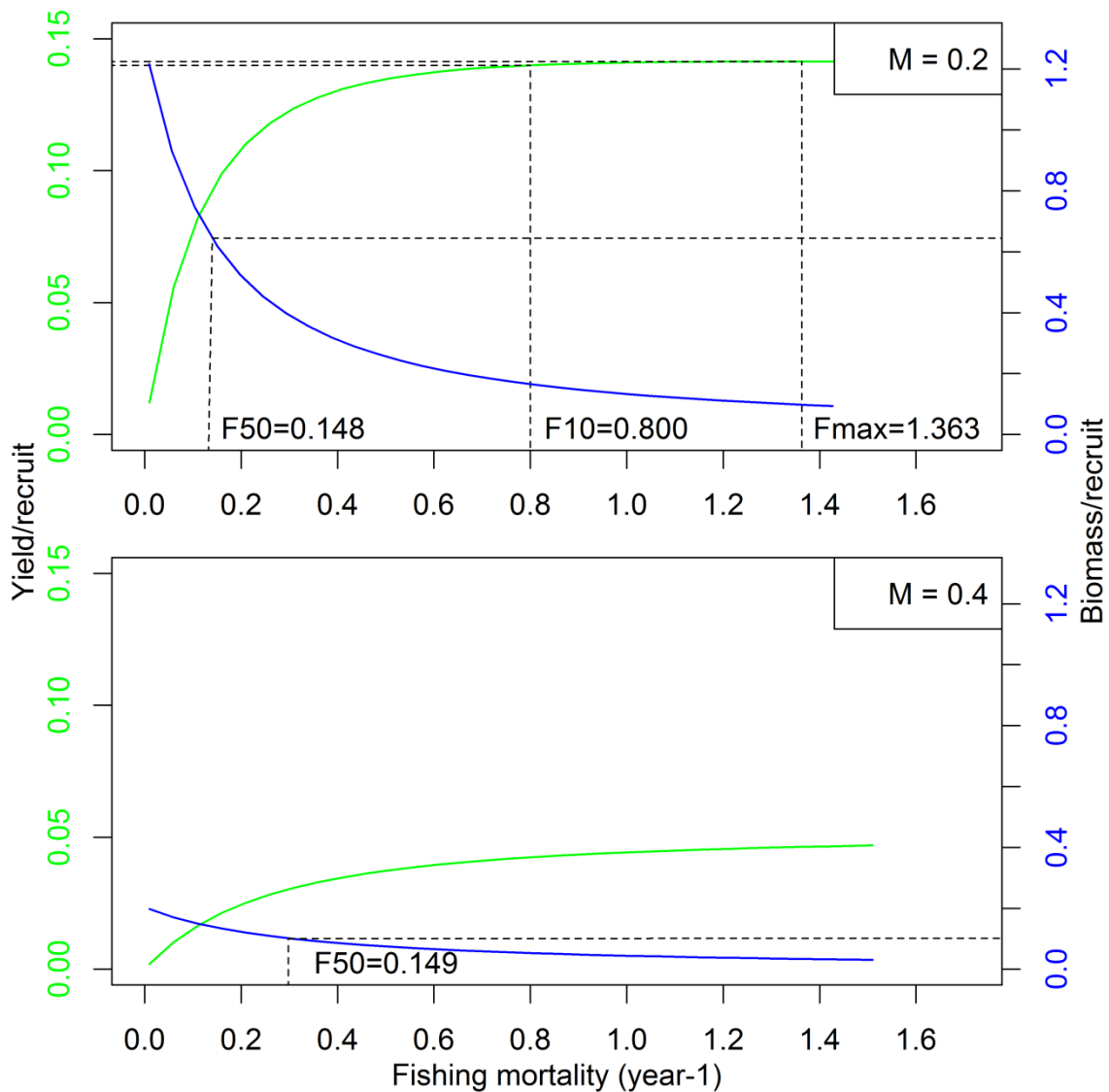

B'/R = (Y'/R)/F

where F = fishing mortality.

Fig. 6: Relative yield and biomass per male recruit at two different levels of natural mortality (M): a) 0.2 year^{-1} and b) 0.4 year^{-1}, and fishing mortality (F). F_{max} (F at a given M and L_c which produces maximum yield, F_{10} (fishing mortality at which the marginal increase of relative yield-per-recruit is 10 % of its value at F = 0) and F_{50} (value of F below which the stock has been reduced to 50 % of its unexploited biomass).

The maximum relative yield-per-recruit is nearly three times as high with an M of 0.2 year^{-1} as with an M of 0.4 year^{-1} (Fig. 6). The size at which the red king crab is targeted by the fishery is high, which means that maximum relative yield-per-recruit is obtained at very high levels of F. With an M of 0.2 year^{-1}, maximum relative yield-per-recruit is obtained at an F of 1.363 year^{-1}, while with an M of 0.4 year^{-1}, it is reached at an infinitely high F (exploitation

rate close to 1) (Fig. 6). However, relative-yield-per-recruit analysis assumes that recruitment to the fishery remains unaffected, regardless of how low the spawning stock is. At high levels of F, the spawning stock biomass-per-recruit (SSB/R) may be very small and it might be very dangerous to allow fishing at this level, since the assumption of constant recruitment may be wrong (Kirkwood and Hoggarth, 2006). At an F of 0.8 year^{-1} the marginal increase of relative yield-per-recruit is 10% (F10) of its value at F = 0. Combined with M, this level of F results in a total mortality of 1.0 which is the same as the observed total mortality of males in period III, when quotas were increased (paper III). Increasing F any further may jeopardize the SSB without significantly increasing the relative yield.

Kruse *et al*. (2000) analysed the potential effects of reducing the size limit in the Bristol Bay red king crab fishery from 137 to 128 mm carapace length. Analysis of red king crab fishery observer data showed that the reduced size limit would result in a decrease in yield per recruit of 5-7 %. Their main conclusion was that the reduced size limit did not appear to be a cost-effective measure for red king crab resource conservation given likely values of handling mortality rates. In 2011, the minimum legal size of Barents Sea red king crab was reduced to 130 mm which led to a decrease in the relative maximum yield-per-recruit of 2.5 %. The level of F resulting in maximum sustainable yield was reduced to 0.931 year^{-1} assuming M= 0.2 year^{-1}. Reducing the minimum legal size any further would jeopardize recruitment, as the males would be targeted at the same time as they reach functional maturity (120-130 mm; Powell and Nickerson, 1965b; Pengilly and Schmidt, 1995).

The second additional analysis is biomass distributions that are constructed two steps. The first step is to construct weight-based von Bertalanffy growth curve (Fig. 7) using the values for parameter L_∞ and k (paper I) in the following equation:

$$W(t) = q* L_\infty^3*[1-\exp(-k*(t-t_0))]^3.$$

where
L_∞ = asymptotic length
k = von Bertalanfy growth coefficient
t = age
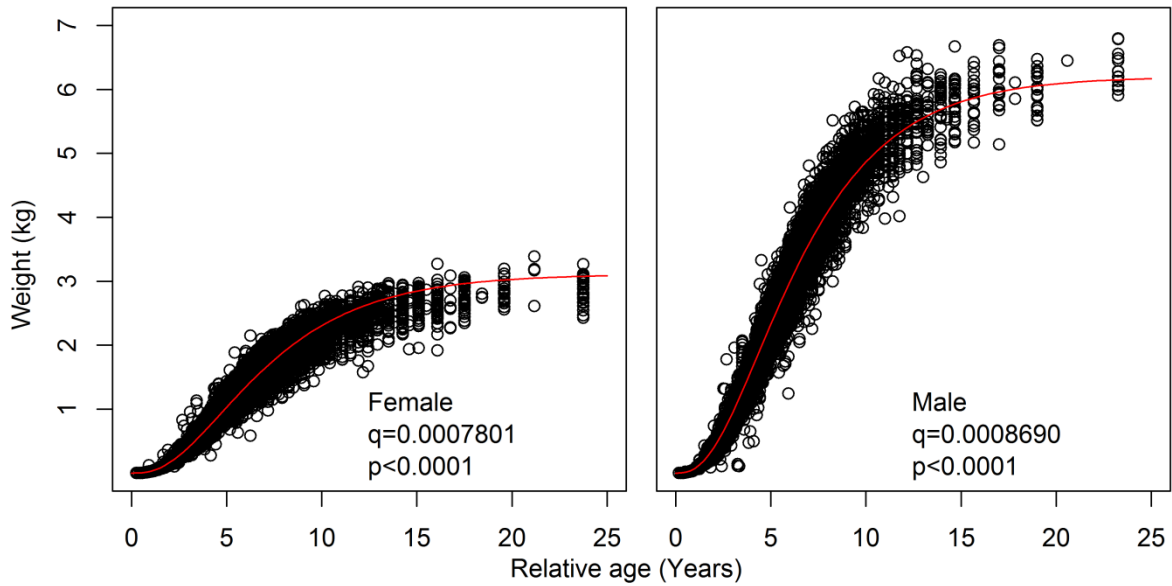t_0 = age at size 0
q = condition factor

Fig. 7: Weight-based von Bertalanffy growth curve of female and male red king crab in Norwegian waters, with significance levels (p). Circles indicate observed weight at estimated age of individual crabs.

In the second step, the weight-at-age data and estimates of Z (paper III) were used to construct biomass distribution plots for males and females in three different periods (I: 1995-2001, II: 2002-2007, III: 2008-2013) (Fig. 8). The Z values estimated in paper III are estimated based on individuals with carapace length larger than 112 mm (full selectivity). This value was used on smaller individuals also.
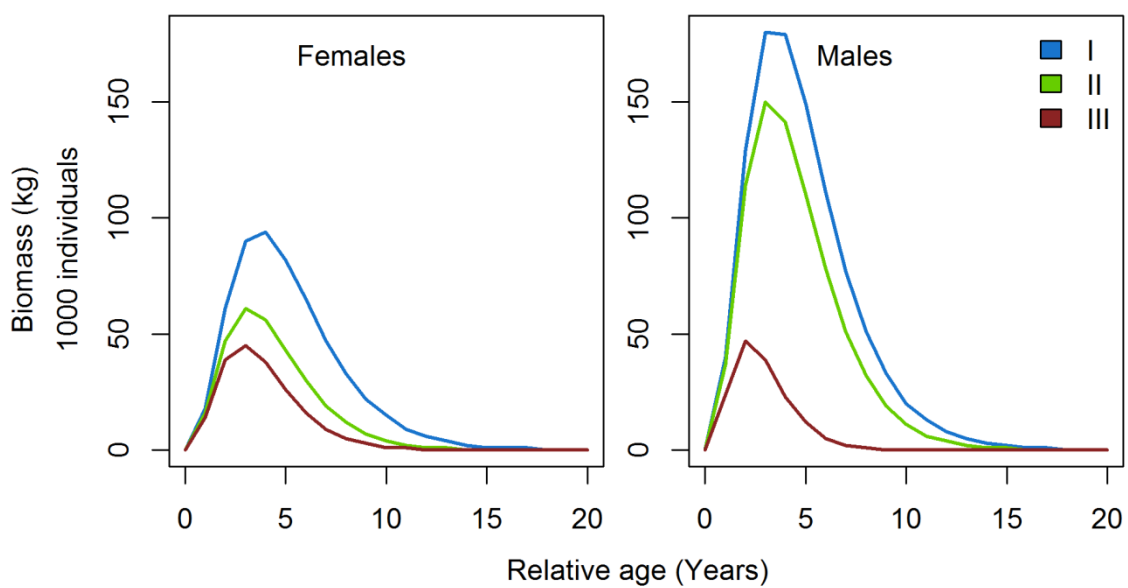
Fig 8: Biomass distribution of initial population of 1000 individuals (in kg) for each period (I: 1995-2001, II: 2002-2007, III: 2008-2013) for male and female red king crab in Norwegian waters.

Orensanz *et al.* (1998) believed that the reason for the collapse of red king crab around Kodiak Island in the Pacific Ocean was that its productivity had been overestimated, due to the long life span of the species. They believe the fishery may have expanded during their initial years by cashing on an accrued biomass of old individuals, thereby basing their catches on the accumulated biomass and not on the productivity of the stock. This is well demonstrated by the reduction in size (reduced mean landing weight) during the initial stock expansion phase. A similar development is now taking place in Norwegian waters. For both sexes, the bulk of the biomass distribution has been shifted towards a smaller age with fewer and fewer large individuals (Fig. 8). The peak of the biomass distribution of males shifts towards a lower age at the onset of the increased quotas in period III while the peak of the biomass distribution of females is found at a lower age every period. The absence of larger individuals is eminent. In period III, only a small fraction of the original population of males survives to the age of 5-6 years which I believe is a good estimate of the age of maturity. There is also a reduction in the fraction of larger females, but to a less extent than for males. This indicates that the Z is too high to allow survival to old age. Hjelset *et al.* (2009) showed that larger females had higher fecundity but were dependent on larger males for survival during moulting and mating (Hjelset et al., 2013). The removal of larger individuals could therefore represent a problem in terms of recruitment.

5 Concluding remarks

Fishery management has different objectives, which can be grouped into four general areas: biological, economic, recreational and social (Hilborn and Walters, 1996). The management of red king crab is challenging due to a conflict between different objectives: reducing further spread and maintaining a commercial fishery.

Catton (1982) defined carrying capacity as "the maximum population of a given species which a particular habitat can support indefinitely". When the carrying capacity is exceeded, a process called overshooting, resources are used up faster than they can be replenished, leading to environmental degradation (Catton, 1982; Postel, 1994). When

resources are reduced, the population will continue to increase for a limited period due to reproductive lag-time, after which the population will inevitably crash until it is realigned with the carrying capacity. The current stock abundance of red king crab is low compared to its peak in 2008 (Anon., 2014) which might have been reach by overshooting the carrying capacity. The red king crab is not native to the Barents Sea and it is possible that it was able to reach such a high abundance by feeding on the accumulated biomass rather than on the productivity of the benthic community. Studies carried out in the Varangerfjord (Oug *et al.*, 2011) indicated that soft-bottom epifauna and infauna have become markedly reduced in crab-invaded areas. Such environmental degradation is one of the first signs of overshooting and may be, at least partly, responsible for the decline in abundance of red king crab. Exploitation rates have been very high since 2008, after which there has been a markedly reduction in stock size. The fact that 50 % of males fail to reproduce in any given season (Dew and McConnaughey, 2005) in combination with the short period of time between maturity and entering the fishery (paper I) may lead to an imbalance in sex ratio. Such an imbalance is believed to be the cause of the reduction in size range and the fall in individual fecundity of egg-bearing females (Hjelset *et al.*, 2012). This has led to a reduction in the reproductive potential of the stock, which may be a part of the explanation of the recent decrease in stock abundance. This decrease in stock abundance in turn may reduce the imminent effect on the ecosystem. However, one of the management goals is to maintain a stock capable of supporting a commercial fishery in the quota-regulated area. If the fishery were to close, the population would be free to increase in number and range. Care must be taken to insure that the stock does not fall to a level unable to support the commercial fishery as the cost of a decimation fishery would be too high to apply along the entire coast of Finnmark. Outside the quota-regulated area, the goal remains to reduce the stock as much as possible to avoid further spread. Paper II indicated that there was a substantial dispersal westward across the border between these two areas, even so the expansion of the RKC seems to be halted. An important reason for the decrease in further spread is most likely the effort of the free fishery and decimation fishery. It is vital that these efforts are continued. By reducing the stock abundance outside the quota-regulated area, the potential risk to the native benthic community and the risk of further range expansion are reduced.

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Paper I

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Paper II

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Paper III

Windsland, K. Total and natural mortality of red king crab (*Paralithodes camtschaticus*) in Norwegian waters: Catch-curve analysis and indirect estimation methods.