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Size composition, reproductive investment, and fecundity of red king crab (*Paralithodes camtschaticus*) in Finnmark fjords, 1994-2022

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And

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Abstract

The release of red king crab (*Paralithodes camtschaticus*) into the Barents Sea by Russian scientists in the 1960s had the goal of establishing a self-sustaining stock for the purpose of commercial harvest. The red king crab has been successfully established as a stock in Norwegian waters where it has become an important commercial resource in the eastern regions of Finnmark. The Norwegian red king crab fishery is separated into two different regimes to meet two management goals, with a free fishery west of North Cape (26ºE) and a quota regulated fishery east of North Cape. This study examines the general size composition of the red king crab, investigates the female reproductive strategy, factors affecting reproductive investment and fecundity over time from when the research fishery started in 1994 till present. The findings presented in this study are general decreasing trends in size composition for both males and ovigerous (roe carrying) females during the sampling period. Clear trends toward a reduction the size where 50% of females are ovigerous in all fjords and over years. Temporal and spatial variability in measured individual egg weight has been demonstrated, and a standardized ovigerous female crab with a 125 mm carapace length (CL) is overall less fecund, compared to previous studies. These changes in population size composition, size at maturity (OL_{50}), reproductive investment and fecundity have been suggested to be result of heavy fishing pressure on large crabs of both sexes, as a result sperm limitation may occur due to low numbers of large males. The decrease in reproductive investment and fecundity could also be related to a reduction in availability of high-quality food items for the crabs.

Acknowledgements

I am sincerely grateful for my supervisors; Einar M. Nilssen (UiT), Ann Merete Hjelset (IMR), and Torstein Pedersen (UiT) for their help, support, and feedback throughout this project. Special thanks to Einar as he initially introduced me to the highly interesting and exciting world of the red king crab as he was the supervisor of my bachelor thesis, and further giving me the opportunity to work together Ann Merete Hjelset and take part in the annual red king crab cruise of 2022. The help I have received has been invaluable. From Einar's statistical expertise helping me through statistical computing, identifying potential outliers of the dataset and some uncertainty calculations in that he computed in Systat. As well as providing the fecundity data estimated by Rasmus Kristoffer Høyning. I'm even more grateful that he took his time to do this as he is currently retired his station at the university. Thanks to Ann Merete Hjelset for not only allowing me to take part of the crab cruise, sharing her fecundity data with me for this study, as well as always being available to give feedback on my progress. I'm grateful for Torstein Pedersen being willing to take over as main supervisor as Einar retired, fully knowing that Torstein is the main supervisor for 3 other master students this semester, and still taking his time to give feedback on my thesis.

When I first set foot onboard FF Kristine Bonnevie I instantly felt welcomed by both the crew and the scientists, making this experience that I will always remember as one of the most exciting parts of my 5-years as a student.

As estimating fecundity for crabs through direct egg counts is a time-consuming task. Therefore, I would like to thank Johanna Hovinen (UiT) for helping me out with my lab work. Further I'm grateful for the help provided by Hanna E. H. Danielsen (IMR) for accessing the IMR database and retrieving the whole data set of every single red king crab sampled from 1994 – 2022, as well as creating a distribution map for the red king crab which is used in this thesis.

At last, a thanks goes out to the people in my life that have supported me through the 5 years at UiT. To my family at home, and all the friends among fellow students I have met during this 5-year period of my life. They have made my time as a student great.

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1 Introduction

1.1 Red king crab and its management

The red king crab (*Paralithodes camtschaticus*) is a non-native species in the Barents Sea and Norwegian waters. It was released into the Barents sea by Russian scientists in the 1960s (Orlov and Ivanov, 1978). In 1977 the first red king crab was caught as bycatch in Varangerfjorden roughly 250 km from where they were released (Orlov and Ivanov, 1978; Anon, 2007; Hjelset et al., 2012). For the first 17 years after the first observation, fishery for the red king crab was banned in both Norwegian and Russian waters, and all crabs caught were to be released back into the sea in order to enable the stock to grow and spread until large enough to be a commercially harvestable fishery resource (Anon, 2007; Hjelset, 2012). Management rules for fishery of the red king crab were non-existent at the time. Therefore a research fishery were implemented which was exempt from fishery regulations that lasted from 1994 till 2001, before a commercial fishery commenced in 2002 (Hjelset et al., 2009).

The red king crab fishery is regulated under a dual approach management system with two main objectives: "*a) a long-term predictable fishery and b) prevention of further spread of the crab" (Hjelset, 2012).* This dual based management approach is however mutually exclusive since a long-term predictable fishery requires a high abundance of crabs which further increases the chance of spread (Hjelset, 2012). The dual based management is separated at the North Cape (26ºE) where the area east of North Cape has a quota regulated fishery in line with the first management goal, whilst wanting to limit the spread west of 26ºE (Anon, 2007; Hjelset, 2012). The second objective is implemented because an invasive species like the red king crab may have strong impacts on the benthic ecosystem which has been both observed and modelled (Falk-Petersen et al., 2011; Pedersen et al., 2018).

It has been speculated that large ovigerous (roe carrying) females migrating to new areas are one of the main contributors to their rapid spread westwards (Hjelset, Personal conversation). In a response to this a female fishery quota was implemented in 2008 with a minimum legal size (MLS) of 137 mm carapace length (CL), the same MLS as that has been used for males since 1994. Furthermore the MLS was lowered from 137 mm down to 130 mm CL in 2011 which is the current MLS regulations used for both sexes (Anon, 2007; Hjelset, 2014).

However, in 2017 the MLS for females were reduced down to 120 mm CL before being reverted back to 130 mm CL in 2019 (Hvingel et al., 2022).

The red king crab is currently a highly profitable fishery both in Russian and Norwegian waters being commercially exploited. The stock in the Barents Sea was exploited for 12 400 metric tonnes of crabs in 2021. Roughly 1800 tonnes were harvested in Norwegian waters, whilst the remaining 11 600 tonnes of crabs were caught in Russian waters (Hvingel et al., 2022; Hjelset, Personal conversations). In 2022 the export of red king crab made up 28% of the income generated from Norwegian crustacean seafood export, corresponding to approximately 840 million NOK (Nokkeltall.Seafood.no, (undated)).

1.2 Reproductive biology of the red king crab

Growth and reproductive effort are often described as two sinks competing for an organism's resources where their life history strategi dictates the amount and how the energy is invested into each sink (Clarke, 1987). Life history strategy is composed of several factors including the somatic growth rate, age-and size at maturity. Reproductive effort (RE) in relation to age and size, age-and size specific fecundity, egg size, mortality rate in relation to size and age, larvae type and development type, and the lifespan of the adult are all important life history characteristics (Stearns, 1992; Llodra, 2002).

1.2.1 Reproduction

The red king crab utilizes internal fertilization, since the female is uncapable of storing sperm, therefore the males must be present when the females undergo moulting (shedding their shell) (McCaughran and Powell, 1977; Nilssen and Sundet, 2006). During this 2–3-day window where the females have a new and soft-shell, fertilization of roe is possible (Hjelset, 2014). The males deliver their spermatophore to the female's ventral surface during copulation. The eggs are fertilized at the time of spawning, thereafter the eggs are incubated on the pleopods tucked under the abdomen for 10-12 months before hatching and thus starting their reproductive moult again (Llodra, 2002; Stevens and Swiney, 2007b; Høyning, 2018).

The red king crab moult and mate in shallow waters in spring, and their spawning event is closely related to their migration pattern between deep and shallow waters throughout the year (Stone et al., 1992). After moulting and mating during spring, the red king crab migrates from shallow to deeper water, before they return to shallow waters again during winter. They slowly migrate to intermediate depths towards the start of spring in order to pre-moult before mating occurs in shallow waters (Stone et al., 1992). Many of these life history strategy characteristics are highly plastic and affected by habitat and the ecosystem the organism inhabits (Llodra, 2002).

Female crabs are dependent on males that are larger than themselves for survival during their soft-shelled period after moulting to make fertilization of eggs possible. Mature females are found to prefer male crabs with a CL roughly 30 mm larger than themselves for mating (Schmidt and Pengilly, 1990). Therefore, it is important from a management perspective to make sure there is a sufficient amount of large male crabs present in the stock for females to mate with. Male crabs are polygamous and can fertilize several females during one mating season, whilst females are monogamous only mating with one male per year (Jewett and Onuf, 1988). Laboratory experiments have shown that one male crab can fertilize as many as 7 female crabs, and it has been assumed that this is transferable to nature (Powell et al., 1974). Under ideal circumstances this could be the case, however with the added stressors that may influence the crab in a natural habitat this number is most likely a bit lower and dependent on the size of the male in question.

1.2.2 Size at maturity

An organism's size and age at maturity is a key life-history trait affecting fecundity and an important parameter in fishery management of exploited populations, and should be estimated regularly (Hjelset et al., 2009). It's important that individuals are protected until they have had the opportunity to reproduce at least once before reaching legal catch size (Somerton, 1980; Donaldson and Donaldson, 1992; Hjelset et al., 2009). For the red king crab, the size at maturity for females is estimated to be at the size where 50% of the females are carrying roe (OL_{50}). This is possible to estimate through looking for presence of roe under the abdomen on the female crab due to the red king crab brooding their eggs before hatching them.

In Norwegian waters the red king crab has been shown to grow faster and mature at larger sizes than in their native areas in the Northern Pacific Ocean whilst their diet remains approximately the same (Jørgensen and Nilssen, 2011; Sundet, 2014). Marukawa (1933) estimated the minimum size at maturity at the coast of Kamchatka to be between 78 – 82 mm CL, whilst Wallace et al., (1949) described the size at maturity to be at 90 mm CL in the

Bering Sea and 105.5 mm CL in the Pacific Ocean. In Norwegian waters the size at maturity through OL_{50} estimates for Varangerfjorden, Tanafjorden and Laksefjorden was shown to have an average OL_{50} of 108.9 mm CL between the fjords (Hjelset et al., 2009), and a OL_{50} value of 111.3 mm CL in Porsangerfjorden 2011 (Lindberg, 2012).

It is well documented in the literature regarding highly exploited fish species that high fishing pressure may lead to a reduction in size and age at maturity as a response to increased mortality among large individuals (Jørgensen et al., 2007; Hjelset et al., 2009).

1.2.3 Reproductive investment and fecundity

Reproductive investment is defined as the amount of energy used in production of reproductive material, in this case roe for the female crab. An estimate of the total dry weight of roe for a female crab will be used as a measurement of reproductive investment in this study.

Fecundity is often defined as the number of offspring produced by a female within a given time period (Llodra, 2002). Fecundity can further be separated into different categories and needs to be defined for each study in order to obtain sufficient information from the data being analysed (Anger and Moreira, 1998; Llodra, 2002). Anger and Moreira (1998) categorized three different types of fecundity in their paper studying decapods; potential, realized and actual fecundity. Potential fecundity refers to the total amount of gametes produced by a female, realised fecundity refers to the total amount of fertilized eggs, and actual fecundity refers to the total amount of hatched larvae. For this study and most fecundity studies of decapods that brood eggs, the realized fecundity is estimated by direct egg counts.

However, fecundity is a highly plastic characteristic that varies depending on numerous factors including external factors such as temperature, food availability and seasonal variability to name a few (Llodra, 2002). Many of the factors' affecting fecundity is related to their life history strategies also known as internal factors: like size and age at maturity, the size of the crab, and the size of males in relation to female size is important for red king crab where the males guard soft shelled females.

There have been several fecundity studies of red king crab in Norwegian waters that have looked into possible differences between areas and over time (Rist, 1999; Hjelset et al., 2012;

Lindberg, 2012; Høyning, 2018). Great variability has been observed both in total roe mass and egg counts for a female crab of approximately equal size and with equal living conditions. This was first demonstrated in Wallace et al., (1949) where he found a variation between 150 000 and 400 000 eggs for ovigerous females of roughly the same size.

It has been described several times that the fecundity of a female red king crab is a function of the size of the individual, that there is an exponential relationship between them, and it is estimated that large females can has as much as 9 times more eggs than smaller crabs (Haynes, 1968; Lindberg, 2012; Høyning, 2018). However, it has often been estimated outliers among small primiparous (first time spawners) and larger multiparous (multiple spawners) crabs that have far less eggs than their size would predict (Dew and McConnaughey, 2005; Swiney and Long, 2015). The tendency for large females to have far less or no eggs at all, has been explained as a case of senescence, or be caused by a lack of larger males to breed with large females causing them to not carry eggs (Sato and Goshima, 2006; Swiney et al., 2012). Indicting that sperm limitation may be a cause for the trends in fecundity seen in Hjelset, (2012) and Høyning (2018).

1.3 Aims and objectives of this study

This study focuses on the four large quota regulated fjords in eastern Finnmark and investigates size composition for ovigerous females and all males, the size where 50% of females are ovigerous, reproductive investment, individual egg weight (IEW) and fecundity for data collected in 2022. This will further the work done by Ann Merete Hjelset (Hjelset, 2012), Ken Ståle J. Lindberg (Lindberg, 2012), and Rasmus Kristoffer Høyning (Høyning, 2018).

This study’s findings will then be compared to previous results, and further used to investigate the variability in the listed variables, both within fjords as well as between fjords over time. It is of great interest to investigate if the findings from this study can be correlated to changes in fishery management, the invasion history of the red king crab, and or related to how the red king crab may have affected the benthic ecosystem composition.

2 Materials and methods

2.1 Sampling area

The sampling area for this study were the four large fjords within the quota regulated area of eastern Finnmark county (Figure 1). The UiT, Arctic University of Norway and The Norwegian Institute of Marine Research (IMR) has since 1994 sampled red king crab on an annual basis in Varangerfjorden, further expanding sampling to Tanafjorden, Laksefjorden, and Porsangerfjorden as the crab spread further westward. From 1994 to year 2000 the king crab survey was carried out by UiT using their research vessel FF Johan Ruud, before the IMR took over sampling responsibility using their vessel FF Kristine Bonnevie. For almost 30 years the UiT and IMR have sampled over 100 000 crabs within these fjords. Data sampling for Varangerfjorden started in 1994, 1999 in Tanafjorden, 2002 in Laksefjorden, and 2005 in Porsangerfjorden (Appendix 1, 2 & 3).

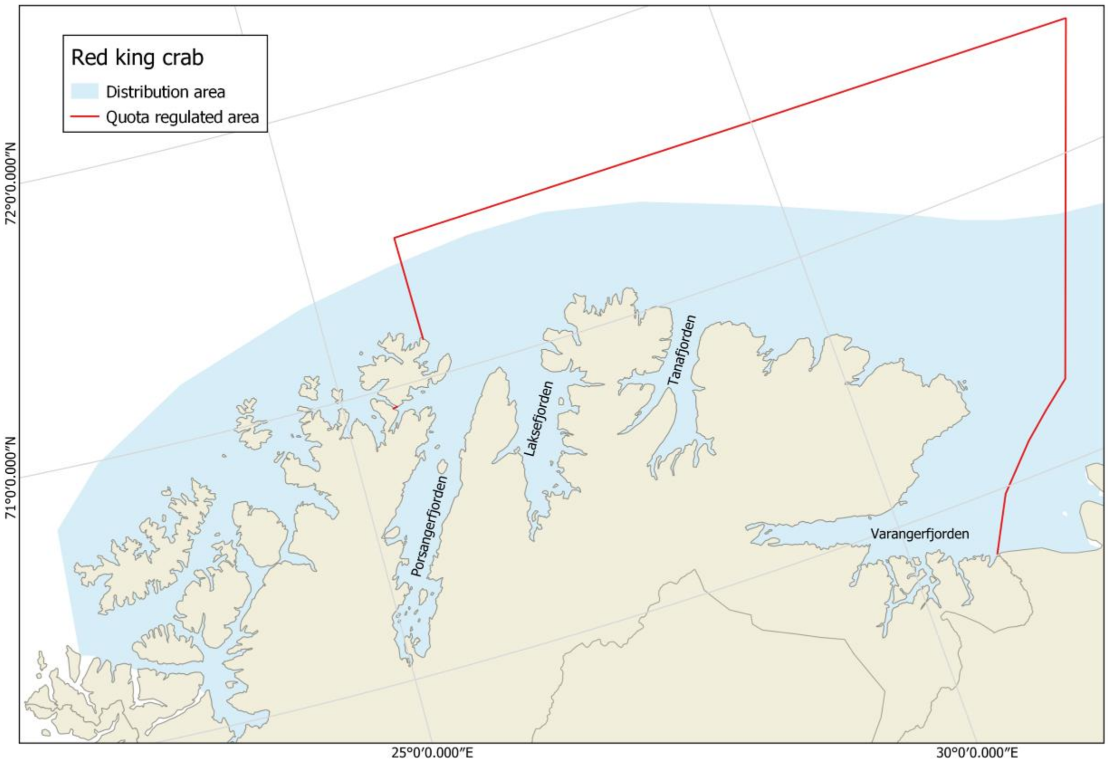

Figure 1. The present red king crab distribution area within Finnmark County (blue). The area within the red lines represents the quota regulated area for commercial fishery (Map created by Hanna Danielsen, IMR).

2.2 Sampling methods

Whilst on board FF Kristine Bonnevie during the annual crab cruise of 2022 in Porsangerfjorden, crabs were sampled from several different stations, depths, and bottom substrates using baited pots and Agassiz trawl described more in detail within Hjelset et al., (2009).

When the traps or trawl were hoisted up and pulled onto deck the crabs were placed into baskets and moved into the onboard laboratory where the crabs' sex was determined, their carapace length was measured using an electronic calliper and then weighed. Other morphological measurement such as moulting stage, presence of roe and missing and/or partially regrown limbs were noted down. A sample of eggs was taken from ovigerous females by laying the ovigerous females on their back and gently prying the abdomen open to access the pleopods carrying roe. The pleopods were cut off using scissors before being placed in a zip-lock bag with station number, serial number, year, and specimen id written on the bag. This bag was then placed into the on-board freezer to preserve the material until it could be processed at a lab.

2.3 Laboratory analysis

All egg samples for the 2022 samples were processed at the saltwater lab at UiT. The eggs were defrosted overnight at 2-4˚C before they were processed. The full egg sample was taken out of the plastic bag they were stored in and put onto a weighing plate. The whole sample including pleopods were weighed, giving us a measure of the total wet weight. Three subsamples were taken from the smallest pleopod to ensure comparable stages of development by carefully separating the eggs from the pleopod using tweezers and placing them into a counting chamber. The counting chamber where then put under a microscope and using a hand counter to count egg numbers, averaging 300 to 400 eggs per subsample for consistency. The subsamples were then weighed before being put into a drying chamber together with the main sample at 60ºC for 48 hours before they were weighed again. The weight of the subsamples was added to the dry weight of the rest of the sample. This procedure was done for 12 to15 crabs across different size groups ranging from smaller to larger crabs from Varangerfjorden 2022 and Porsangerfjorden 2017 and 2022 to get an estimate on the IEW and total egg count for the fjord across different size groups. Based on previous findings concluding that IEW is not affected by size of the crab within a fjord there is no need to take subsamples from every single crab (Hjelset et al., 2012). Therefore, for the remaining egg samples only the total wet weight and dry weight was measured by separating the pleopods from the eggs and measuring the wet weight and then drying the egg mass for 48 hours before measuring the total dry weight of roe.

2.4 Data treatment

Whilst all data sampling and morphological measurement were done as part of annual cruises by UiT and IMR, the fecundity measurement are from a combination of previous work done by Ann Merete Hjelset (Hjelset, 2012) for Varangerfjorden 2000 – 2007, Tanafjorden 2000 – 2007, and Laksefjorden 2004 – 2007. Rasmus Kristoffer Høyning (Høyning, 2018) for Varangerfjorden 2008, 2010, 2011, 2013, 2015, and 2016 in cooperation with UiT and IMR. This thesis focuses on extending on the data series till 2022. For consistency in data, only crabs sampled in autumn and early winter (from August till the end of the year) were used. The treatment of raw data was performed in Microsoft Office Excel (Microsoft Corporation, 2018), whilst the creation of figures was performed in RStudio (RStudio Team, 2022) which is an application of R (R Core Team, 2022). Total numbers of crabs used for calculation for all data are given in Appendix 1 as well as for all females (Appendix 2 left), only ovigerous females (Appendix 2 right), and for all male crabs (Appendix 3).

2.4.1 Size composition of the red king crab

Computation of the size composition of ovigerous female crabs were done by removing all female crabs without roe from the data set. To present an overview of the size competition for all ovigerous females (n = 22 670) the 5th and 95th percentiles and median CL values were calculated for each year for all fjords pooled together as well as for each fjord separately for the whole sampling period (1994 – 2022).

These data were then presented as time series and were plotted using the “ggplot2” (Wickham, 2016) and “ggridges” (Wilke, 2022) packages in R showing both the CL quantiles and the frequency of data across different CL values over time using a binwidth of 3mm. First in form of CL composition time series plots with quantile values for all fjords pooled together and for each fjord separately. Then plots of quantile values from all fjords were presented to compare possible differences between areas.

The same approach was used for size composition over time for all male crabs regardless of maturity stage. When presenting size composition for males in form of a size composition plot over time a binwidth of 5 mm was used for male crabs. The differences in binwidth are used for cosmetic reasons as ovigerous female CL composition spans a narrower range of CL values.

Since females are dependent on males larger than themselves for protection during mating, the correlation between male and ovigerous female size composition was investigated using the estimated 95th percentiles of CL ranges from all fjords pooled together for all years. These were plotted against each other to investigate possible changes in the CL gap over time.

2.4.2 Individual egg weight and fecundity ranges

The IEW was calculated by taking the dry weight of roe estimated from the subsamples and dividing by the number of eggs in the subsample (Equation 1).

$$Individual\ dry\ egg\ weight\ (g) = \frac{Dry\ weight\ of\ roe\ (g)}{Egg\ count}$$

Equation 1

The mean value of the three subsamples were estimated for each of the ovigerous female red king crab where subsamples were taken.

For the crabs where IEW were calculated this specific value was used to calculate their fecundity, whilst the mean IEW estimated for Varangerfjorden 2022 and Porsangerfjorden 2017 and 2022 was used to calculate the fecundity of the rest of the females where IEW were not specifically measured. This can be done since it’s been proven that IEW is not influenced by the size of the female (Hjelset et al., 2012). Fecundity of a female is calculated by dividing the dry weight of roe by the individual dry egg weight (Equation 2).

$$Fecundity = \frac{Dry\ weight\ of\ \ (g)}{Individual\ dry\ egg\ weight\ (g)}$$

Equation 2

Individual dry egg weight in grams (g) are used to calculate fecundity, whilst when presented in plots and tables individual dry egg weight is presented in milligrams (mg) for cosmetic reasons.

2.5 Statistical analysis

The majority of statistical analysis were done in R using the R-studio application, some calculations of local regression confidence intervals were done in SYSTAT (Systat-Software-Inc., (undated)).

2.5.1 Size at 50% ovigerous length

For the OL_{50} estimates, only female crabs between the 80- and 140-mm CL were used, the same CL range used in Lindberg (2012). This was done to remove outliers among small crabs that are ovigerous, and any potential large females without eggs hawing to strong an influence. The OL_{50} was estimated through logistic regression using the "glm" function in R to make a model with presence of roe as a function of CL and using the argument "family = binomial" which tells R to compute a logistic regression (Equation 3)

$$Presence\ of\ roe = \frac{e^{a+b(CL)}}{1 + e^{a+b(CL)}}$$

Equation 3.

In Equation 3 *a* and *b* are the regression constant (intercept) and regression coefficient (slope) respectively. Since the response variable (presence of roe) works with ultimate binary values (1 with roe and 0 without roe), one can estimate at which CL a crab has 50% chance of carrying roe (Y = 0.5). Using the "dose.p" command within the "Mass" package (Venables and Ripley, 2002) in R on the logistic regression model. This gives an estimate at which X (CL) value, Y (Presence of roe) equals 0.5 and the standard error of the estimate which is used to calculate 95% Confidence intervals (CI). This gives an estimate at which CL value a randomly selected female has a 50% chance of being ovigerous.

These calculations were done for each year and fjord where data was available. OL_{50} estimates with standard errors were calculated for Varangerfjorden (1994 – 2022), Tanafjorden (2000 – 2015 & 2017 – 2022), Laksefjorden (2002 – 2022), and Porsangerfjorden (2007 – 2022). There was no sample for Tanafjorden 2016 since IMR did not sample Tanafjorden that year. There were also no estimated OL_{50} value for Porsangerfjorden due to only sampling three crabs all being ovigerous in 2005 and 2006 with 19 crabs sampled only two being non-ovigerous (Appendix 4).

The OL_{50} estimates were then plotted as a time series to investigate any trends. Fjords were determined to show trends in OL_{50} if and there were statistically significant differences in estimated OL_{50} values (No overlap in 95% CI) between early measurements and 2022 measurements (Whitlock and Schluter, 2009).

Further the data was pooled into 3 subsets based on different fishery management regimes. The first time series being from 2002 to 2007 used to represent the time before a female fishery quota was introduced. Choosing to start in 2002 for this time series and not back in 1994 was due to not wanting Varangerfjorden to have several years where it is the only fjord contributing with samples, and also excluding the values from the research fishery from 1994 – 2001. The second time series is from 2008 to 2010 and represent the time between the introduction of a female quota and before the MLS was reduced in 2011. The third and last time series is from 2011 to 2022 and represent the time after the introduction of female quota and reduction in MLS to 130 mm CL. The two-year period where the MLS of females were reduced to 120 mm CL will not be estimated as it is only a two-year period in the middle of the third time series (2011 – 2022). This was done to investigate if the changes in fishery management had any effect on the OL_{50} for female crabs in the quota regulated area as a whole.

2.5.2 Models for individual egg weight

Analysis of covariance (ANCOVA) was used to test for any temporal and spatial effects on IEW where P-values were used to determine the statistical significance in variability of a given variable (Whitlock and Schluter, 2009). To run the analysis the years between 2008 and 2016 for Varangerfjorden were excluded due lack of variability in IEW values for that time period in Varangerfjorden (Høyning, 2018). Furthermore, the AICc values for linear models including all possible different predictor variables were compared to find the best fitting model for investigating variance in IEW.

2.5.3 Reproductive investment and fecundity data analysis

Reproductive investment is a measurement of how much energy a mature female invests into egg production. In this case the total dry roe weight is a valid measurement of reproductive investment. To investigate which crab size invests the most energy into reproduction relative to their size, a roe index (RI) was calculated for all ovigerous crab with estimated dry roe weights. The RI is calculated by dividing the total dry roe weight by CL to the power of three as presented in Lindberg, (2012) (Equation 4).

$$Roe\ index = \frac{Dry\ weight\ of\ roe\ (g)}{CL\ (mm)^3}$$

Equation 4

The RI was presented graphically by plotting it as a function of CL (multiplying RI by 100 000 for cosmetic plotting reason). To visualize trends in RI as a function of CL, a local regression (loess) smoothing line was fitted with standard error around the line visible (Cleveland, 1979).

The relationship between dry roe mass and size was investigated through linear regression analysis using the size of the crab (CL) as predictor variable and dry roe mass (in grams) as response variable. To meet the assumptions of normality and homogeneity of variance both variables were log transformed to the natural logarithmic (ln) scale. Using the regression constant and coefficient from in R regression output to calculate the ln of total egg mass from a specific size of crabs (Equation 5).

$$ln(Dry\ weight\ of\ roe\ (g)) = \ln(a) + b * \ln(CL)$$

Equation 5

The linear relationship between size and dry weight of roe was then estimated for all fjords and years where necessary CL and roe mass data were available. The regression output was assessed and noted down (regression constant (a), regression coefficient/slope (b), standard error of b (SE), the r^2, f-value of b, and the p-value of b) (Appendix 5). To avoid any confounding factors regarding possible changes in size distribution, reproductive investments was estimated for a standardized female crab. The average sized crab among ovigerous females for the whole sampling period was estimated to be 122 mm CL, a reduction compared with Hjelset et al., (2012) who estimated this to be 125 mm CL. To make this study's results more comparable to previous work a 125 mm CL ovigerous females will be regarded as a standardized ovigerous female also in this study.

This CL value was fed into Equation 5 with the ln of the regression constant (a) and regression coefficient (b) values for each year to calculate reproductive investment for a standardized ovigerous female over time. Whilst the estimated reproductive investment was calculated in R, the confidence intervals around the estimate were calculated locally using SYSTAT. The estimate and confidence intervals were transformed from ln scale to normal values then to total egg count using the mean IEW value for that fjord and year presented in Appendix 6 (Equation 2). Regression output and standardized ovigerous female estimates are presented in Appendix 5.

3 Results

3.1 Size composition of red king crabs

3.1.1 Size composition of ovigerous female crabs

All fjords pooled together show a declining trend in 95th percentile and median values for ovigerous females, whilst the 5th percentile remains approximately constant. The 95th percentile starting off at a high level 160 – 180 mm CL from 1994 – 2001, before gradually declining down and flattening out after 2008 at just above the MLS of 130 mm CL from then till 2022 (Figure 2). The size composition time series show similar trends across all fjords with the 95th starting off at a high level before gradually decreasing. As for 2022 the estimated 95th percentile in Varangerfjorden, Tanafjorden and Laksefjorden are above the MLS whilst in Porsangerfjorden it is below MLS (Figure 3, left). The median values for the four fjord have a drop early in the sampling period for the given fjord before settling close to the same value for all fjords between 115 and 125 mm CL in 2022 (Figure 3, left) (for size composition plots for each fjord separately see Appendix 7 – 10).

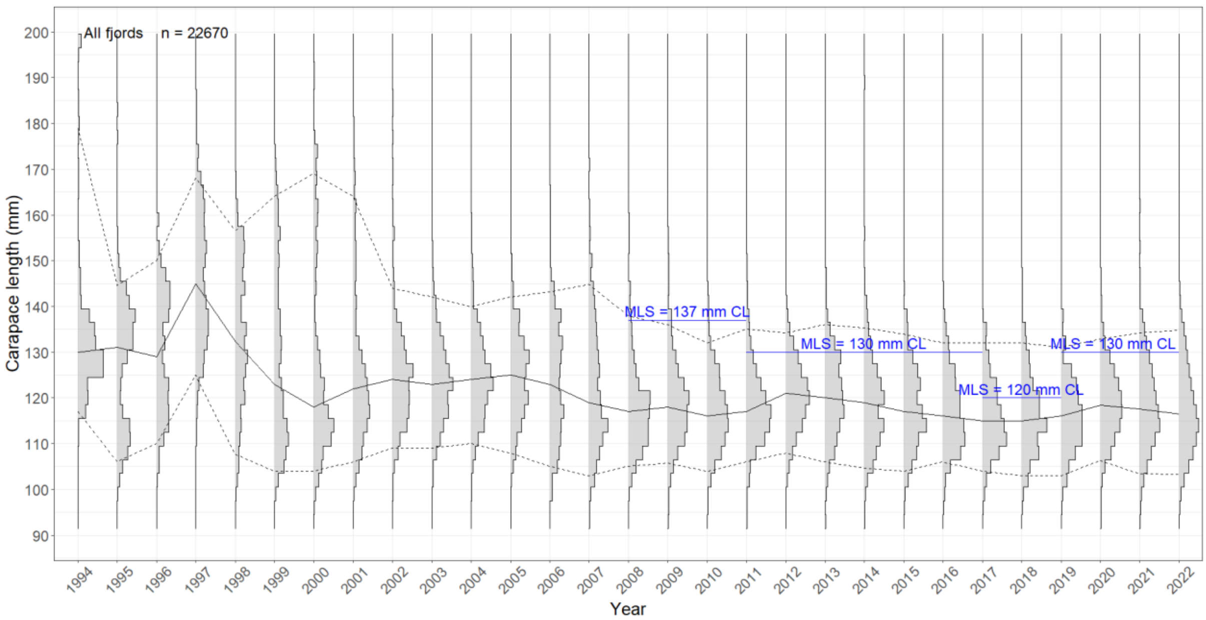

Figure 2. Size composition plot for ovigerous female crabs in all fjords over time based on a total of 22 670 measured crabs. Solid black line represents median, dotted lines the 95th and 5th percentile CL values. Blue solid line with text represents the minimum legal size for fisheries for females in the periods 2008 – 2010, 2011 – 2016, 2017 – 2018, and 2019 – 2022.

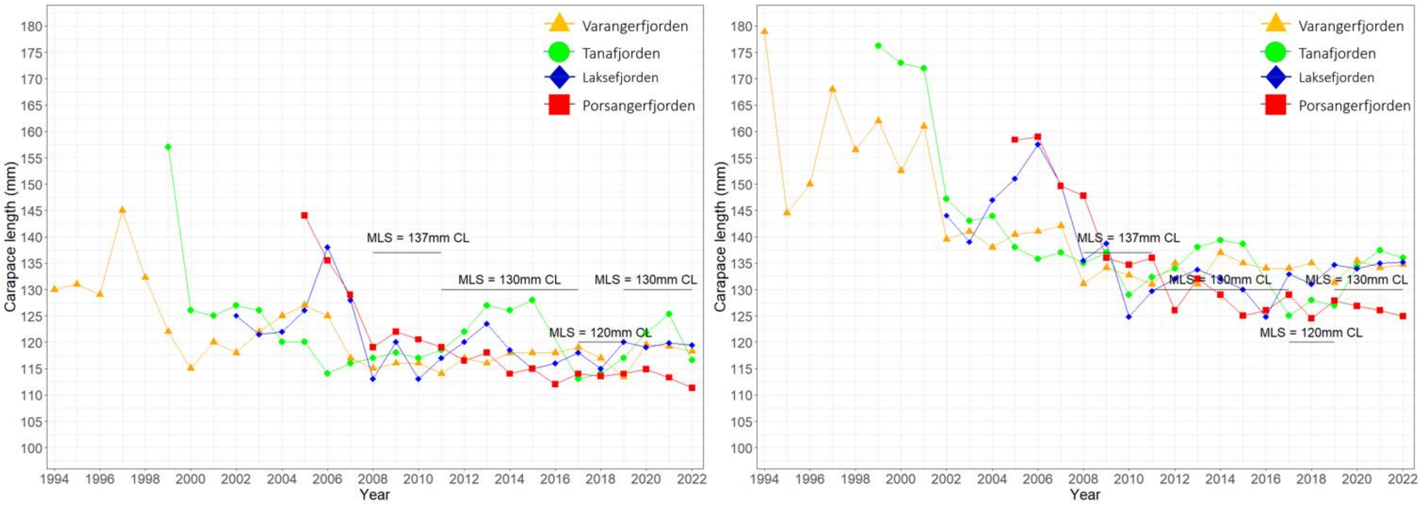

Figure 3. The median (left) and upper 95th percentile (right) for CL estimates of ovigerous females over time for the four fjords. The black line with text represents the minimum legal size for fisheries for females in the periods 2008 – 2010, 2011 – 2016, 2017 – 2018, and 2019 – 2022.

3.1.2 Size composition of male crabs

Quantile estimates for males show overall declining trends for 95th percentile and median CL estimates over time. The 95th percentile peaks in 1997 before gradually decreasing, then flattening out at approximately 150 mm CL from 2011 till 2022. The median estimated value follows the same trend as the 95th percentile flattens out at approximately 110 mm CL from 2011 to 2022. The 5th percentile remains consistent at approximately 70 mm CL for the whole sampling period except for an estimated value below 40 mm CL in 1997 (Figure 4). The 95th percentile and the median values for all fjords over time and all fjords roughly follow the same gradually negative trends with some variability between the fjords as the 95th percentile and median values flattens out after 2008 (Figure 5) (for size composition plots for each fjord separately see Appendix 11– 14).

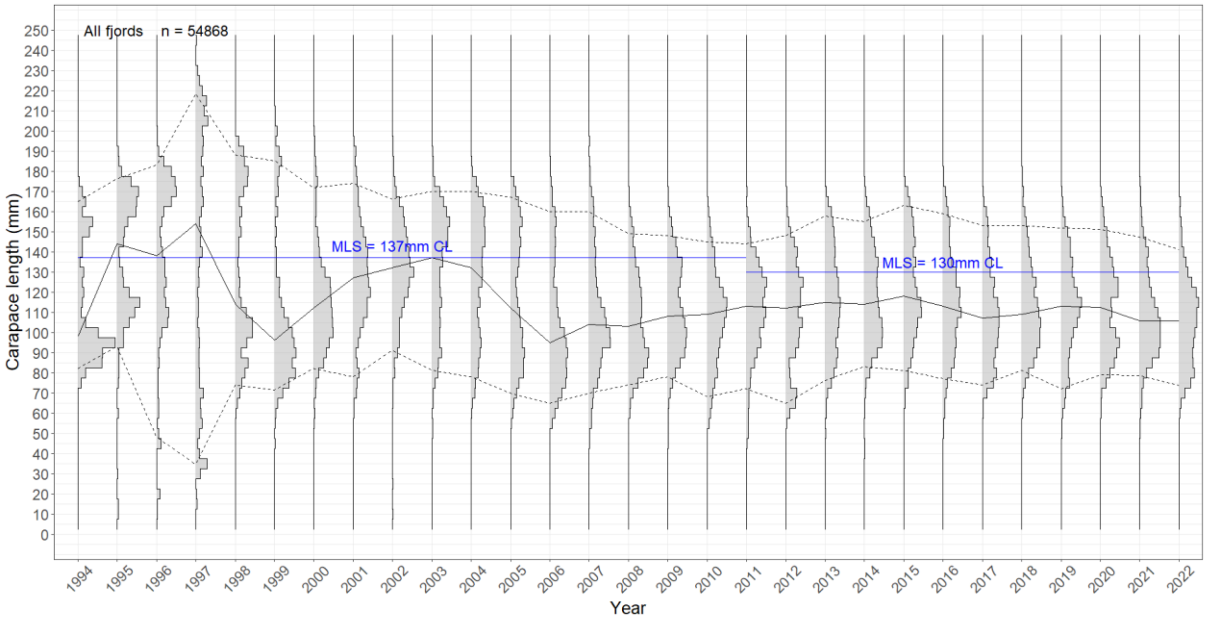

Figure 4. Size composition plot for male crabs from all fjords pooled together. Solid black line represents median, dotted lines the 95th and 5th percentile CL values. Blue solid line with text represents MLS in the fisheries for male crabs in the periods 1994 – 2010 and 2011 - 2022.

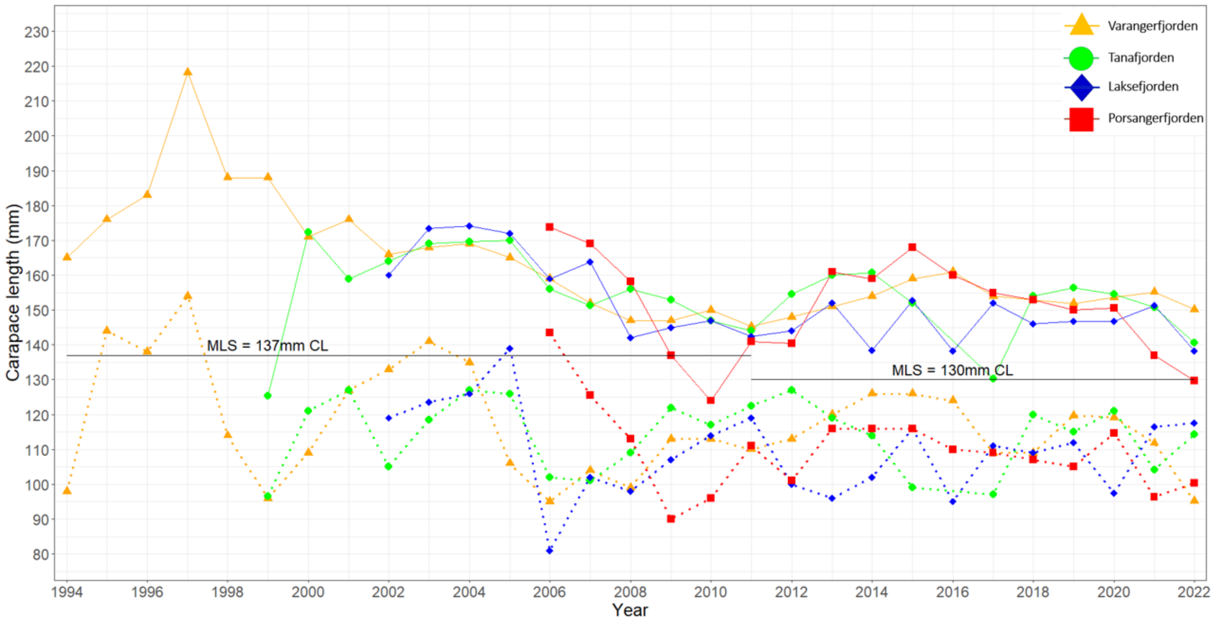

Figure 5. Presentation of 95th (solid lines) percentile and median (dotted lines) CL values for males within all fjords over time. Back line represents the minimum legal catch size for fisheries in the periods 1994 – 2010 and 2011 - 2022.

3.1.3 Relationship between ovigerous female and male maximum sizes

In the first year of sampling (1994) the 95th percentile for ovigerous female crabs is higher than the 95th percentile for males, this is the only year where this is the case (Figure 6). Another extreme value is in 1997 where a lot of large male crabs were sampled ending with a

95th percentile of 218.2 mm CL. After 2008 the CL gap between male and ovigerous female 95th size percentile narrows down. As for 2022 the difference between male and female 95th percentiles are only 6.4 mm CL. There has been a clear reduction in the gap between male and ovigerous female 95th percentile CL estimates, the size composition of ovigerous females have been consistent from 2002 till 2022 whereas the male size composition has consistently decreased and gotten closer to the female upper limit (Appendix 15).

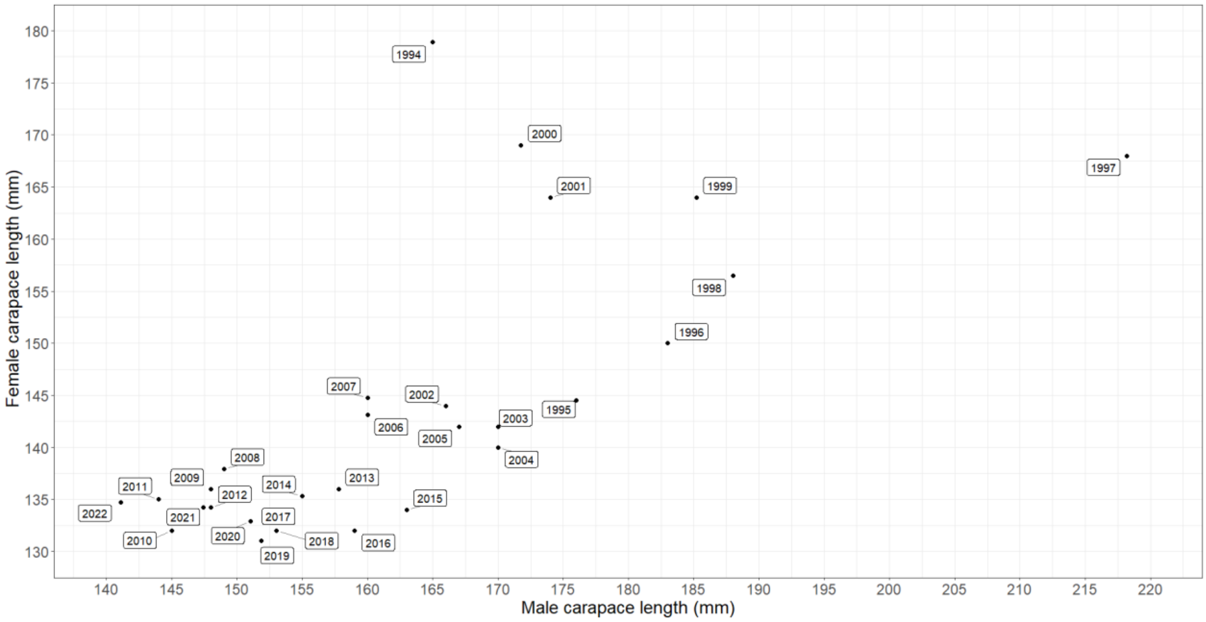

Figure 6. Scatter plot of the relationship between the ovigerous female 95th CL percentile as a function of male 95th CL percentile for each year with data from all fjords pooled together.

3.2 Size at 50% ovigerous length

The CL at which a randomly selected female has a 50% probability of being ovigerous was estimated to be 108.7 mm CL (0.066 mm SE) for all fjords through the whole sampling period (Appendix 16). Time series of OL_{50} from the fjords show negative trends in OL_{50} within all fjords measured (Figure 7), where the estimated values in 2022 is statistically significantly different, with no overlap in confidence intervals between the first and last estimated OL_{50} value (see Appendix 17 each fjord plotted separately with 95% CI).

Varangerfjorden follow a pattern of high and stable OL_{50} values for the first 3 years, before spiking at a value 118.6 mm CL in 1997, then dropping down till its lowest estimated value of 103.5 in 1999. Before increasing to a value of 111.6 mm in 2005, then gradually decreasing until 2022 (Appendix 17, top left). Tanafjorden start off with its highest estimated value of

117.6 mm CL in 1999, then decreasing quite fast. Then peaking again in 2015, before decreasing (Appendix 17, top right). Laksefjorden starts off with an estimated OL_{50} value of 112 mm CL in 2022 before gradually decreasing with a lot of variability through the year down to its lowest estimated value of 106.6 mm CL in 2022 (Appendix 17, bottom left). Porsangerfjorden show the most distinct negative trend in OL_{50} peaking at 115.6 mm CL in 2008 before gradually decreasing down from then on (Appendix 17, bottom right). As of 2022 the estimated OL_{50} for Varangerfjorden and Tanafjorden were statistically significantly different from each other with Varangerfjorden having a higher OL_{50} estimate (Appendix 18). No statistically significantly differences in estimates were found between Varangerfjorden, Laksefjorden and Porsangerfjorden nor between Tanafjorden, Laksefjorden and Porsangerfjorden.

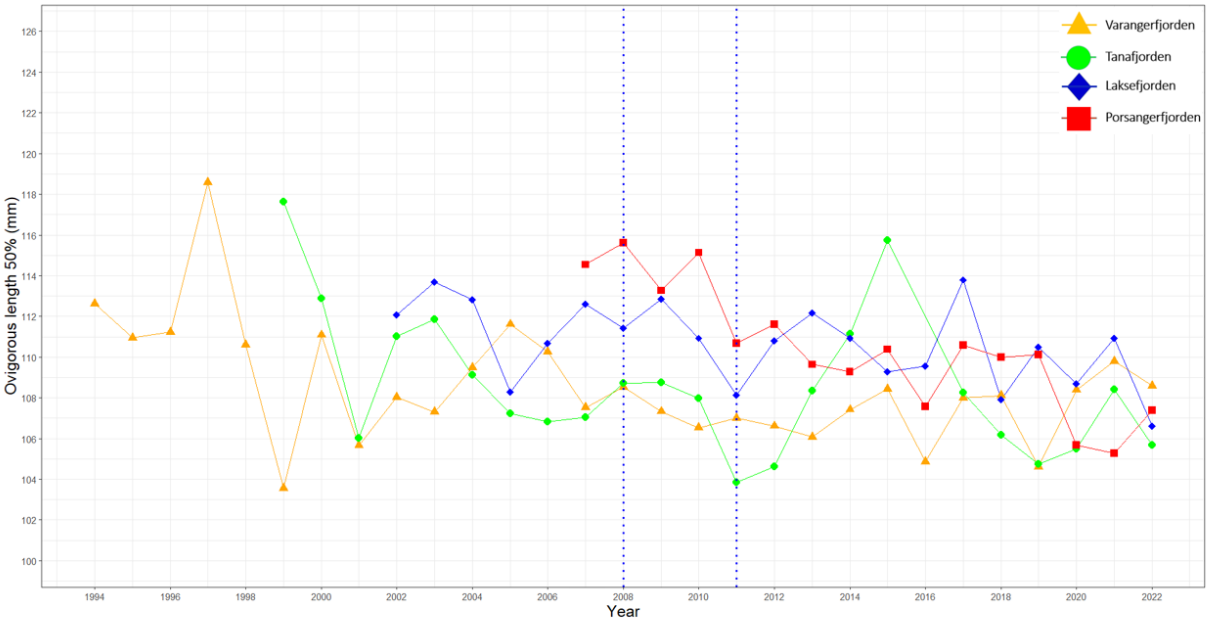

Figure 7. 50% ovigerous length estimates over time for Finnmark fjords over time. Blue dotted vertical lines indicate the changes in fishery introducing a quota on female crabs in 2008 and reduced minimum legal catch size in 2011.

Pooling three different time periods; before female quota (2002 – 2007), the three-year period between the introduced female quota and the reduction in MLS (2008 -2010), and after the reduction in MLS to 130 mm CL (2011 – 2022), OL_{50} estimates show statistically significantly differences between the three periods (Figure 8). The two first time periods do not differ significantly with estimated values of 109.52 mm and 109.91 mm CL respectively. However, the last period from 2011 till 2022 has statistically significantly lower OL_{50} (108.04 mm CL) than the two before (Figure 8).

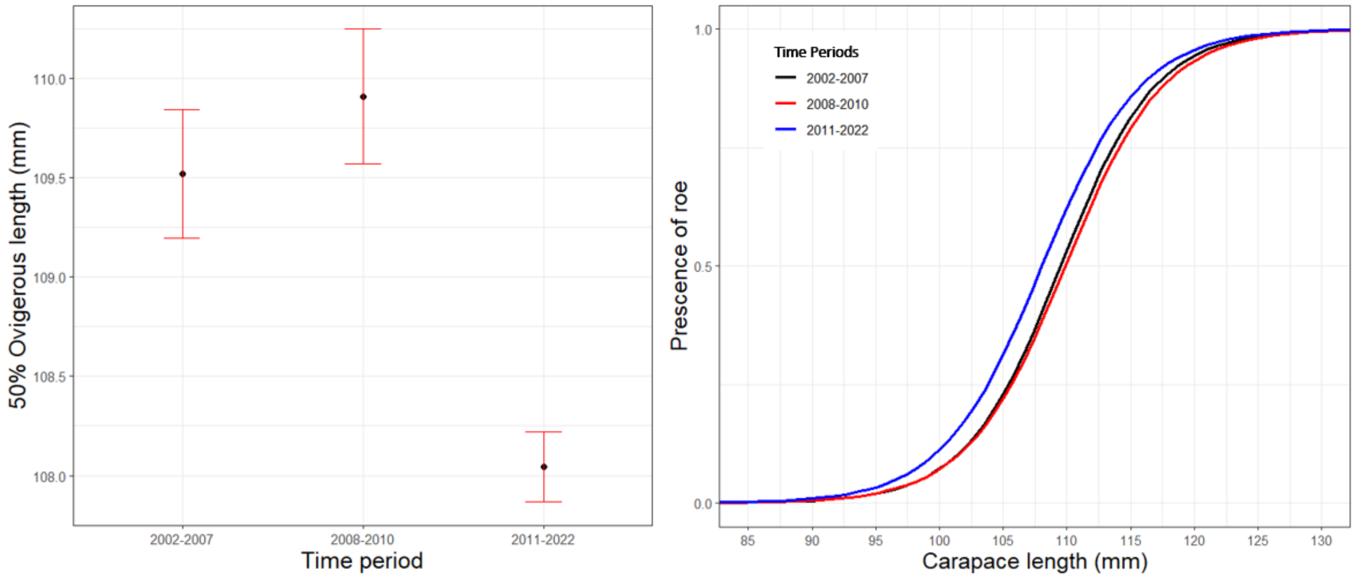

Figure 8. OL_{50} estimates from all fjords pooled into three different time periods: 2022-2007, 2008-2010, and 2011-2022. Size at maturity (mm) plots with estimated 95% confidence interval as error bars for each period (left). Binary logistic regression curves for presence of roe as a function of CL for each period (right).

3.3 Reproductive data overview

There is observed noticeable reduction in the CL ranges for the female crabs sampled for fecundity measurements from 2000 to 2022 in Varangerfjorden and Tanafjorden (Table 1). The lower range of CL values remains approximately the same over time, whilst the upper ranges has decreased. In Varangerfjorden the maximum CL values has dropped from 170 – 180 mm CL in the 2000 and 2001 then gradually dropping down to 140 – 150 mm CL in 2022. Similar trend is demonstrated by Tanafjorden from 2000 to 2007 where the upper range of CL estimates goes down from 186 mm down to 144 mm.

The negative trends in upper ranges of CL clearly affects both the upper ranges in dry weight of roe and fecundity which is demonstrated in Varangerfjorden and Tanafjorden, whilst Laksefjorden show no noticeable trends in CL or fecundity. Porsangerfjorden demonstrates a negative trend in fecundity, however it can't be tied to reduced CL values as there are no CL estimates in 2017. The total number of eggs per crab sampled ranged from 558 000 down to 38 000 in Varangerfjorden, from 498 000 down to 32 000 in Tanafjorden, from 387 000 down to 86 000 in Laksefjorden, and 321 000 down to 49 000 in Porsangerfjorden. Whereas the Varangerfjorden, Tanafjorden, and Porsangerfjorden demonstrates negative trends in upper fecundity ranges, Laksefjorden show a weak increasing trend in the upper ranges of CL, reproductive investment and fecundity. The upper CL range in Laksefjorden increases from

158 mm in 2004 to 170 mm CL in 2007. So does the upper fecundity range for Laksefjorden where the maximum egg count in 2004 were 369 000 eggs, it has then increased to 477 000 eggs in 2007.

There were no noticeable trends in IEW ranges for any of the fjords, and it does not seem to be affected by the reduction in upper CL ranges. The estimated fecundity ranges from this study estimate that crabs from Varangerfjorden 2022 have between 328 000 and 59 000 eggs, Porsangerfjorden 2017 have between 321 000 and 72 000 eggs, whilst in 2022 the range has decreased down to between 183 000 to 49 000 eggs.

Table 1. Overview for reproductive data measurements from each fjord and year. With the number of crabs (n) and minimum and maximum ranges for CL, dry roe mass (g), individual egg weight (mg) and egg count in thousands.

Year	Fjord	n	CL range (mm)	Dry weight of roe (g)	Individual egg weight range (mg)	Fecundity range (total egg count in thousands)	Source
2000 – 2022	ALL	1314	91 – 187	7.01 – 123.11	0.11 – 0.358	32 – 558	
2000	Varangerfjorden	34	99 – 173	17.78 – 106.03	0.204 – 0.272	70 – 477	Hjelset et al., (2012)
2001	Varangerfjorden	47	98 – 183	13.41 – 123.11	0.192 – 0.265	58 – 558	
2002	Varangerfjorden	50	103 – 156	10.03 – 76.25	0.198 – 0.284	51 – 316	
2003	Varangerfjorden	45	99 – 170	8.85 – 75.39	0.16 – 0.274	42 – 334	
2004	Varangerfjorden	47	99 – 161	7.55 – 67.02	0.103 – 0.267	38 – 347	
2005	Varangerfjorden	46	100 – 150	12.56 – 61.98	0.168 – 0.245	52 – 339	
2006	Varangerfjorden	54	93 – 155	8.25 – 83.83	0.193 – 0.26	32 – 345	
2007	Varangerfjorden	45	98 – 144	8.84 – 44.88	0.176 – 0.258	38 – 218	
2008	Varangerfjorden	31	100 – 133	9.56 – 43.87	0.241	40 – 182	Høyning (2012)
2010	Varangerfjorden	57	100 – 152	10.13 – 55.52	0.232	44 – 240	
2011	Varangerfjorden	52	95 – 149	11.23 – 58.12	0.233	44 – 249	
2013	Varangerfjorden	44	93 – 147	7.46 – 48.9	0.234	32 – 209	
2015	Varangerfjorden	56	91 – 145	9.73 – 50.6	0.257	38 – 197	
2016	Varangerfjorden	68	98 – 145	13.93 – 49.4	0.236	59 – 209	
2022	Varangerfjorden	44	103 – 144	12.48 – 64.41	0.182 – 0.24	59 – 328	This study
2000	Tanafjorden	41	102 – 178	16.85 – 115.86	0.212 – 0.289	73 – 474	Hjelset et al., (2012)
2001	Tanafjorden	47	97 – 186	18.62 – 119.71	0.214 – 0.287	69 – 498	
2002	Tanafjorden	34	105 – 187	16.15 – 102.51	0.214 – 0.285	64 – 392	
2003	Tanafjorden	42	101 – 143	17.57 – 77.34	0.204 – 0.264	76 – 338	
2004	Tanafjorden	46	99 – 166	9.37 – 82.32	0.19 – 0.273	49 – 383	
2005	Tanafjorden	52	96 – 156	7.88 – 74.76	0.209 – 0.358	32 – 322	
2006	Tanafjorden	53	96 – 162	12.81 – 66.22	0.205 – 0.264	62 – 287	
2007	Tanafjorden	37	105 – 144	7.01 – 50.3	0.179 – 0.279	34 – 220	
2004	Laksefjorden	25	105 – 158	25.48 – 86.97	0.214 – 0.242	112 – 369	
2005	Laksefjorden	44	108 - 166	25.61 – 89.91	0.115 -0.265	98 – 380	
2006	Laksefjorden	55	101 - 170	22.68 – 91.44	0.162 – 0.308	86 – 387	
2007	Laksefjorden	58	99 – 170	12.25 – 116	0.173 – 0.351	55 – 477	
2017	Porsangerfjorden	17	NA	18.39 – 77.38	0.221 – 0.273	72 – 321	This study
2022	Porsangerfjorden	77	96.3 – 135	10.84 – 40.46	0.189 – 0.245	49 – 183	

3.4 Reproductive investment

The RI represented by the loess regression line show a small peak at approximately 125 mm CL. The standard error of the loess line become larger among crabs smaller than 110 mm CL and larger than 150 mm CL (Figure 9).

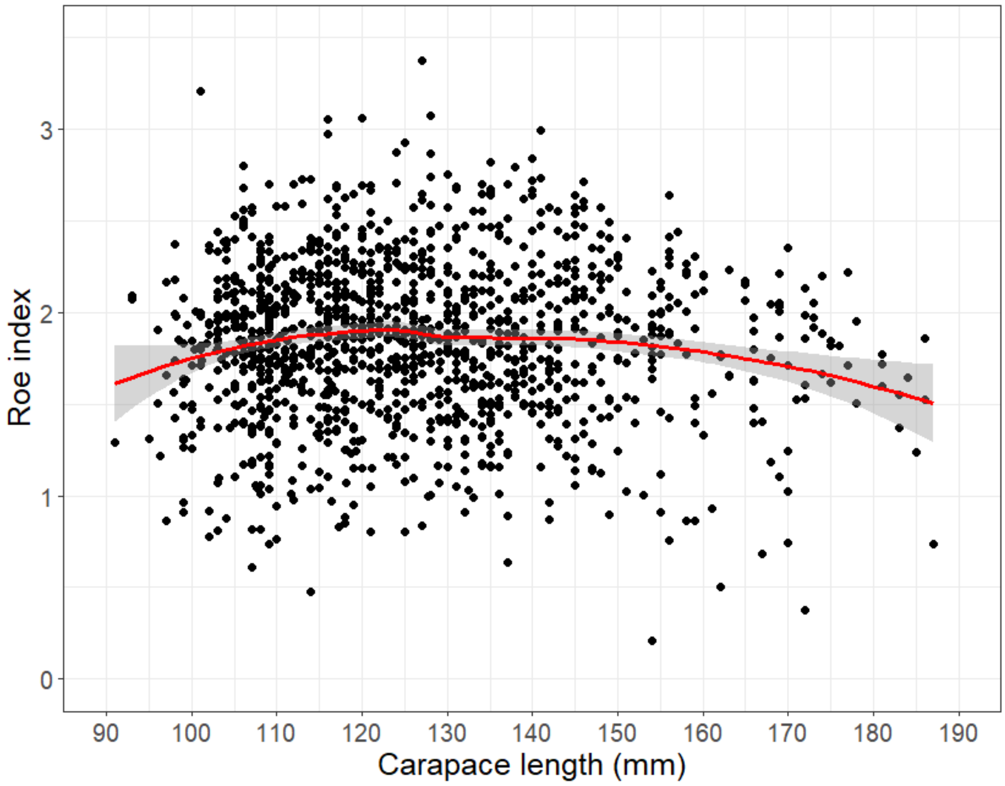

Figure 9. Roe index as a function of CL. Fitted loess regression line (red) with one standard error.

There is a clear correlation between dry egg mass and CL, and that that energy invested into reproduction increases exponentially with increasing CL ($p < 0.001$) (Figure 10). The fitted loess line (red) deviates from the regression line (black) among smaller and larger CL values. Estimates for the regression coefficient (*b*) for each year and fjord showed variability both within fjords from year to year as well as between fjords, with only Laksefjorden having one estimate for 2007 being statistically significantly different from its 2005 estimate and Varangerfjorden's 2004 estimate (Appendix 19 & 20).

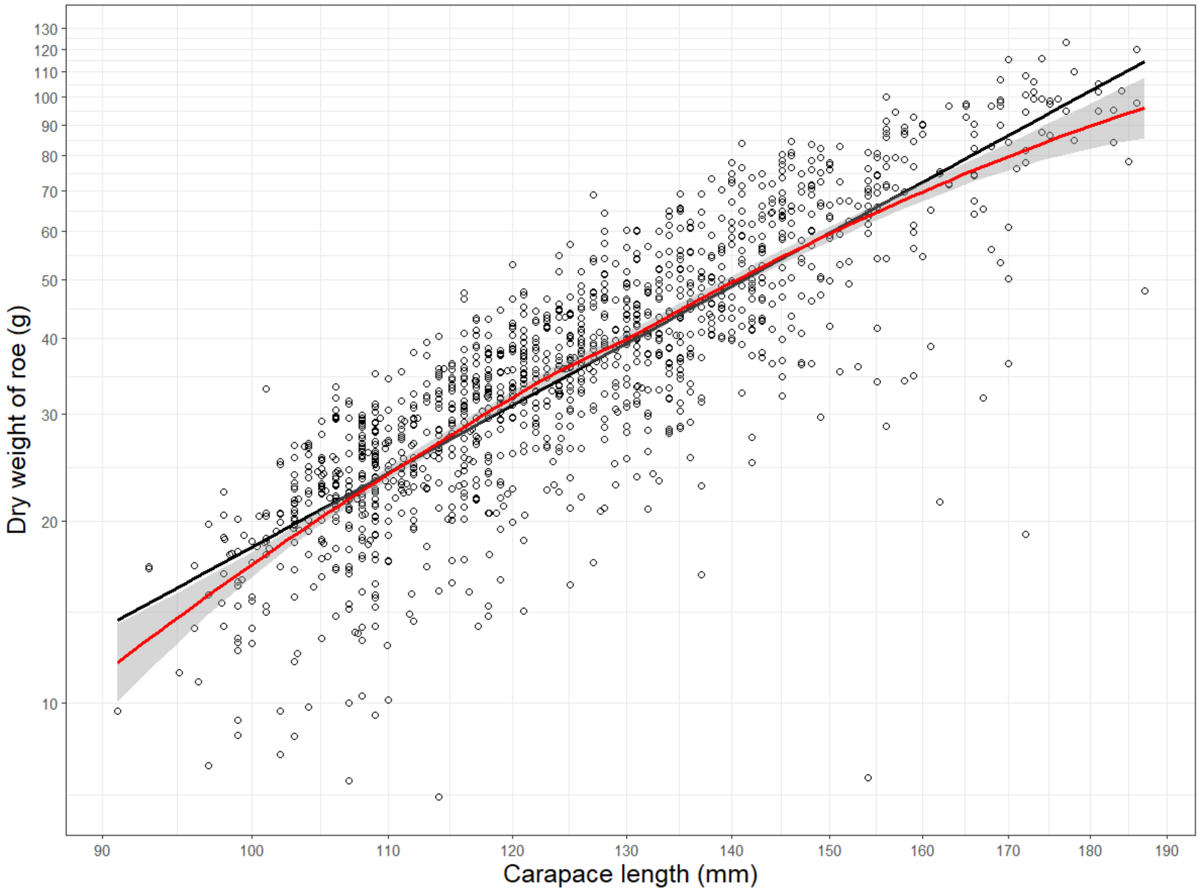

Figure 10. Dry weight of roe (g) as a function of CL from all fjords and years pooled together. Both variables are log transformed. Both axis values converted to normal scale. Estimated regression line (black). Loess regression line (red) with one standard error.

3.5 Individual egg weight

The mean weight of one egg were estimated to be 0.23 mg for the whole sampling period. The ANCOVA show that there are variations in mean IEW over time ($p < 0.001$), between fjords ($p < 0.001$), and between fjords over time ($p = 0.03$) (Table 2). However, variance in mean IEW can't be explained by CL ($p = 0.47$). The model with the lowest AICc value for investigating variance in IEW included the interaction between Year and Fjord as parameters (Appendix 21). The variation in mean IEW is further illustrated with the mean value of each year and fjord with 95% CI around the mean in Figure 11. All fjords show clear variation between years where the mean value for a given year is statistically significantly different from another year. There are significant differences in mean IEW between fjords in the years between 2000 and 2007. For Porsangerfjorden, IEW is significantly different between 2017 and 2022. There was no notable difference between Varangerfjorden and Porsangerfjorden in 2022.

Table 2. ANCOVA for individual egg weight against listed parameters from Varangerfjorden (2000 – 2007, and 2022), Tanafjorden (2000 – 2007), Laksefjorden (2004 – 2007), and Porsangerfjorden (2017 and 2022). Listed model parameters are; degrees of freedom (df), f-value and p-value.

Period	Parameters	Model Parameters		
		df	F-value	p-value
2000 – 2022	Year	1	13.5	< 0.001
	Fjord	3	7.3	< 0.001
	CL	1	0.5	0.47
	Year × Fjord	2	3.4	0.03
	Residuals	955		

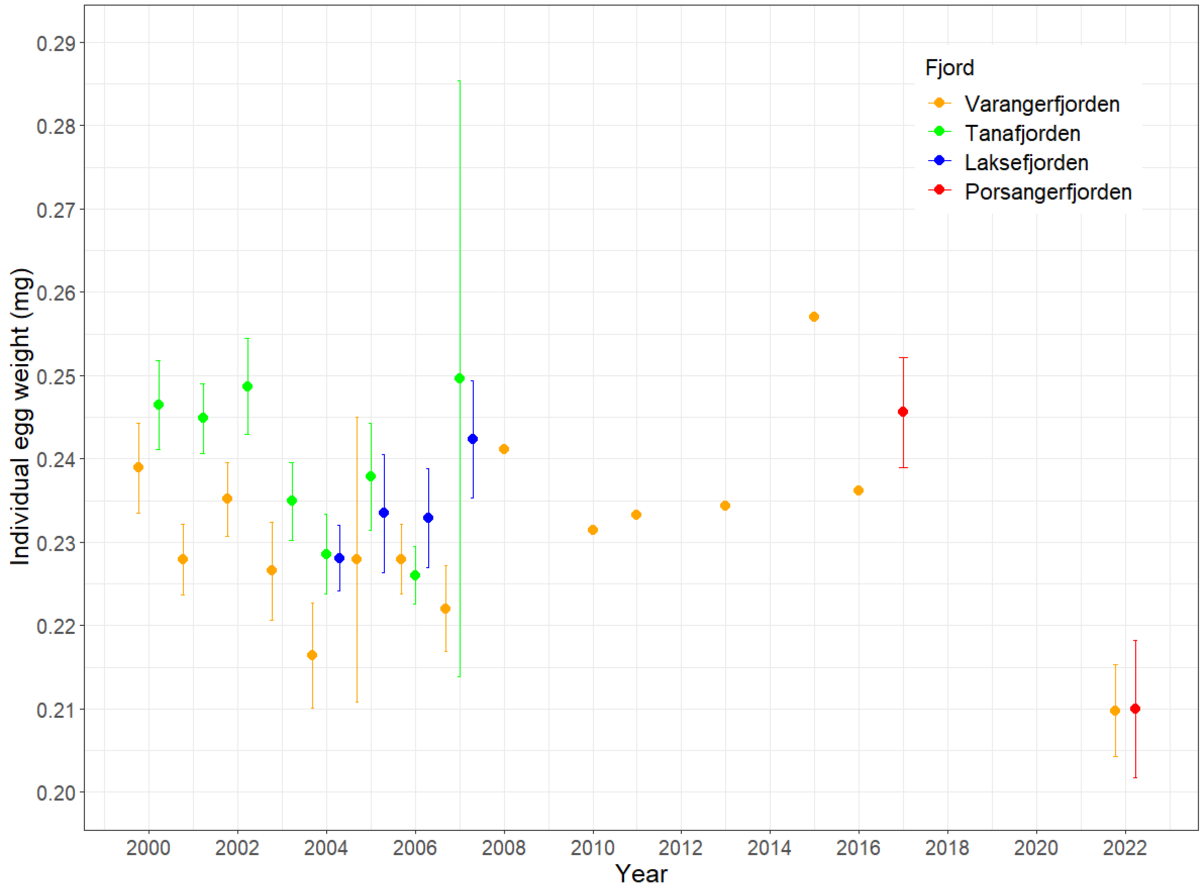

Figure 11. Mean individual egg weight (mg) with 95% CI for each fjord from year 2000 till 2022 (See Appendix 6 for exact values and Standard errors).

3.6 Reproductive investment and fecundity of a standardized ovigerous female

All fjords measured for several year show initial negative trends for both dry weight of roe and fecundity for a standardized ovigerous female (125 mm CL) (Figure 12 & Appendix 22). For Varangerfjorden, Tanafjorden and Laksefjorden, the measured values follow the same initial negative trends in the start before the sampling periods ends for Tanafjorden and Laksefjorden in 2007. Both dry weight of roe and fecundity for Varangerfjorden flattens out from 2006 till 2022 where both Varangerfjorden and Porsangerfjorden have similar estimated values.

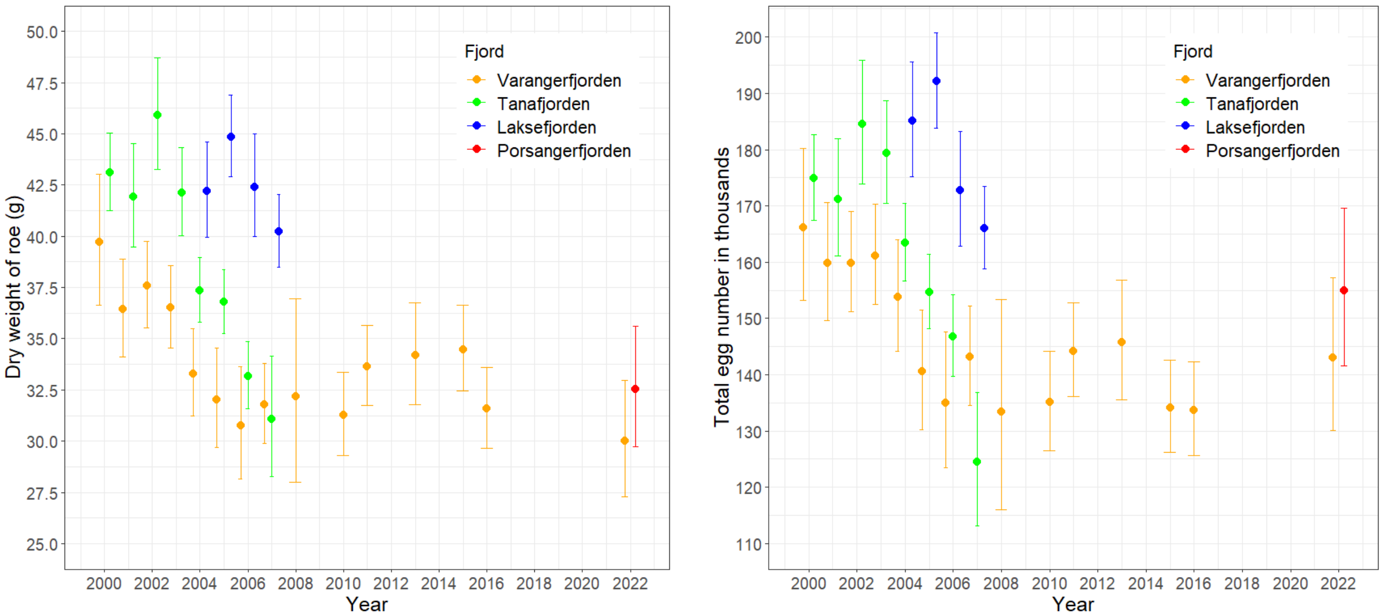

Figure 12. Estimated total dry roe mass in grams (left) and total egg counts in thousands (right) for a standardized 125 mm carapace length crab with 95% CI for each fjord over time.

4 Discussion

As this study is based on a dataset spanning almost 30 years of sampling (1994 – 2022), a considerable amount of hard work has gone into sampling each year and fjord, and further estimating fecundity for a total of 16 years through laboratory procedures. Based on the groundwork laid down by Hjelset (2012), Lindberg (2012) and Høyning (2018), this study has furthered the time series of size composition, OL_{50} values, variance in individual egg weight, reproductive investment, and fecundity for red king crab within the four largest fjords in eastern Finnmark county.

This study's findings are in line with what has been described earlier in Hjelset (2012), Lindberg (2012), and Høyning (2018). Initial reduction in size composition for both sexes across all fjords before flattening out with a further reduction in the number of large males and large ovigerous females (Figure 2, 3, 4, & 5). A tendency towards a reduction in the size where a randomly selected female has a 50% chance of being ovigerous (OL_{50}) (Figure 7), where the introduction of a female quota and reduction in MLS have affected OL_{50} (Figure 8). There is still no correlation between CL and IEW however there are variances between years and fjords (Table 2 & Figure 11). A standardized ovigerous (125 mm CL) female is generally less fecund now than a crab of the same size was in 2000. This trend is categorized by an initial reduction right after sampling started before flattening out in approximately 2008 and remaining approximately consistent from 2008 till 2022 (Figure 12). The fjord seems to follow an east to west trend where the fjords follow the same trends with a few years lag between them. This is consistent with the invasion history of the red king crab gradually moving westward over time. This is the same conclusion made by Hjelset, (2012).

The agassiz trawl and pots used for sampling crabs do a great job of sampling a representative size composition of ovigerous females, however it does leave out a considerable amount of the smaller size ranges of male crabs (< 70 mm CL) (Lindberg, 2012). The male crabs do not just appear as approximately 70 mm CL of size as the size composition figures may suggest, and there are smaller crabs in the population that does not get sampled annually using these methods.

There are some concerns regarding the invasiveness of the equipment and methods used for red king crab sampling. The use of pods have previously shown an injury rate of 2%, and a

0.1% mortality rate on crabs (Byersdorfer et al., 1992). Whilst commercial trawls have shown an instant mortality rate as high as 47% on red king crab (Stevens, 1990). Lindberg (2012) noted that whilst in Porsangerfjorden that the use of trawls inflicted more serious injuries and mortality than pods do. The process of cutting off pleopods for roe samples before releasing the female back to the ocean may sound brutal, whilst it is not a fatal procedure for the crab as they possess the ability to regrow lost limbs. It is overall a taxing experience for the female as it has to invest energy into regrowing the lost pleopods, and therefore may not have the excess energy to produce roe for the coming spawning event.

During both lab work and data treatment, several challenges were encountered. From the estimating of IEW at laboratory where egg membranes would break, either when being detached from the pleopod, or when separating from each other within the counting chamber to make it easier and less time consuming to count. This would not affect the overall estimated dry weight of the subsample, however reducing the number of eggs counted resulting in potentially a higher IEW for 2017 and 2022 estimates, further leading to a lower calculated fecundity. This is however something both Lindberg (2012) and Høyning (2018) has identified as possible issue in their theses as well. So overall it should not affect the greater fecundity results that were dependant on IEW values. As these study’s estimated IEW for 2022 is the lowest estimated so far, the notion that a considerable number of eggs may have been destroyed during laboratory procedures can be discarded. However, the general level of uncertainty introduced through egg handling at lab is not expected to have a significant impact on the results as the breaking of eggs seems to be a reoccurring problem.

As notable in the fecundity data overview (Table 1) there is no CL range for Porsangerfjorden 2022. This is either due to an error at the time of sampling where the serial number were not noted down onto the zip-lock bag, or the serial number were not noted down during laboratory procedures of this study. Either way there is as of now no way to connect the crab from the fecundity dataset to the crabs within the IMR database as the serial number is missing from the fecundity dataset, which is unfortunate, because it leads to this study only having one point for reproductive investment and fecundity for Porsangerfjorden.

The decision to exclusively use dry weights for IEW, reproductive investment and fecundity estimates where made after the realization that when the whole wet roe mass sample were placed on the laboratory weight, the weight would gradually decrease as water slowly evaporated. To add further uncertainty to the wet estimates, adding water to the counting chamber made the separation of eggs from the hairs that connected them easier. Further making the counting of subsamples less time consuming and reduced the likelihood of egg membranes getting punctured. Increasing uncertainty around wet weight estimate but reducing the uncertainty for dry IEW estimates.

Several challenges arose from the general patchiness of the fecundity data as the dataset now was a combination from three different contributors, having their data set up in different ways. Making the datafiles compatible with each other was a generally time-consuming procedure. As mentioned in materials and methods the IEW values for Varangerfjorden 2008 – 2016 only consisted of the mean value given to every crab for a given year meaning no variance around the mean value for each year. Therefore, these data needed to be excluded from the ANCOVA of IEW, because including these data would lead to the conclusion that there was no variance in IEW between years.

All in all, the inclusion of the fecundity data provided to this study by Hjelset (Hjelset, 2012) and Høyning (Høyning, 2018) has contributed greatly to the visualization of trends in reproductive investment, IEW and fecundity across fjords and years. As visualizing trends in fecundity with only data from 2017 and 2022 would not suffice.

4.1 Size composition

The decision to pool all data together for both male and ovigerous females to illustrate trends in size composition were made because all fjords followed similar trends and the estimated percentiles were relatively close to each other after 2008. Presenting the spread of data over time as a size composition plot gives an insight into variability among size estimates, and clearly demonstrates the narrowing tendencies of CL ranges in the bulk of the stock over time. This is clear in the start of the sampling period for both sexes that there were distinct age classes that have been evened out over time as the larger crabs disappear.

As of 2022 there are few large male crabs left in the fjords, where only 2.5% of the male crabs sampled and only one (0.25%) ovigerous female was considered large (≥ 150 mm CL). This trend is present within each fjord ass well, where in Tanafjorden and Laksefjorden there were caught more females larger than the MLS than there were males larger than the MLS.

Using ovigerous females as the baseline for sexually mature females introduces a level of uncertainty. Whilst one guaranties that the ovigerous females are sexually mature, there are a few large non-ovigerous crabs being excluded that are most likely sexually mature. Within the 2022 samples, there were a few female crabs larger than 130 mm CL that were non-ovigerous and therefore excluded from the data (Appendix 23). Out of the roughly 49 000 female crabs from the whole sampling period there were 2590 non-ovigerous crabs larger than the estimated OL_{50} of 108.7 mm CL, meaning that as a “worst-case” scenario, 5% of female crabs that are sexually mature ends up being considered non ovigerous and therefore excluded from the dataset. However, the true value of sexually mature female crabs that are being falsely identified as immature is probably much lower than this and does not significantly affect the results of this study.

The size composition for ovigerous females has gradually decreased across the fjords over time. Starting with initial negative trends in size composition before female quota was introduced, indicating that the implementation of a female commercial fishery quota in 2008 may not be the primary reason behind the reduction in size distribution for ovigerous females. However, it is clear that close to 95% of the ovigerous female crabs are smaller than the MLS, and their distribution has been like that since the introduction of the female quota (Figure 3). Only in the initial years of sampling (before 1998) was the median value of ovigerous females larger than the minimum legal catch size of today (Figure 2 for all fjords together & Appendix 7 – 10 for each fjord individually).

The four fjords demonstrate similar negative trends in size composition of males. This seems to consistently happen right after the first few samplings take place and fishing pressure is induced on the stock. As of 2022, the majority of male crabs are smaller than the minimum legal catch size whereas the median value has been as high as 160 mm CL from 1996 till 1998 before the median value started decreasing (Figure 4). For males the lower fifth percentile stays relatively consistent through all fjords over time. This can be explained by the sampling equipment not being designed to catch crabs smaller than roughly 70 mm CL.

The gap between male and ovigerous female 95^{th} CL percentiles has narrowed over time, and as of 2022 the gap between them were 6.4 mm. The 2022 value is the lowest 95^{th} percentile CL ever measured for males, approximately 12 mm CL larger than the MLS, and it is a gradually but noticeable decrease in the amount of large male crabs even though the CL ranges have remained approximately constant (Figure 4). The reduction of the size gap between the largest individuals can affect the reproductive potential of the stock. As females are dependent on larger males for protection during mating a skewed sex composition among larger individuals could lead to an increased amount of large non-ovigerous females and a decrease of the reproductive stock. As the male crab are polygamic a skewed population sex structure would not affect the reproductive potential of the stock as a few large males could even out the skewed sex composition (Jewett and Onuf, 1988). The concern arises when considering that the handshaking in mating couples spans roughly 30 – 40 mm CL (Schmidt and Pengilly, 1990; Nilssen and Sundet, 2006), and as there are only a few males that are large enough to mate with the largest females, this could become a problem and lead to a higher number of females failing to mate as a result of high fishing pressure on male crabs (McMullen, 1967; McMullen, 1968). As of 2022 the vast majority among large females are ovigerous with a few exceptions (Appendix 23). Investigating a possible increase in large non-ovigerous females is outside this thesis focus it would be interesting to investigate further.

As the effects of fishery pressure is concerned, the introduction of a female quota in 2008 does not seem to have greatly affected the size composition of ovigerous females as the quotas are far smaller than male quotas (Figure 2 & 3) (Hvingel et al., 2022). However, the reduction in ovigerous female size composition seem to follow the changes in male size composition. It has been theorized that the high fishing pressure on male crabs have resulted in a higher injury-induced mortality among females caught during fishery that could lead to a decline in size composition (Kruse, 1993; Hjelset, 2014). All in all the reduction in size composition seen in both male and ovigerous females are likely caused by high fishing pressure (Hjelset, 2014), and that the majority of the crabs are now smaller than the MLS since the landings have stabilized in the 1 300 – 1 700 tonnes range for males and 100 – 120 tonnes range for females in recent years (Hvingel et al., 2022).

4.2 Size at 50% ovigerous length

Determining sexual maturity based on the presence of eggs is a simple yet effective method involving the inspection of the females abdomen allowing for large sample of crabs to be determined as ovigerous or non-ovigerous in a short amount of time, and little effort (Hjelset et al., 2009). This study's results display great year to year variations in OL_{50} estimates within all fjords seen in both estimates, and 95% CI adding to the uncertainty of the estimated trends (Figure 7 & Appendix 17). The year-to-year variability within fjords can be explained by variance in sampling as well as strong year classes. Latitude, temperature, food availability and growth has also been confirmed as factors leading to regional variability in size at maturity (Otto et al., 1990; Hjelset et al., 2009). Large females that are falsely identified as non-ovigerous could lead to an increase in the OL_{50} estimate.

This is the reason behind why the 50% ovigerous length estimates was calculated by only using crabs between 80- and 140-mm CL to avoid any possible large female crabs that most likely are mature that were classified as non-ovigerous. Removing the crabs smaller than 80 and larger than 140mm CL did affect the overall results since before removing them Laksefjorden did not show a statistically significant trend, and the negative trend within Tanafjorden became more distinct after removing the small and large crabs.

It has been described several times that red king crab from "pods" with crabs of roughly the same sizes (Powell and Nickerson, 1965; Dew, 1990). It's been described that adult and juvenile red king crabs prefer different types of substrates, whilst juvenile crabs are found to prefer hard bottom substrates, adult crabs have been found to prefer soft bottom substrates (Marukawa, 1933; Wallace et al., 1949). Immature crabs tend to stick to more shallow waters and have rarely been observed among mature crabs in deeper waters (Wallace et al., 1949). Meaning that the spatial distribution of red king crab is highly dependent on their sex, size and their current maturation stage (Lindberg, 2012). Therefore, all data used were from autumn samplings where the mature red king crabs is known to be more stationary (Hjelset, Personal conversation).

All the fjords examined demonstrated negative trends in OL_{50} with their estimated value for 2022 being statistically significantly lower from their first estimated value. To tie the changes seen in OL_{50} to fishery management three different time periods based on management shifts were investigated. This showed that the last time period (after 2011) was statistically significantly different than the first to periods (Figure 8). This would lead to the conclusion that a reduction in minimum legal catch size has affected the OL_{50} value. However, the second time period (2008 – 2010) is only spanning over three years. Three years is too short a time for the introduction of a female quota to influence the OL_{50}, meaning that the observed reduction in OL_{50} can probably be attributed to the combination of female quota and reduction in minimum legal catch size.

The negative trends seen in all the fjords, and in the last time period (2011 – 2022) may not be biologically significant differences even though they are statistically significantly different. This is due to the way king crabs grow through increments when moulting. Studies has shown that the female growth rate is inconsistent in comparison to the growth rate of males. Laboratory experiments with females in captivity, showed that pubertal females (crabs with mature ovaries, just prior to their maturity moult) has a growth increment of 16.2 mm CL (Stevens and Swiney, 2007a; Hjelset et al., 2009). As this is the approximate size range that is identified in the OL_{50} estimates, this means that the changes observed in these fjords and time periods may only be within a single moult increment and therefore not biologically significantly different. Therefore, one cannot conclude that there is a biologically significant difference in size at maturity even though the estimates are statistically significantly different. Further primiparous crabs have a growth increment of 7.5 mm and multiparous females have a growth increment of 4.7 mm (Stevens and Swiney, 2007a). This reduction in increments makes identifying year to year classes from the size composition with increasing size in ovigerous females (Hjelset et al., 2009). Hjelset et al., (2009) wrote down that the fluctuations in OL_{50} are most likely caused by differences in year class strength. Therefore, polling data together were recommended to even out year to year variation (Otto et al., 1990).

Reduction in size and age at maturity due to heavy fishing pressure on larger individuals has been observed in some heavily exploited cod stocks (Andersen et al., 2007; Jørgensen et al., 2007). The commonality between red king crab fisheries and cod commercial fisheries is that the exploited portion of the population are the larger individuals. It is therefore interesting to investigate if high fishing pressure could have had similar effects on the Norwegian king crab population. Meaning that a reduction in OL_{50} for red king crab due to high fishing pressure is entirely possible if fishery pressure increases. With there being high variability in size at maturity in the red king crabs' native areas, and these also sexually mature at a much smaller size than in Norwegian waters, indicating that the red king crabs have the capability to mature at much smaller sizes (Marukawa, 1933). A reduction in size at maturity would decrease the growth rate of females giving them the chance to reproduce more times before being of legal catch size, but with a lower total reproductive potential. With the current MLS for fisheries a female crab may have the chance to reproduce 3 – 4 times before reaching MLS (Lindberg, 2012).

Hjelset, (2012) concluded that the size at maturity has been stable throughout the sampling periods and that the larger size at maturity compared to native waters may be caused by good growth conditions, and is not influenced by the change in level of exploitation. This could entail that the reduction shown in OL_{50} estimates could be related to a decrease in benthic biomass and high-quality food items, which has been described as a result of the red king crab invasion (Otto et al., 1990; Falk-Petersen et al., 2011). However, more likely is that the tendency towards a reduction is size at maturity is correlated to the reduction in size composition in both males and females that likely correlated to fishery management.

4.3 Individual egg weight

The variation demonstrated in IEW can't be related to the reduction in the 95th CL percentile since the variance in IEW cannot be explained by variance in CL values ($p = 0.47$). Figure 11 can be regarded as a visualization of the best model available for investigating variation in IEW. All data for Varangerfjorden are included in this visualisation of the model, however datapoints between 2008 and 2016 have no confidence intervals due to the variation around the mean being equal to zero. The model allows for identifying which years that differ from each other but also how fjords differ from each other. Even though there are statistically significant differences between fjords and years, there is no clear trends in IEW over time. New 2022 IEW values in Varangerfjorden and Porsangerfjorden are the lowest estimated values for the whole sampling period from 2000 to 2022. These two values from the two fjords were not significantly different from each other and there was overlap between the 95% CI for Varangerfjorden 2004, 2005, and 2022. The two points for Porsangerfjorden from 2017 and 2022 may indicate a significant decrease in IEW over time for this fjord, but this assumption is likely be incorrect due to the variation between years displayed by the other fjords.

4.4 Reproductive investment and fecundity

The loess regression line gave a rough approximation of which crab size invested the most of their energy budget into the production of eggs. This can be seen in Figure 9 where a slight peak at approximately 125 mm CL that would indicate that based on this study's data, the size an ovigerous female invests the most energy relative to its size is at 125 mm CL. However, the error bars are quite large in this figure without a strong curve of the regression line adding a lot of uncertainty towards the estimate. The conclusion that an ovigerous female has its optimum for reproductive investment between the CL values of 120 and 130 mm is documented in Lindberg (2012). Further it has been described that the overall condition of female crabs started to decrease as they passed the 130 – 140 mm CL threshold (Rafter, 1996; Rist, 1999). This has been further documented where a reduction in total dry weight of roe were observed when crabs passed 130 – 140 mm CL (Paul and Paul, 1997). A reduction in reproductive potential of the red king crab stock could be a possible result as female crabs reach their optimal size for reproduction at the same size as they become legally harvestable.

Whilst the corelation between how much a female crab invests into reproduction increases exponentially with increasing CL, there were quite a few outliers in the data set (Figure 10). The outlier is mainly among the smaller than110 mm CL and larger than 150 mm CL crabs, whilst the medium sized crabs have fewer outliers. Looking at the residuals for the plots it is prevalent that the outliers among larger crabs have a stronger pull than the outliers among smaller crabs, however there are more outliers among smaller crabs (Appendix 24). These tendencies are further illustrated by the red Loess line which deviates from the black regression line among smaller and larger crab sizes seen in Figure 10.

The outliers among smaller females are likely primiparous crabs, it is known that they are consistently producing less eggs than multiparous crabs (Dew and McConnaughey, 2005; Swiney et al., 2009; Lindberg, 2012). Primiparous crabs have greater egg loss through their brooding period, this is caused by primiparous and multiparous crabs having slightly differently shaped abdomens. Where the abdomen of primiparous crabs are less concave than for the multiparous crabs (Matsuura, 1985). Distinguishing between primiparous and multiparous crabs in situ is not a feasible task (Hjelset et al., 2012). However, these primiparous crab can affect the estimate correlation between reproductive investment from year to year depending on the proportion of primiparous crabs in a catch if by chance one were to get a lot of primiparous crabs within a sample. This is one of the reasons why roe samples were taken from approximately the same number of crabs across different size ranges.

The log linear model with estimated dry roe mass instead of total egg count was due to there being greater uncertainty among the prediction for smaller and larger crabs when using fecundity as response variable (Appendix 25). This is notable when comparing the two regressions in form of plots where the loess lines deviate further from the regression line in Appendix 25 using egg count as response variable than in Figure 10 using dry weight of roe as response variable. Therefore, estimating fecundity of a standardized ovigerous female through regression analysis using dry weight of roe, then transforming this estimate to fecundity gives a more certain prediction.

The discrepancies between the estimated dry roe mass through the regression model and the actual dry roe mass of a given crab become more prevalent as crabs pass 130 mm CL and become even more prevalent the larger the females get as indicated by the loess line's increased deviation from the regression line (Figure 10). This is consistent with the findings by Lindberg (2012), where he wrote that with greater CL the more variation in number of eggs is observable. This tendency towards larger females to carry fewer eggs could be correlated to the reduction in the upper size ranges of male crabs.

There are clear trends towards a reduction in reproductive investment and fecundity since year 2000 till 2022 (Figure 12). This is especially prevalent for Varangerfjorden which has the most complete time series of the four fjords. For Varangerfjorden a 125 mm CL ovigerous female invests less energy into roe production and is overall less fecund in 2022 than a crab of the same size was back in 2000. This general negative trend before flattening out found within Varangerfjorden could possibly be transferred to the other fjords based on what we see in the 7- and 4-year period of sampling in Tanafjorden and Laksefjorden, where we see the start of a s negative trend at the from 2000 till 2007 and 2004 till 2007 respectively (Figure 12). One could theorize that the values from these fjords would also flatten out after reaching the 30- till 35-gram dry roe mass or the 120 000 till 150 000 eggs range as seen within Varangerfjorden.

Since there is only one estimated point for reproductive investment and fecundity from Porsangerfjorden in this study, one can't make any conclusion regarding any trends this fjord may have followed. Lindberg (2012) estimated a 125 mm CL ovigerous female from Porsangerfjorden to have 37.24 g of dry roe mass and 167 000 eggs in autumn of 2011. These estimated values for 2011 are higher than the 155 000 eggs estimated for Porsangerfjorden 2022. However, Lindberg (2012)'s fecundity estimated value is just above the upper range of Porsangerfjorden's 2022 confidence interval estimate of 169 600 eggs (Appendix 5). Even though it was not listed in the thesis, there is almost certainly overlap between the confidence intervals of this studies 2022 fecundity estimate and Lindberg (2012) 2011 fecundity estimate for Porsangerfjorden. Therefore, one can't say that these two estimates differ significantly from each other. It is possible to theorize that Porsangerfjorden may have followed the same trend as Varangerfjorden thereby remaining at an approximately constant level from 2011 till 2022.

Investigating the distribution of residuals along the regression line as CL values increase for each fjord and year gives, insight into the uncertainties of the predicted values. What is clear from these is that they tend to curve down among smaller and larger crabs, this is the case for almost every year with a few exceptions were the lack of large grabs sampled may have affected the regression model (Appendix 26 – 29). This show that using a log linear regression model for predicting reproductive investment for ovigerous females gives good estimates for medium sized crabs between the sizes of 110- and 150- mm CL, whilst it becomes too uncertain for accurate reproductive investment predictions among crabs smaller and larger crabs outside this CL interval.

4.5 Investigating the quality of this studies measurements

It's important to investigate how roe data sampled in in this study overall compares to the data that has been processed before. When looking at the 2022 estimates of the relationship between reproductive investment and size for each fjord over time estimated regression coefficient (*b*) values for Varangerfjorden and Porsangerfjorden in 2022 do not significantly differ from the rest (Appendix 19). However, they do have some of the larger confidence intervals among the estimates, but not as large to be of any concern toward the legitimacy of the estimate as high CI is also present in earlier estimates.

The estimates for mean individual egg weight (Figure 11) show that the 2022 estimates from Varangerfjorden and Porsangerfjorden are the lowest estimated values so far. There are some overlap in confidence intervals between Varangerfjorden in 2022 and 2004 – 2005. Since there is no way for me to calculate the confidence intervals for the mean Varangerfjorden values between 2008 and 2016 one can't make any conclusion regarding decreasing trends in IEW for this fjord. However, for the two estimates for Porsangerfjorden (2017 and 2022) they are statistically significantly different from each other which would suggest that crabs from this fjord now invested more into each egg in 2017. Comparing Porsangerfjorden 2022 estimates to findings by Lindberg, (2012) where he estimated the mean individual egg weight to be 0.223mg with a standard deviation of 0.019mg in autumn 2011. This estimate is right above the 2022 estimate and there most likely being overlap in the 95%CI. This puts the Porsangerfjorden 2017 estimate into question due to it being quite a lot higher than the other two estimates, this could be due to that estimate only being made up by 17 crabs as a practise sample to try before estimating the 2022 samples, or that the samples from 2017 was from the upper spectrum of individual egg weight ranges just by chance as there has been displayed great variability between years in the rest of the fjords.

There is not much to say about the estimated 2022 values for reproductive investment and fecundity where total dry roe and total egg count are consistent with the values from 2006 till 2016, where the dry mass and egg count for a standardized ovigerous female has flattened out (Figure 12).

5 Concluding remarks and further outlook

This study has demonstrated a decrease in presence of many large individuals of both female and male crabs in the stock. During the last 10 plus years, the maximum size of both females and males has been flattening out. A further decrease in availability of large male crabs, could possibly influence the reproductive investment and fecundity in females. There are clear trends towards a reduction in the CL at which 50% of females are ovigerous for all fjords. A further reduction in size span of the ovigerous females can also reduce the reproductive life span of the stock. Temporal and spatial variability in measured individual egg weight has been demonstrated, and a standardized 125 mm CL ovigerous female is overall less fecund now, compared to previous studies.

Continuing the monitoring of size composition of both sexes is important because further decreases of large individuals left in the crab stock. Further investigating if the amount of large non-ovigerous females increases as this is an indicator of the mating success of the stock and could lead to a further decrease in stock recruitment. Size at maturity should continue to be monitored regularly to either confirm or discard the legitimacy of the negative trends seen in this study. Routinely checking the fecundity of a standardized ovigerous female crab, can say something about the reproductive potential of the stock and allows for monitoring differences between fjords. Investigating the fecundity for standardized ovigerous female in both Tanafjorden and Laksefjorden would be of interest as the status of the reproductive potential in these fjords are currently unclear.

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7 Appendix

Data tables with counts for all crabs (Appendix 1), all females (Appendix 2 left) ovigerous females (Appendix 2 right). Appendix 2 using the abbreviations; Var (Varangerfjorden), Tan (Tanafjorden), Lak (Laksefjorden), and Por (Porsangerfjorden). Then all males (Appendix 3). All crabs used for measurement were sampled in autumn from 1994 to 2022.

Appendix 1. Data table with number of crabs measured from the four fjords from 1994 to 2022 for both sexes, mature and immature crabs. All crabs sampled were in autumn.

Year	Varangerfjorden	Tanafjorden	Laksefjorden	Porsangerfjorden
1994	647	0	0	0
1995	1325	0	0	0
1996	1397	0	0	0
1997	1544	0	0	0
1998	1677	0	0	0
1999	1293	329	0	0
2000	2771	591	0	0
2001	4116	1282	0	0
2002	2062	780	236	0
2003	1702	958	524	0
2004	3598	837	517	0
2005	2980	784	392	4
2006	1954	421	375	47
2007	2293	600	1103	296
2008	1846	873	1582	618
2009	1710	1340	1140	1116
2010	1761	805	637	1842
2011	1441	398	656	1869
2012	1109	772	804	53
2013	1129	362	838	1901
2014	1432	236	1363	854
2015	1263	325	678	1474
2016	993	0	370	1272
2017	911	607	411	1069
2018	1184	489	638	1307
2019	1195	573	658	1489
2020	999	607	933	1510
2021	1161	868	915	2606
2022	2177	1348	1106	2597

Appendix 2. Data tables with number of female crabs measured from the whole sample period (1994 – 2022). Both non-ovigerous and ovigerous female crabs (left table), only ovigerous female crabs (right table). All crabs were sampled in autumn.

Year	Var	Tan	Lak	Por
1994	466	0	0	0
1995	809	0	0	0
1996	687	0	0	0
1997	938	0	0	0
1998	916	0	0	0
1999	833	171	0	0
2000	1289	306	0	0
2001	1864	613	0	0
2002	496	487	175	0
2003	618	550	252	0
2004	1240	448	180	0
2005	1300	480	151	3
2006	915	213	168	19
2007	979	302	537	88
2008	746	489	682	279
2009	692	743	482	545
2010	788	442	225	881
2011	665	194	284	1117
2012	520	544	369	31
2013	369	258	369	727
2014	505	129	687	342
2015	449	174	251	538
2016	509	0	142	524
2017	378	332	183	368
2018	603	262	298	462
2019	427	300	272	640
2020	432	412	427	680
2021	532	563	476	1533
2022	1041	970	667	1316

Year	Var	Tan	Lak	Por
1994	303	0	0	0
1995	511	0	0	0
1996	414	0	0	0
1997	649	0	0	0
1998	479	0	0	0
1999	477	29	0	0
2000	306	195	0	0
2001	1367	380	0	0
2002	350	320	123	0
2003	434	335	88	0
2004	667	302	81	0
2005	452	345	80	3
2006	212	73	18	17
2007	324	155	165	28
2008	127	211	71	93
2009	339	415	108	114
2010	286	295	85	114
2011	334	154	167	601
2012	225	507	118	16
2013	205	203	66	307
2014	239	87	180	108
2015	258	39	126	127
2016	382	0	25	221
2017	121	93	32	89
2018	291	151	131	66
2019	256	192	107	123
2020	175	340	136	385
2021	229	350	277	665
2022	226	706	536	357

Appendix 3. Data tables with numbers for all male crabs sampled form 1994 – 2022 from all fjords. Crabs were sampled in autumn.

Year	Varangerfjorden	Tanafjorden	Laksefjord	Porsangerfjorden
1994	181	0	0	0
1995	516	0	0	0
1996	698	0	0	0
1997	600	0	0	0
1998	758	0	0	0
1999	460	158	0	0
2000	1482	285	0	0
2001	2252	669	0	0
2002	1566	293	61	0
2003	1084	408	272	0
2004	2358	389	337	0
2005	1680	304	241	1
2006	1039	208	191	38
2007	1314	298	566	208
2008	1100	384	900	339
2009	1018	597	658	571
2010	973	363	412	961
2011	776	204	372	752
2012	589	228	435	22
2013	760	104	469	1173
2014	927	107	676	512
2015	814	151	427	936
2016	484	0	228	748
2017	532	275	228	701
2018	581	227	340	845
2019	768	273	386	849
2020	567	195	506	830
2021	629	305	439	1073
2022	1136	378	439	1281

Appendix 4. Data table showing estimates of 50% ovigerous length (mm) with standard error (SE) of each fjord and each year after sampling of crabs started in the given fjord.

Year	**Varangerfjorden**		**Tanafjorden**		**Laksefjorden**		**Porsangerfjorden**	
	OL_{50}	SE	OL_{50}	SE	OL_{50}	SE	OL_{50}	SE
1994	112.619	1.067						
1995	110.946	0.499						
1996	111.222	0.590						
1997	118.580	1.192						
1998	110.613	0.586						
1999	103.562	0.545						
2000	111.085	0.405	117.629	3.843				
2001	105.657	0.378	112.878	0.897				
2002	108.036	0.677	106.003	1.060	112.075	1.309		
2003	107.301	0.671	111.003	0.746	113.683	1.042		
2004	109.486	0.457	111.850	0.624	112.812	0.937		
2005	111.609	0.538	109.137	0.640	108.284	2.725		
2006	110.260	0.659	107.232	0.641	110.677	3.284		
2007	107.516	0.432	106.836	0.917	112.587	0.789	114.541	2.508
2008	108.525	0.567	107.036	0.742	111.424	0.727	115.605	0.779
2009	107.327	0.473	108.729	0.483	112.859	0.833	113.267	0.809
2010	106.523	0.534	108.759	0.396	110.932	1.053	115.129	0.661
2011	107.004	0.465	107.971	0.605	108.122	0.808	110.663	0.408
2012	106.614	0.593	103.842	1.536	110.807	0.631	111.605	2.568
2013	106.078	0.686	104.617	1.638	112.176	1.106	109.635	0.468
2014	107.421	0.558	108.354	1.433	110.931	0.577	109.284	0.654
2015	108.440	0.700	111.131	1.183	109.274	0.700	110.378	0.614
2016	104.870	0.688			109.563	1.114	107.577	0.516
2017	108.004	0.673	108.238	0.654	113.795	1.527	110.572	0.664
2018	108.110	0.478	106.165	0.766	107.905	0.704	109.984	0.743
2019	104.622	0.648	104.757	0.967	110.475	0.780	110.116	0.537
2020	108.381	0.671	105.485	0.983	108.698	0.731	105.666	0.517
2021	109.803	0.536	108.420	0.601	110.932	0.527	105.281	0.322
2022	108.588	0.545	105.674	0.563	106.595	0.653	107.377	0.368

Log linear regression model with dry roe mass (g) as response variable and carapace length as predictor variable and estimates for fecundity for a standardized 125 mm CL ovigerous female. This was done for all years and fjords pooled together, for each fjord separately with all years pooled together, and for each fjord and each year separately (Appendix 5). For dry weight of roe (g) the abbreviation RW is used in this table.

Appendix 5. Data table for regression output for each fjord, each year and pooled together. Then also the estimates for a standardised ovigerous female crab of 125 mm CL. The number of crabs used for the regression output (N). The intercept of the regression on natural logarithmic scale (ln(A), the slope of the regression (b), standard error and 95%CI of the slope (SE(b) and 95%CI(b)), the r-squared of the regression (r^2), the F-value , P-value of the slope, estimate roe weight (RW) and 95%CI of a 125mm cl crab on ln scale (ln(Roeweight), low 95%CI ln(Roeweight), and Hi 95%CI ln(Roeweight)), then transformed to normal numbers and then for total egg counts.

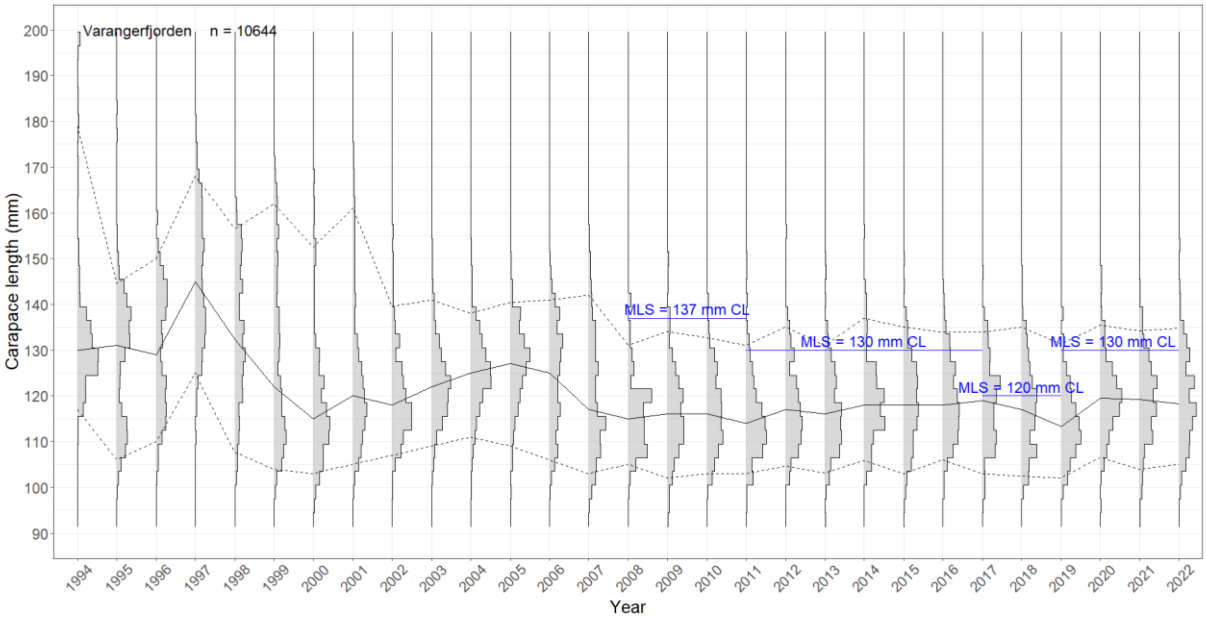
Fjord	Year	N	Ln(A)	b	Se(b)	95%Ci(b)	r^2	F-value	P-value	Ln(RW)	Low 95%CI Ln(RW)	Hi 95%CI Ln(RW)	RW (g)	Low95%CI RW (g)	High 95%CI RW (g)	Total egg count	Low 95%CI eggcount	High 95%CI eggcount
Var	2000	33	-8.8552	2.596	0.217	0.429	0.822	143.428	<<0.001	3.677	3.596	3.757	39.698	36.618	43.039	166172	153277	180153
Var	2001	46	-9.818	2.777	0.153	0.303	0.882	329.670	<<0.001	3.591	3.525	3.656	36.425	34.118	38.886	159806	149685	170602
Var	2002	48	-7.279	2.258	0.239	0.474	0.659	89.082	<<0.001	3.622	3.566	3.678	37.591	35.545	39.754	159858	151159	169057
Var	2003	41	-7.764	2.352	0.188	0.373	0.800	156.279	<<0.001	3.593	3.538	3.648	36.508	34.547	38.581	161157	152498	170308
Var	2004	45	-7.024	2.180	0.246	0.487	0.646	78.463	<<0.001	3.500	3.436	3.564	33.277	31.213	35.479	153756	144215	163927
Var	2005	47	-10.412	2.874	0.336	0.664	0.620	73.341	<<0.001	3.462	3.387	3.537	32.027	29.698	34.539	140520	130301	151539
Var	2006	54	-11.345	3.059	0.373	0.739	0.564	67.153	<<0.001	3.422	3.333	3.511	30.770	28.146	33.638	134971	123459	147549
Var	2007	43	-9.773	2.740	0.280	0.555	0.699	95.544	<<0.001	3.454	3.393	3.516	31.783	29.888	33.796	143145	134611	152212
Var	2008	30	-9.401	2.665	0.621	1.230	0.396	18.391	<<0.001	3.466	3.327	3.605	32.166	27.987	36.971	133410	116075	153335
Var	2010	56	-7.359	2.236	0.288	0.570	0.528	60.429	<<0.001	3.438	3.373	3.503	31.262	29.281	33.376	135062	126505	144194
Var	2011	52	-9.409	2.676	0.235	0.466	0.721	129.430	<<0.001	3.511	3.454	3.569	33.637	31.755	35.631	144196	136128	152742
Var	2013	43	-10.712	2.949	0.339	0.671	0.649	75.667	<<0.001	3.527	3.454	3.600	34.176	31.768	36.767	145820	135546	156877
Var	2015	56	-9.453	2.690	0.253	0.501	0.677	113.042	<<0.001	3.536	3.475	3.596	34.474	32.446	36.627	134149	126259	142528
Var	2016	68	-7.887	2.348	0.282	0.559	0.512	69.258	<<0.001	3.448	3.385	3.510	31.571	29.656	33.611	133686	125575	142322
Var	2022	42	-10.824	2.945	0.486	0.962	0.479	36.790	<<0.001	3.397	3.302	3.491	29.998	27.282	32.983	142979	130035	157204
Tan	2000	40	-9.994	2.849	0.103	0.204	0.953	764.129	<<0.001	3.759	3.715	3.803	43.115	41.272	45.040	174916	167436	182724
Tan	2001	47	-8.376	2.508	0.135	0.268	0.884	343.846	<<0.001	3.731	3.670	3.791	41.920	39.458	44.536	171215	161156	181897
Tan	2002	32	-7.324	2.309	0.169	0.335	0.861	186.235	<<0.001	3.822	3.762	3.881	45.907	43.249	48.727	184593	173902	195930
Tan	2003	41	-9.038	2.646	0.191	0.378	0.831	192.311	<<0.001	3.736	3.685	3.787	42.137	40.043	44.340	179364	170449	188743
Tan	2004	44	-10.251	2.872	0.167	0.331	0.875	294.520	<<0.001	3.616	3.574	3.658	37.366	35.821	38.977	163464	156706	170513
Tan	2005	50	-9.680	2.751	0.185	0.366	0.82	221.053	<<0.001	3.600	3.558	3.643	36.781	35.239	38.390	154637	148155	161403
Tan	2006	52	-9.296	2.650	0.192	0.381	0.791	189.545	<<0.001	3.497	3.448	3.547	33.178	31.582	34.856	146793	139729	154216
Tan	2007	37	-11.866	3.169	0.476	0.944	0.558	44.170	<<0.001	3.432	3.337	3.526	31.064	28.252	34.158	124434	113169	136825
Lak	2004	25	-11.406	3.137	0.237	0.469	0.884	175.677	<<0.001	3.738	3.683	3.793	42.217	39.961	44.600	185094	175204	195543
Lak	2005	44	-8.799	2.609	0.186	0.369	0.824	196.342	<<0.001	3.798	3.754	3.843	44.852	42.913	46.879	192124	183822	200809
Lak	2006	55	-9.572	2.758	0.211	0.418	0.763	170.657	<<0.001	3.743	3.684	3.802	42.416	39.981	44.998	172702	162790	183218
Lak	2007	56	-12.402	3.333	0.167	0.330	0.881	398.771	<<0.001	3.690	3.646	3.734	40.227	38.498	42.034	166002	158868	173457
Por	2022	66	-9.523	2.693	0.310	0.614	0.541	75.439	<<0.001	3.478	3.387	3.568	32.537	29.720	35.622	154938	141523	169628
Var	2000-2022	719	-9.458	2.681	0.0778	0.154	0.623	1186.280	<<0.001									
Tan	2000-2007	353	-10.732	2.970	0.0830	0.164	0.785	1279.671	<<0.001									
Lak	2004-2007	182	-10.491	2.944	0.116	0.230	0.780	639.783	<<0.001									
All fjords	2000-2022	1321	-10.649	2.942	0.0524	0.104	0.705	3144.672	<<0.001									

Mean individual egg weight is an estimate of how much an ovigerous female invests into each offspring. The mean individual egg weight of each year is used to calculate the total egg count from roe mass as a true measurement of fecundity. The mean individual egg weight is calculated from the fjords and years data was available. Year 2008-2016 for Varangerfjorden is missing standard errors due to that was already calculated for Høyning (2018) and all crabs given the same IEW value (Appendix 6).

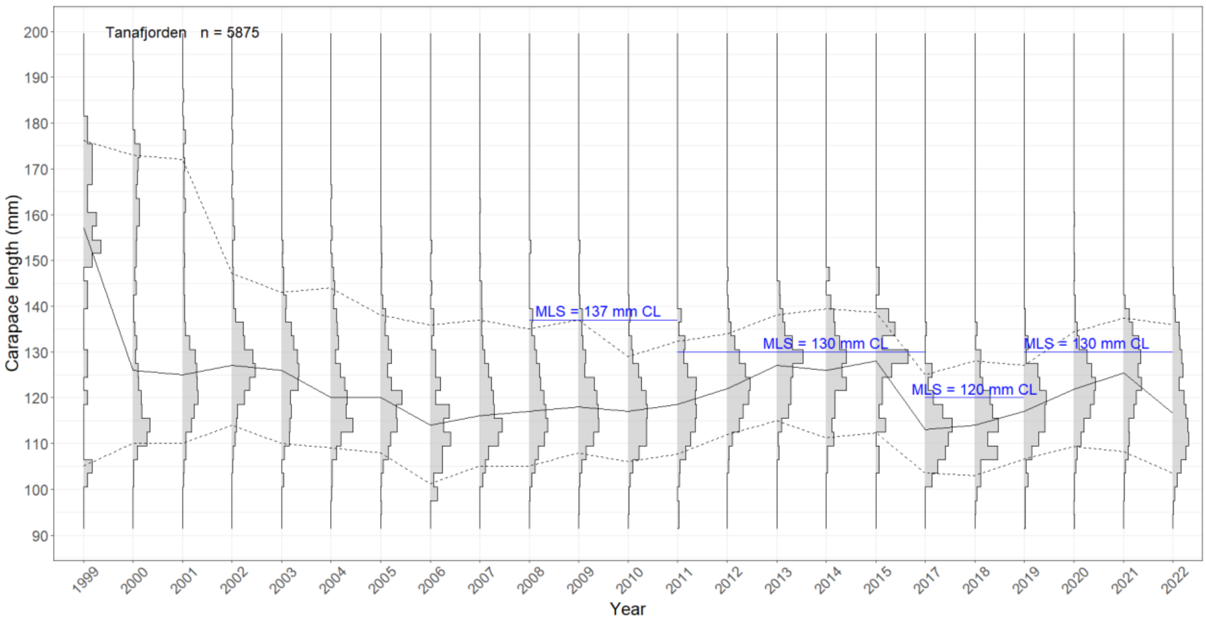
Appendix 6. Data table for the mean dry individual egg weight (mg) and standard error (SE) of the mean for each fjord and each year.

Year	Varangerfjorden		Tanafjorden		Laksefjorden		Porsangerfjorden	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
2000	0.239	0.00267	0.246	0.00273				
2001	0.228	0.00211	0.245	0.00266				
2002	0.235	0.00221	0.249	0.00210				
2003	0.227	0.00292	0.235	0.00289				
2004	0.216	0.00316	0.229	0.00233	0.228	0.00196		
2005	0.228	0.00854	0.238	0.00240	0.233	0.00353		
2006	0.228	0.00210	0.226	0.00321	0.233	0.00296		
2007	0.222	0.00259	0.250	0.01788	0.242	0.00350		
2008	0.241							
2010	0.231							
2011	0.233							
2013	0.234							
2015	0.257							
2016	0.236							
2017							0.246	0.00331
2022	0.210	0.00273					0.210	0.00412

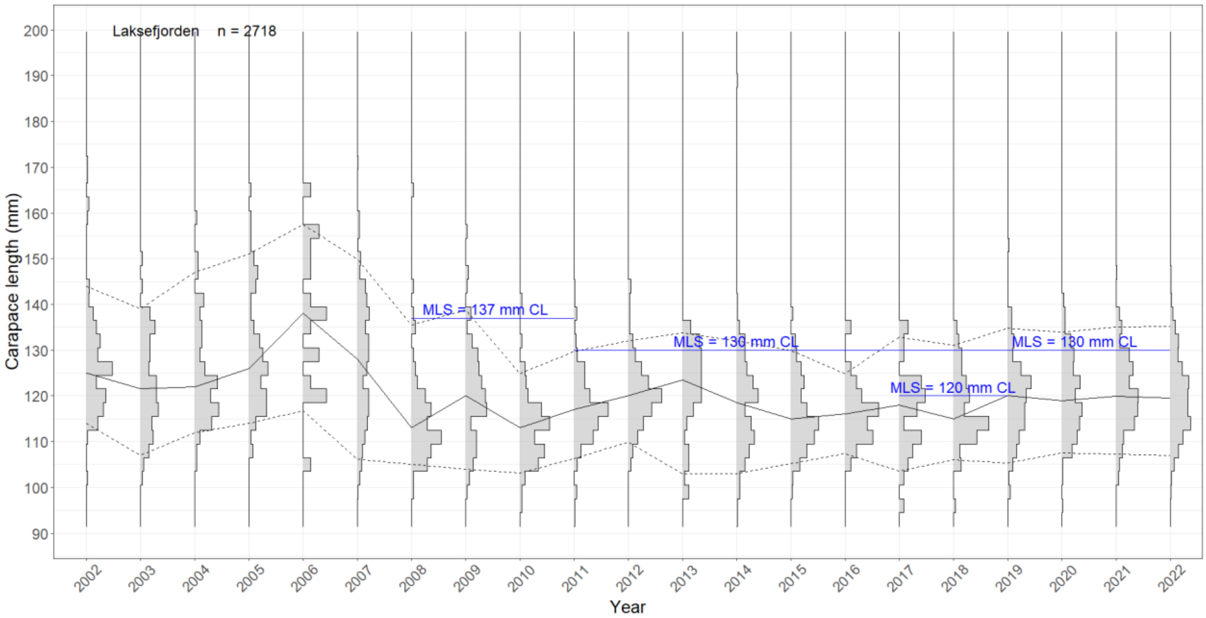
Size composition plots for mature females from each fjord for each sample year with a bin width of 3 mm Cl (Appendix 7 - 10). The total amount of crab contributing to the plot are shown in the top left of each plot with Varangerfjorden having 10644 crabs, Tanafjorden with 5875 crabs, Laksefjorden with 2718 crabs, and Porsangerfjorden with 3430 crabs. Porsangerfjorden 2005 being removed due to only 3 mature female crabs being sampled.



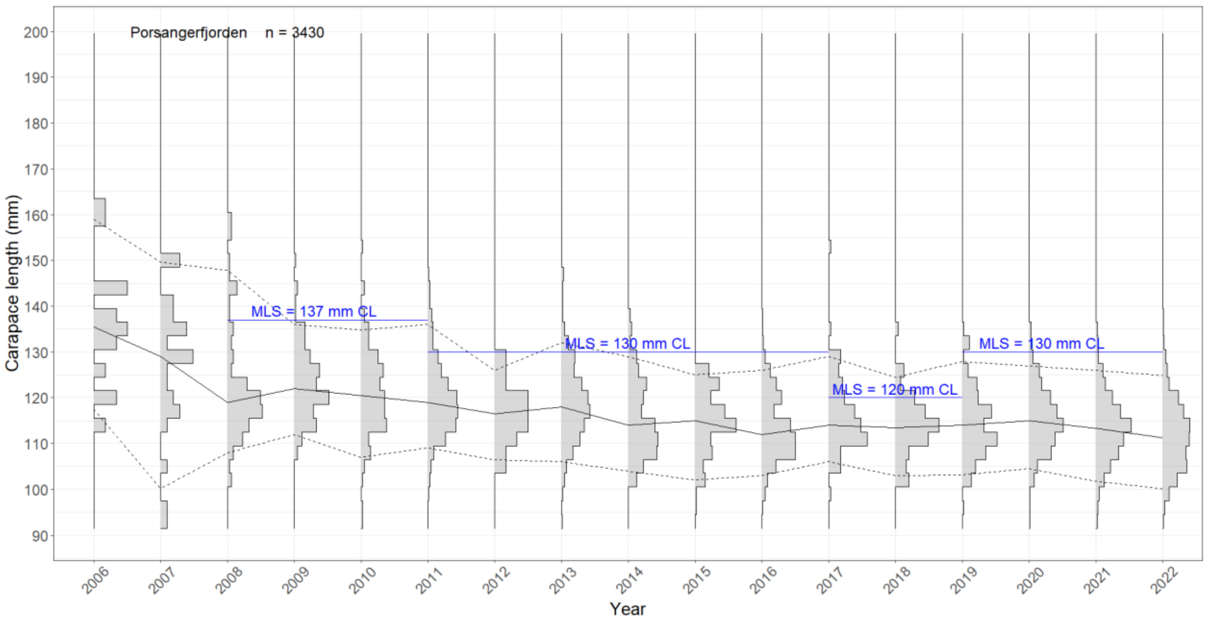
Appendix 7. Size composition over time for ovigerous females within Varangerfjorden. Solid black line represents median carapace length values, dotted lines the 95th and 5th percentile carapace length values. Blue solid line with text represents the minimum legal size for female fisheries for the periods 2008 – 2010, 2011 – 2016, 2017 – 2018, and 2019 – 2022.



Appendix 8. Size composition over time for ovigerous females in Tanafjorden. Solid black line represents median carapace length values, dotted lines the 95th and 5th percentile carapace length values. Blue solid line with text represents the minimum legal size for female fisheries for the periods 2008 – 2010, 2011 – 2016, 2017 – 2018, and 2019 – 2022.

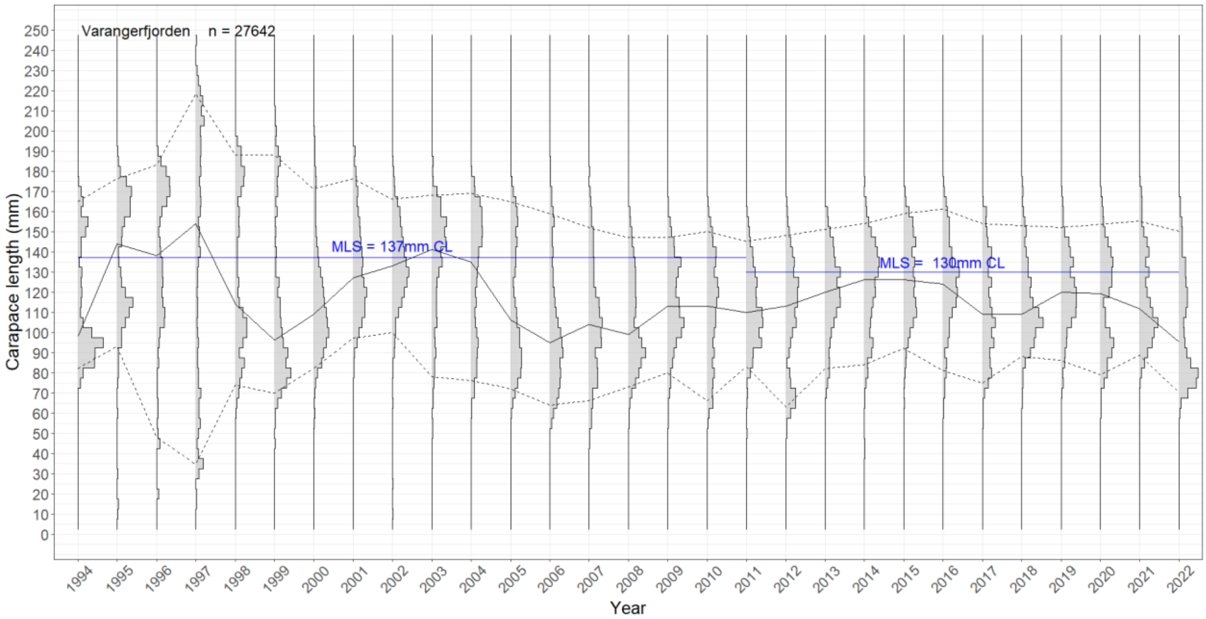


Appendix 9. Size composition over time for ovigerous females in Laksefjorden. Solid black line represents median carapace length values, dotted lines the 95th and 5th percentile carapace length values. Blue solid line with text represents the minimum legal size for female fisheries for the periods 2008 – 2010, 2011 – 2016, 2017 – 2018, and 2019 – 2022.

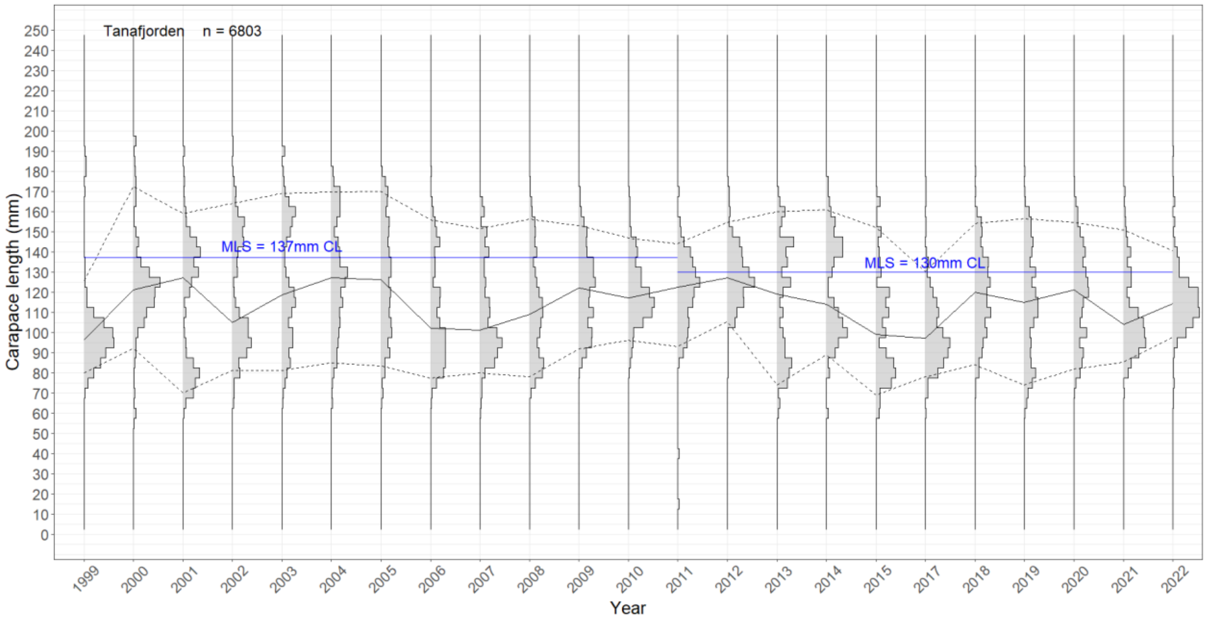


Appendix 10. Size composition over time for ovigerous females in Porsangerfjorden. Solid black line represents median carapace length values, dotted lines the 95th and 5th percentile carapace length values. Blue solid line with text represents the minimum legal size for female fisheries for the periods 2008 – 2010, 2011 – 2016, 2017 – 2018, and 2019 – 2022.

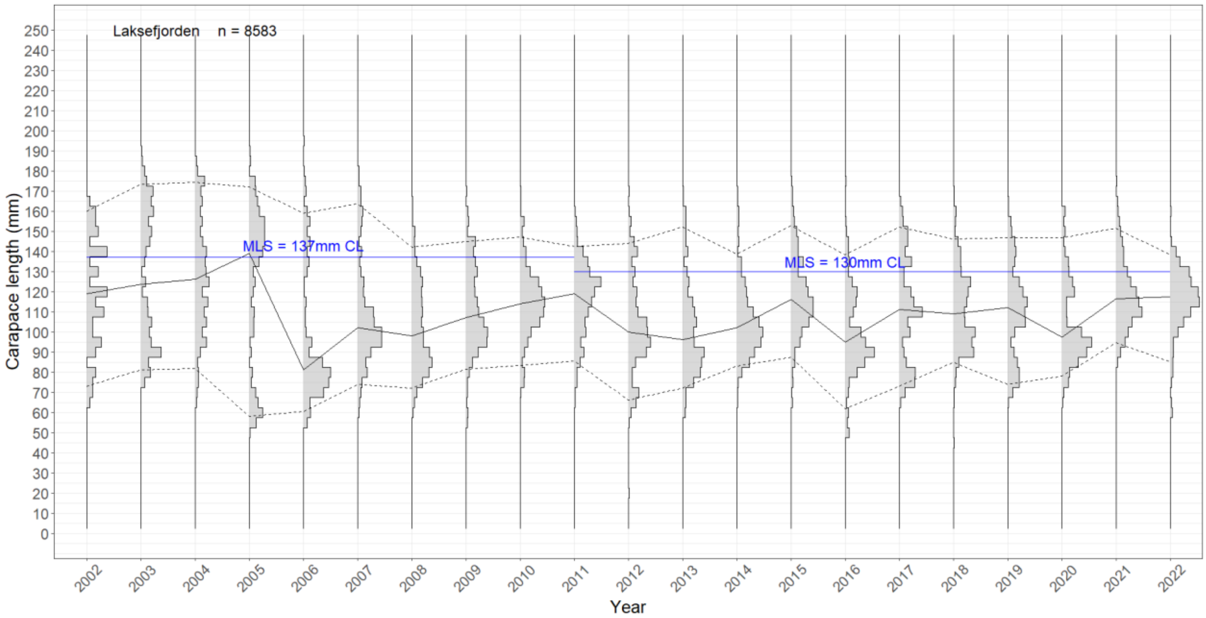
Size density plots for both sexually mature and immature males from each fjord for each sample year with a bin width of 5 mm Cl (Appendix 11 - 14). With the calculated quantiles being only for mature crabs. The total amount of crab contributing to the plot are shown in the top left of each plot with Varangerfjorden having 27642 crabs, Tanafjorden with 6803 crabs, Laksefjorden with 8583 crabs, and Porsangerfjorden with 11839 crabs. Porsangerfjorden 2005 being removed due to only 1 male crab were sampled.



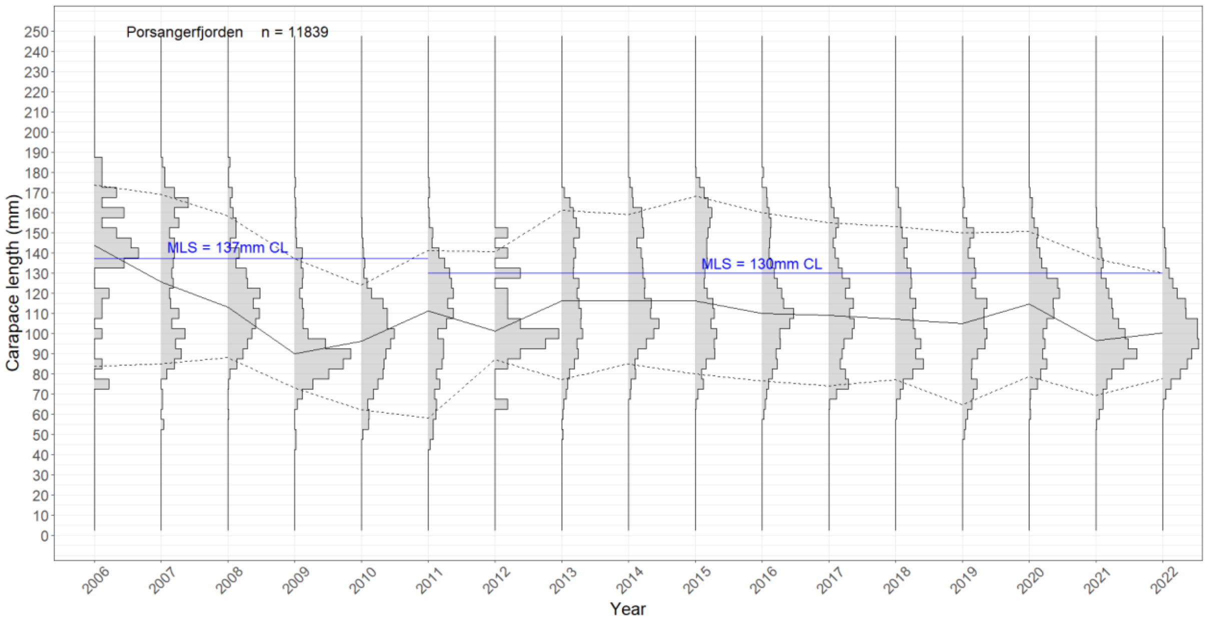
Appendix 11. Size composition over time for all males in Varangerfjorden. Solid black line represents median carapace length values, dotted lines the 95th and 5th percentile carapace length values. Blue solid line with text represents MLS for fisheries in the two periods 1994 – 2010 and 2011 – 2022.



Appendix 12. Size composition over time for all males in Tanafjorden. Solid black line represents median carapace length values, dotted lines the 95th and 5th percentile carapace length values. Blue solid line with text represents MLS for fisheries in the two periods 1994 – 2010 and 2011 – 2022.

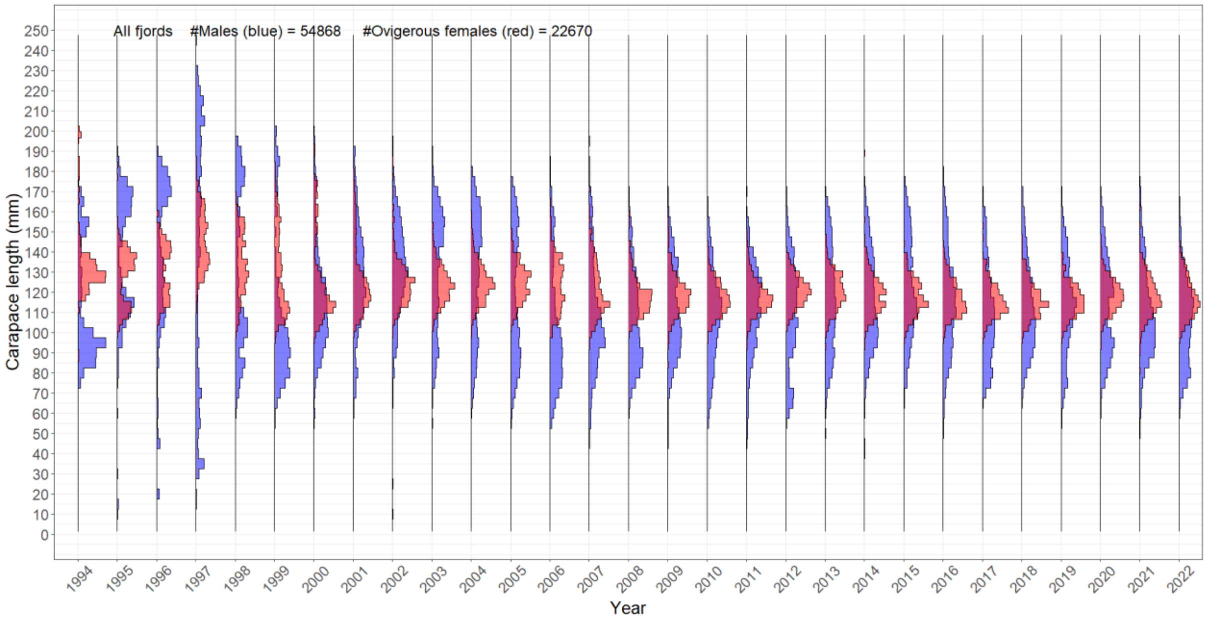


Appendix 13. Size composition over time for all males in Laksefjorden. Solid black line represents median carapace length values, dotted lines the 95th and 5th percentile carapace length values. Blue solid line with text represents MLS for fisheries in the two periods 1994 – 2010 and 2011 – 2022.



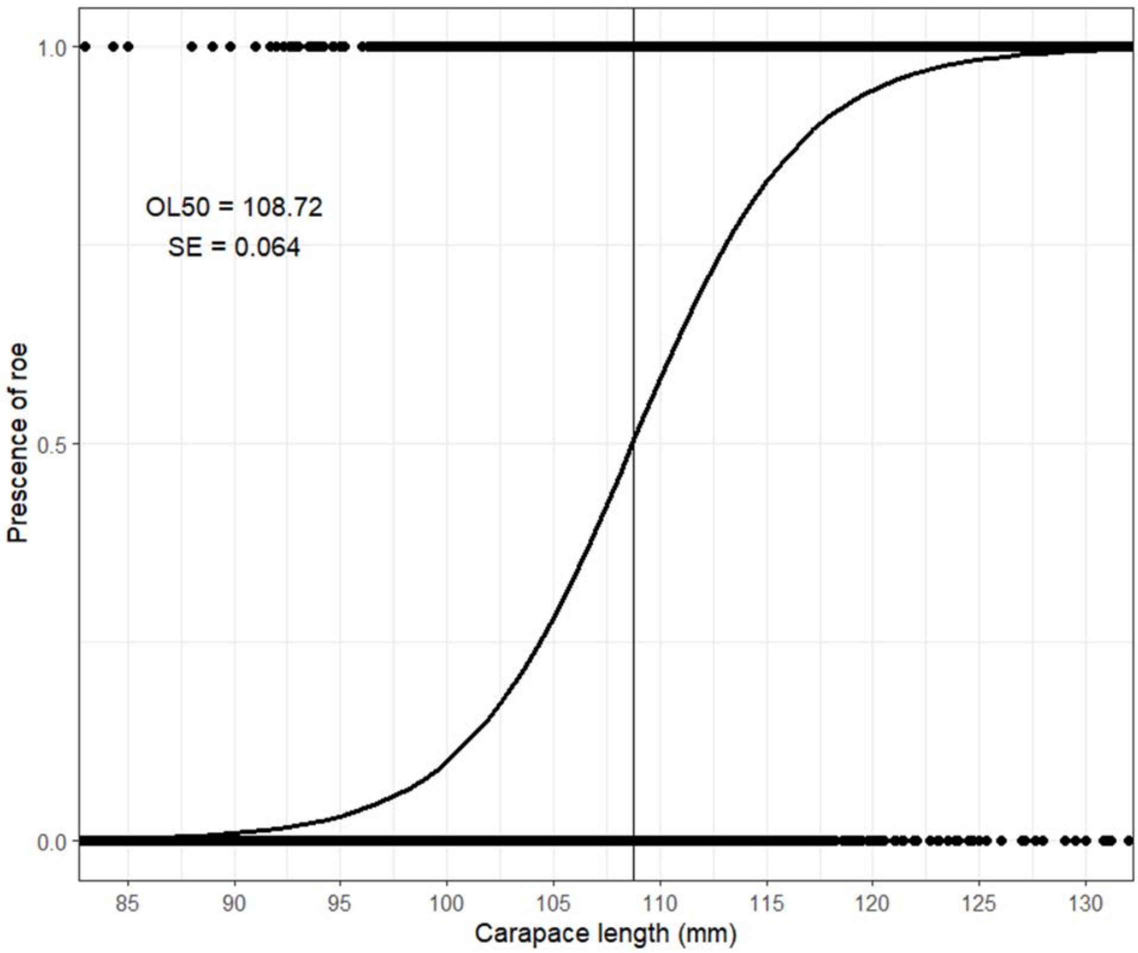
Appendix 14. Size composition over time for all male crabs in Porsangerfjorden. Solid black line represents median carapace length values, dotted lines the 95th and 5th percentile carapace length values. Blue solid line with text represents MLS for fisheries in the two periods 1994 – 2010 and 2011 – 2022.

Size composition of males and ovigerous females combined into one plot (Appendix 15). This plot shows the relationship between male and ovigerous females over time. The general trend is that whilst the size composition of ovigerous females decreased initially, it has remained constant since 2002 the size composition of males showed that the 95th percentile had flattened out and the maximum values have remained approximately constant over time, the amount of these large crabs have decreased since 2000.



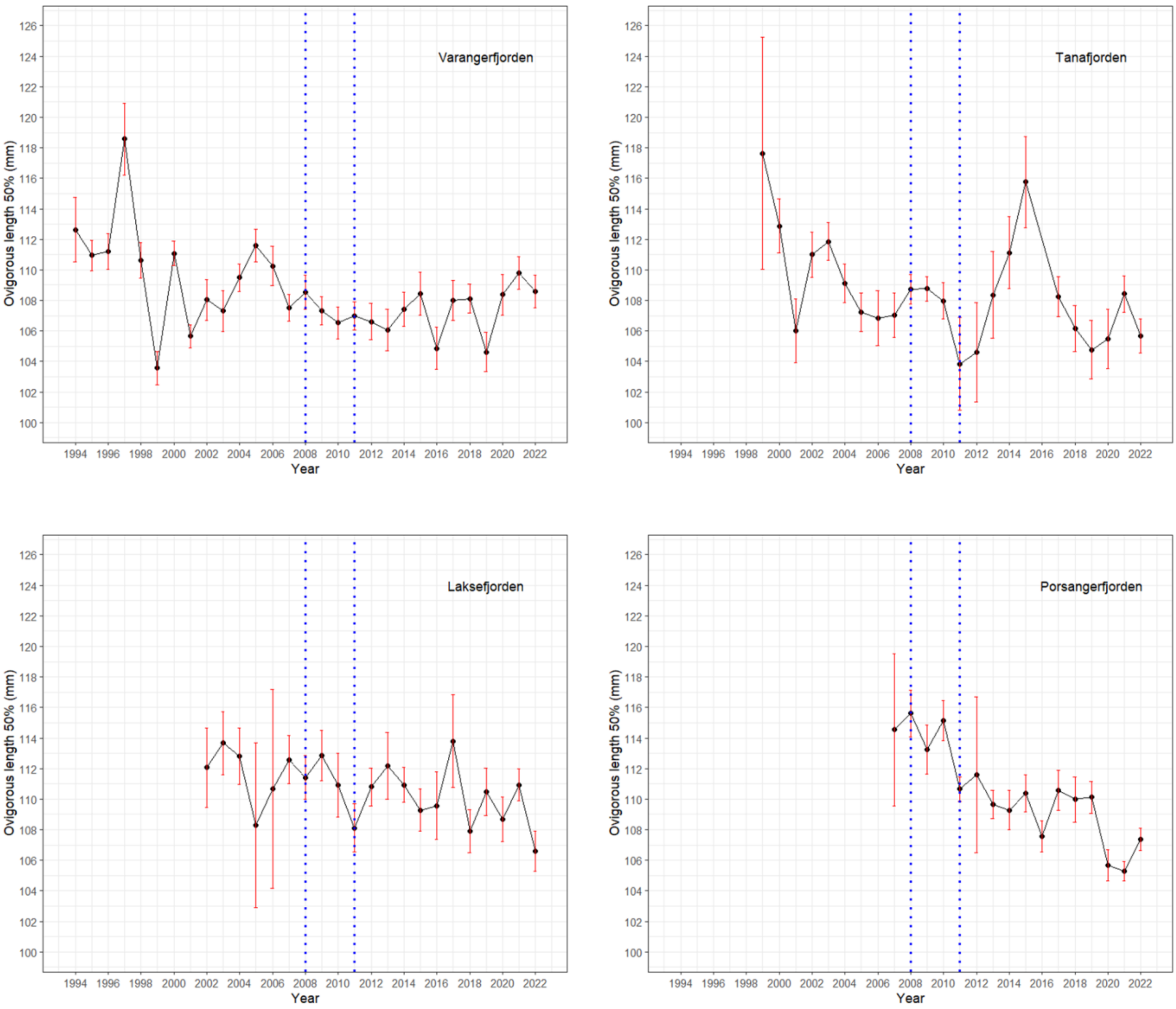
Appendix 15. Size composition plot for all males (blue) and ovigerous females (red) from all fjords over time.

Presentation of OL_{50} for all years and fjords pooled together estimating OL_{50} = 108.7 mm CL with SE of 0.064 (Appendix 16). The same OL_{50} value as estimated in Hjelset (2009). Quite a few females above 120 mm CL which are most likely sexually mature just not ovigerous as of sampling. Also a few ovigerous crabs smaller the 80 mm CL that are ovigerous and have a strong pull on the regression slope.



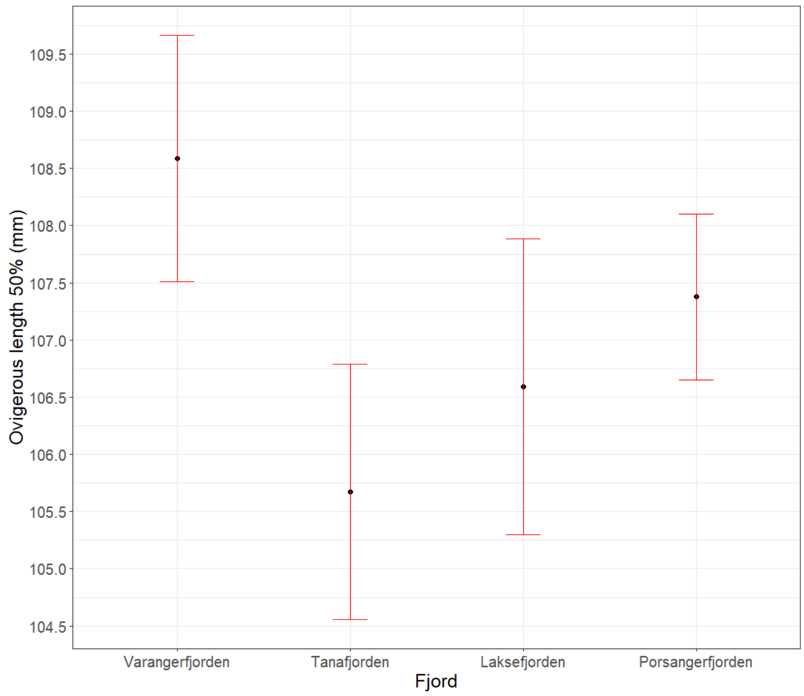
Appendix 16. Size at 50% ovigerous length estimated through binary logistic regression with carapace length on the x axis and presence of roe on the y axis from all fjords and years pooled together. OL_{50} was estimated to be 108.74mm cl with a standard error (SE) of 0.066 mm.

Time series of OL_{50} estimates for each fjord separately with 95% CI as error bars (Appendix 17). The 95% CI allows for identifying statistically significant differences between years. OL_{50} estimates for Varangerfjorden top left, Tanafjorden top right, Laksefjorden bottom left, Porsangerfjorden bottom right. Through these figures the statistically significant difference within each fjord is visible.



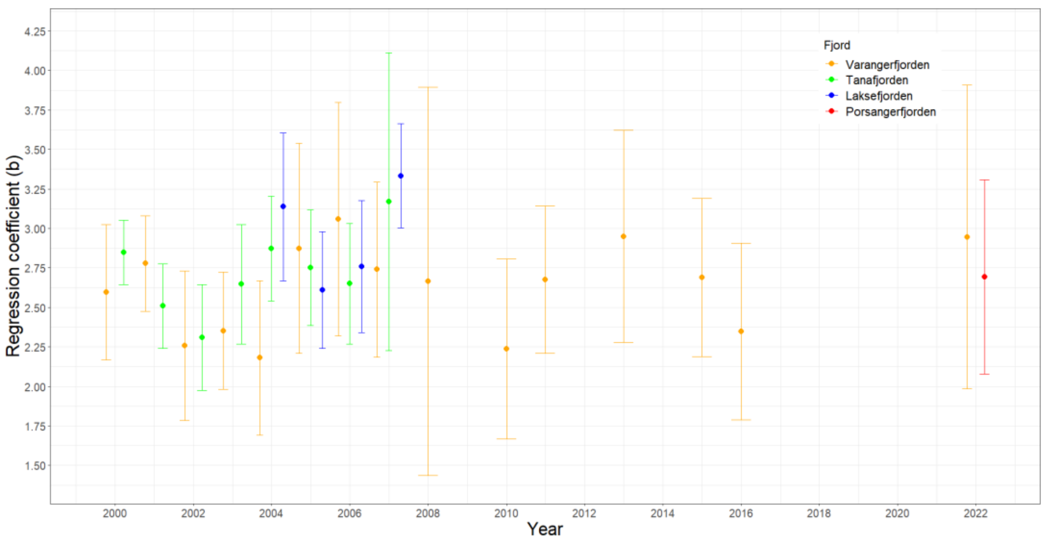
Appendix 17. 50% ovigerous length (mm) with 95% CI over time for Varangerfjorden (top left), Tanafjorden (top right), Laksefjorden (bottom left), and Porsangerfjorden (bottom right). Blue dotted vertical lines at 2008 and 2011 represent the changes fishery management.

OL_{50} estimates from 2022 show that Varangerfjorden and Tanafjorden are statistically significantly different from each other. Whilst both Varangerfjorden and Tanafjorden are not statistically significantly different from Laksefjorden and Porsangerfjorden (Appendix 18).



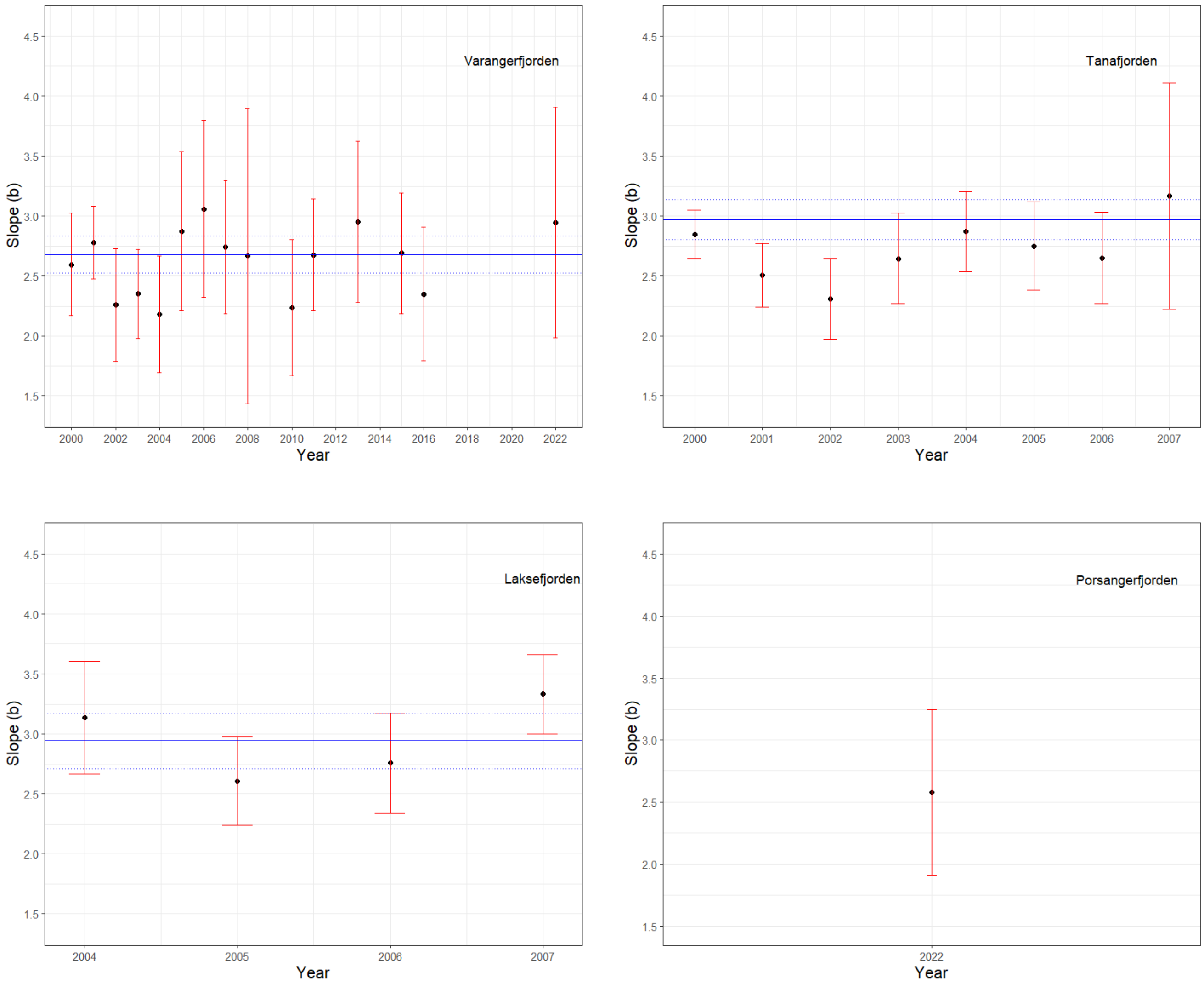
Appendix 18. OL_{50} estimates for 2022 for the fjords with 95% CI as red error bars.

Estimated regression coefficients (*b*) for the correlation between size and dry roe mass for each year and fjord with 95%CI as error bars (Appendix 19). Laksefjorden 2007 is statistically significantly different from Laksefjorden 2005. Some statistically significant differences between Laksefjorden 2007 and Tanafjorden 2002 – 2004.



*Appendix 19. Estimated regression coefficient (*b*) for the relationship between total roe mass and CL with 95% CI from each fjord over time (Se Appendix 5 for exact values for (b) and 95% Confidence intervals).*

Regression coefficients (*b*) for each fjord separately indicates that there are few significant differences within fjord except Laksefjorden 2005 and 2007 (Appendix 20 bottom left). Tanafjorden 2001 and 2002 are differ significantly from the estimated regression coefficient from the whole fjord pooled together (Appendix 20 top right)



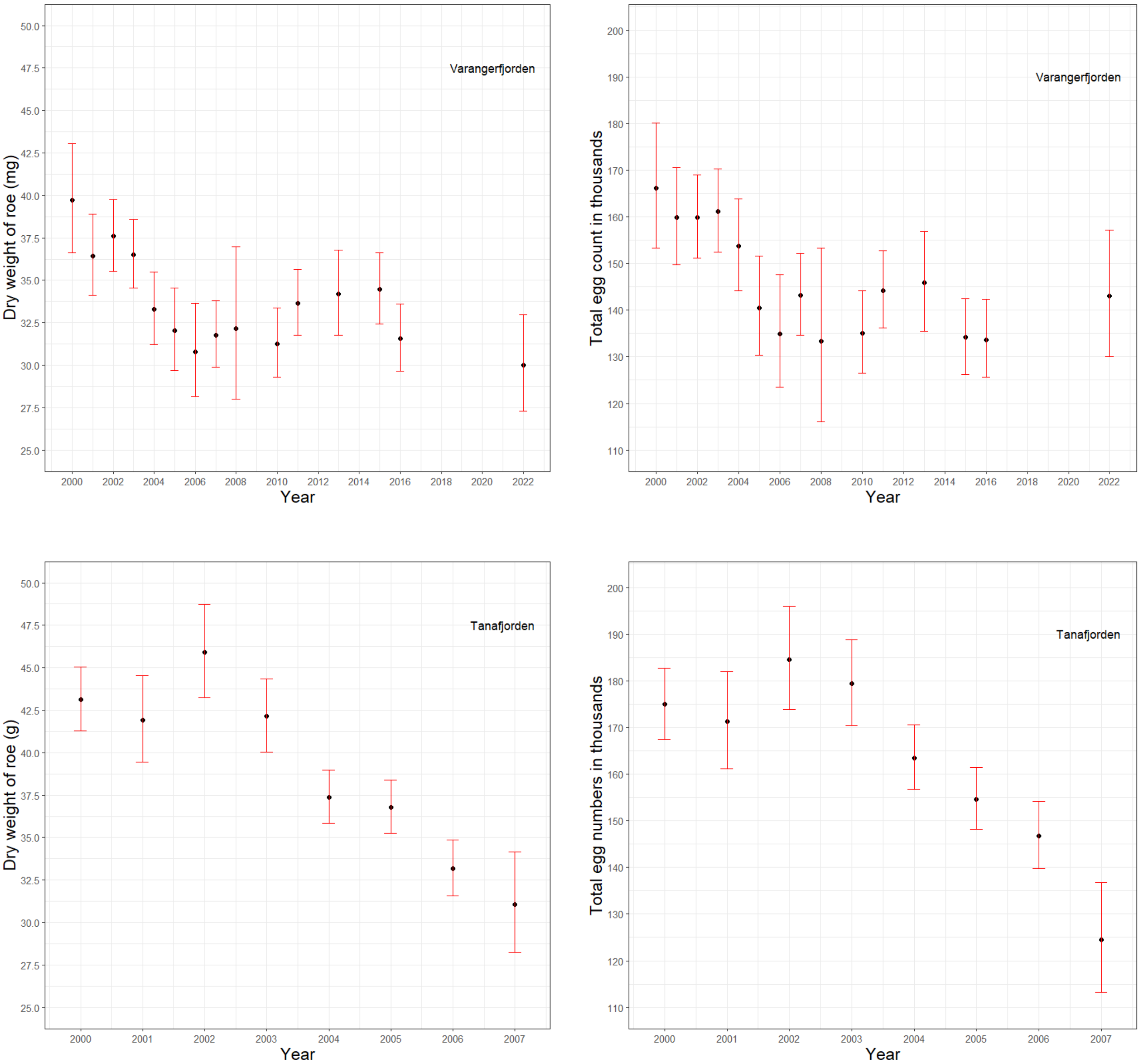
Appendix 20. Comparison of the estimated regression slope with 95% CI between dry roe mass and carapace length for Varangerfjorden (top left), Tanafjorden (top right), Laksefjorden (bottom left), and Porsangerfjorden (bottom right) over time. Blue solid line represents the estimated slope for the whole fjord pooled together with blue dotted lines as 95% CI.

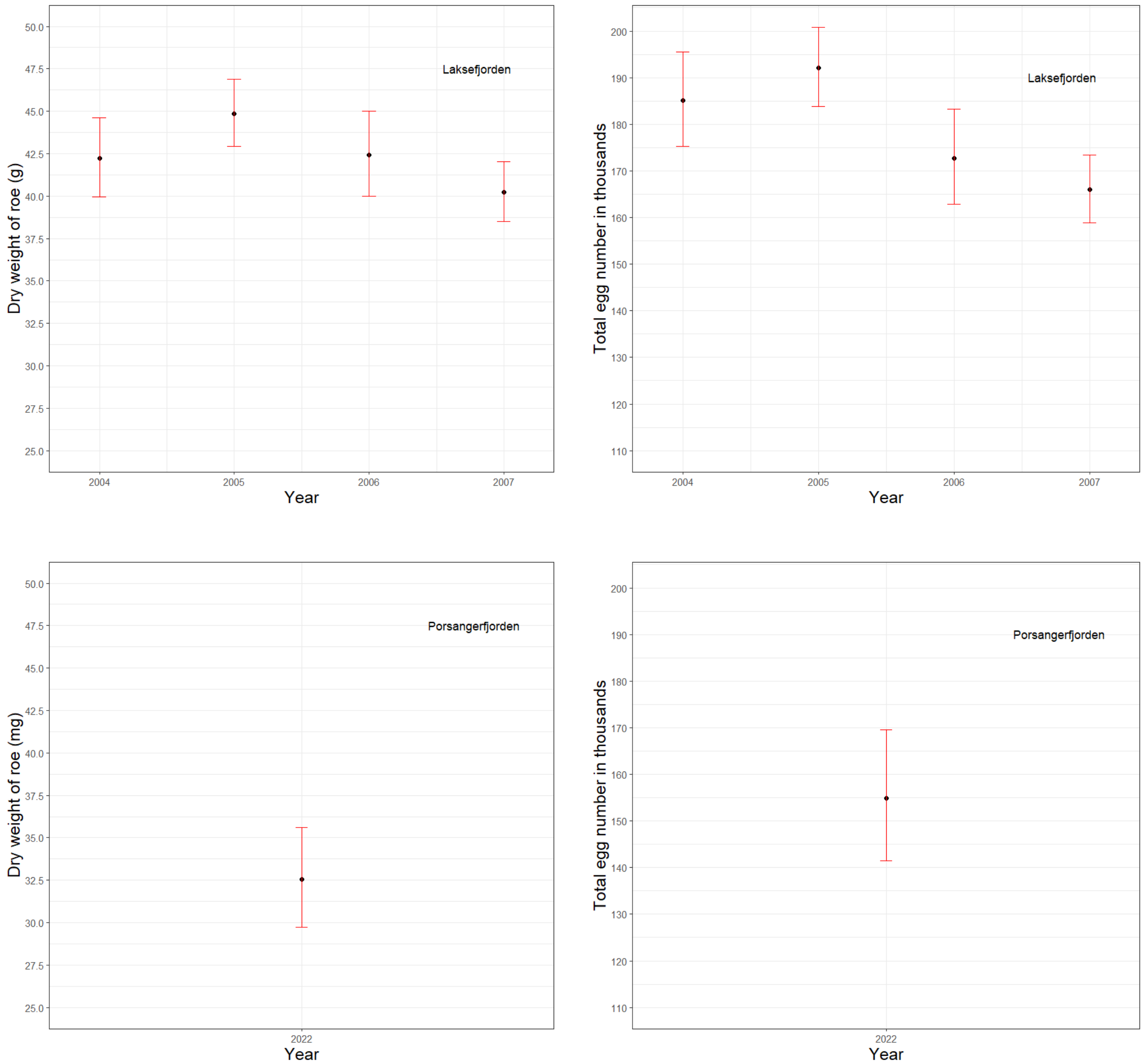
The model selection table for investigating differences around the mean IEW show that the best model is the one using the parameters fjord and year with the correlation between them. The worst model for explaining variance in IEW is the model using only CL as a parameter (Appendix 21).

Appendix 21. Model selection table for investigating variance around the mean individual egg weight.

Model selection table							
Intercept	**CL**	**Fjord**	**Year**	**Year × Fjord**	**df**	**ΔAICc**	**Weight**
-0.0085420		+	4.376e-06	+	8	0.00	0.498
-0.0084650	-5.323e-08	+	4.341e-06	+	9	1.10	0.288
0.0021700		+	-9.646e-07		6	2.47	0.144
0.0022680	-4.128e-08	+	-1.011e-06		7	3.92	0.070
0.0002354		+			5	15.68	0
0.0002341	9.642e-09	+			6	17.67	0
0.0023410			-1.052e-06		3	19.55	0
0.0024010	-2.619e-08		-1.080e-06		4	21.34	0
0.0002326					2	42.02	0
0.0002267	4.541e-08				3	43.30	0

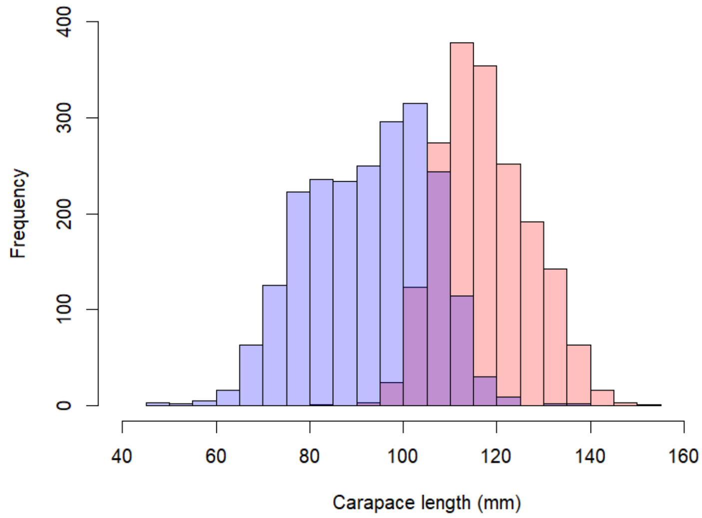
Both Varangerfjorden and Tanafjorden show distinct negative trends in reproductive investment and fecundity for a standardized ovigerous female (Appendix 22).





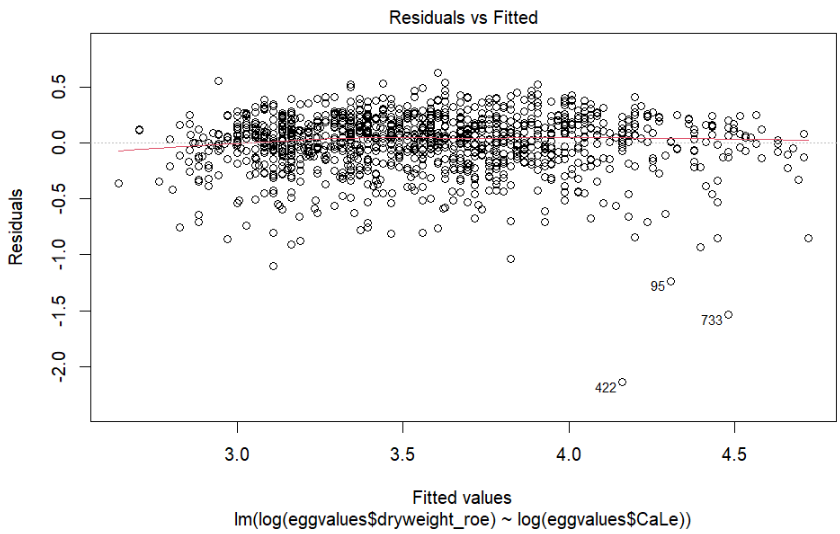
Appendix 22. Estimated dry roe dry weight (left) and total egg count in thousands (right) with 95% CI for each fjord and year from Varangerfjorden, Tanafjorden, Laksefjorden, and Porsangerfjorden (moving from top to bottom).

Size composition for all females show that there are a few non-ovigerous female crabs that most likely are mature being excluded from the size composition and could affect the OL_{50} measurements (Appendix 23).



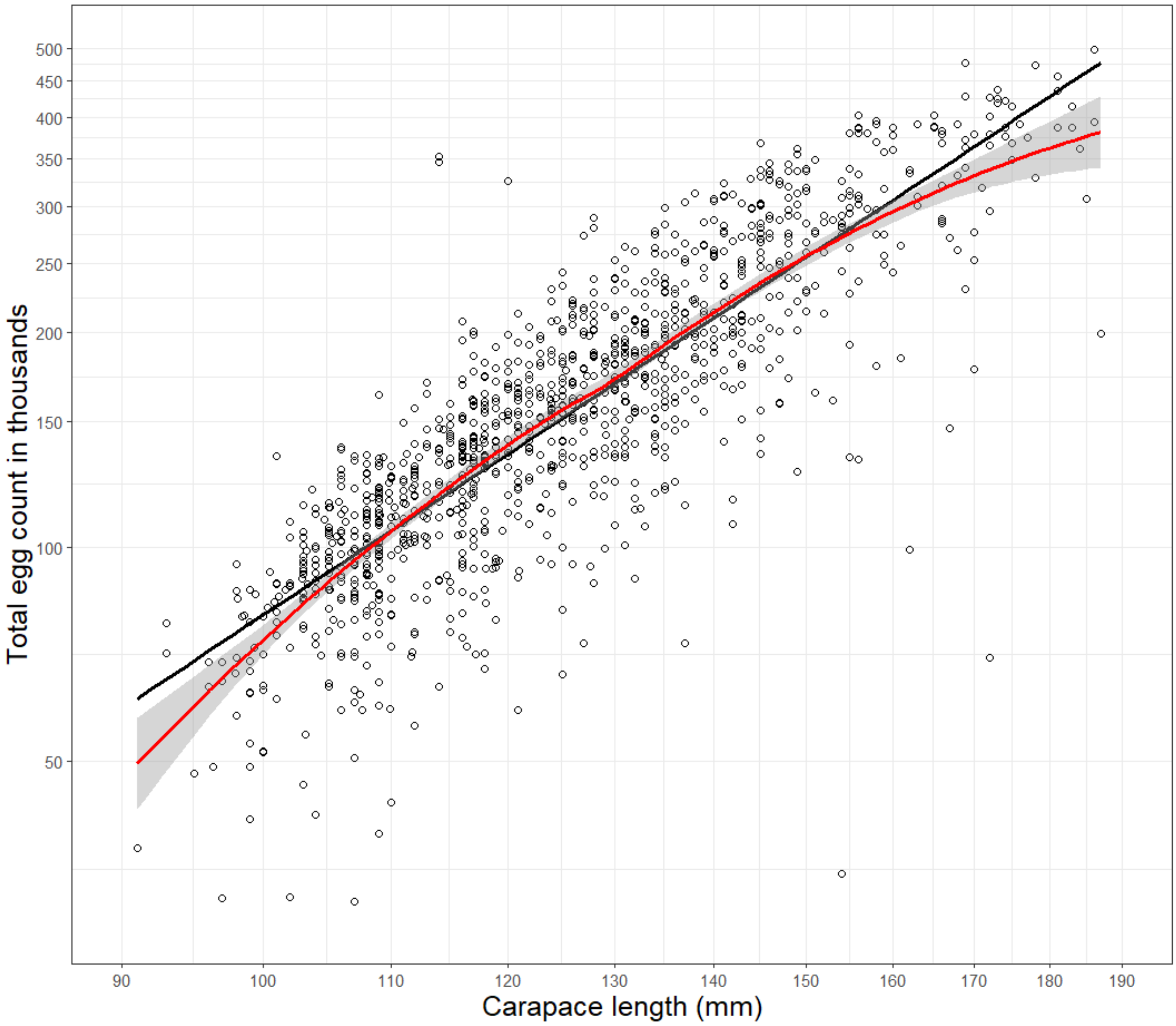
Appendix 23. Size composition of non-ovigerous (blue) and ovigerous (red) female red king crabs for all fjords 2022.

Plotting a residual vs fitted for the regression presented in Figure 10 show that the most extreme outliers are among the larger crabs as indicated as case 95, 422, and 733 in Appendix 24. The red line slightly curving away from 0 in the start of the fitted values indicates that the regression slightly overestimates the reproductive investment for smaller crabs.



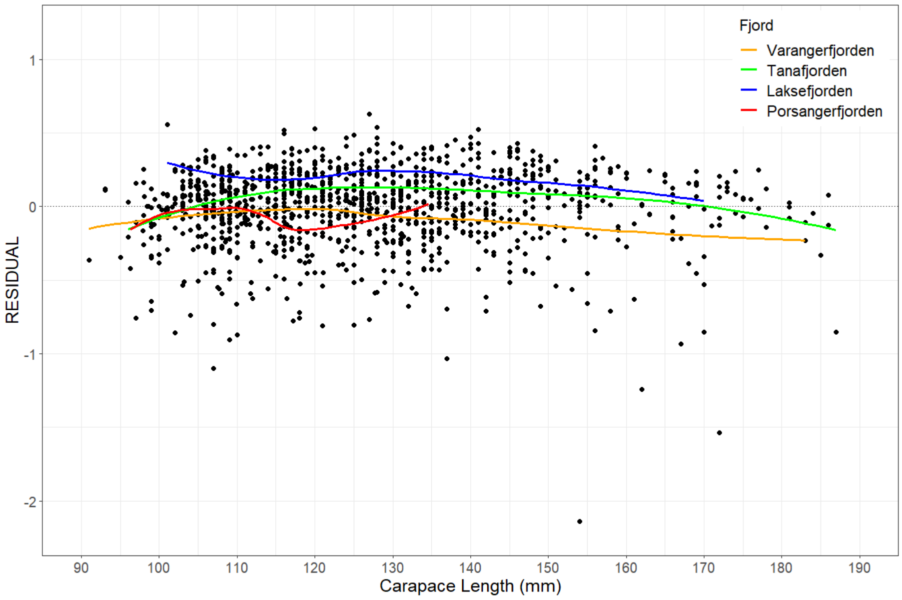
Appendix 24. Residual vs fitted plot for the log linear regression between dry weight of roe and the size of the crabs (Figure 10).

Plotting the correlation between fecundity and CL both ln transformed (Appendix 25) show a similar plot as plotting the correlation between reproductive investment and CL ln transformed (Figure 10). The red loess line shows the same trend as in Figure 10 among smaller and larger crabs, however it deviates further from the regression when estimating fecundity than when estimating reproductive investment.

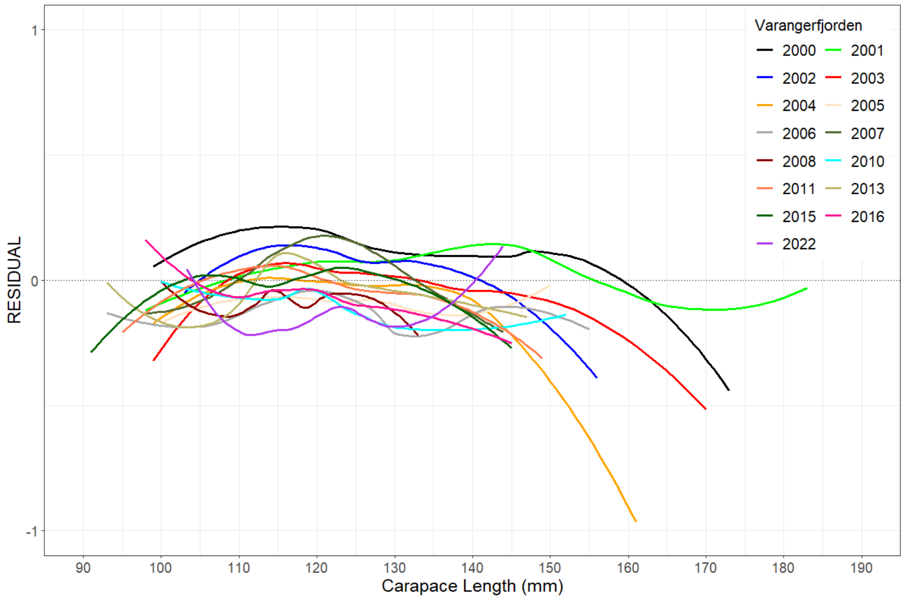


Appendix 25. Presentation of a log linear model with fecundity as a function of CL. Black line is the estimated regression line whilst the red line is a Loess line with standard error.

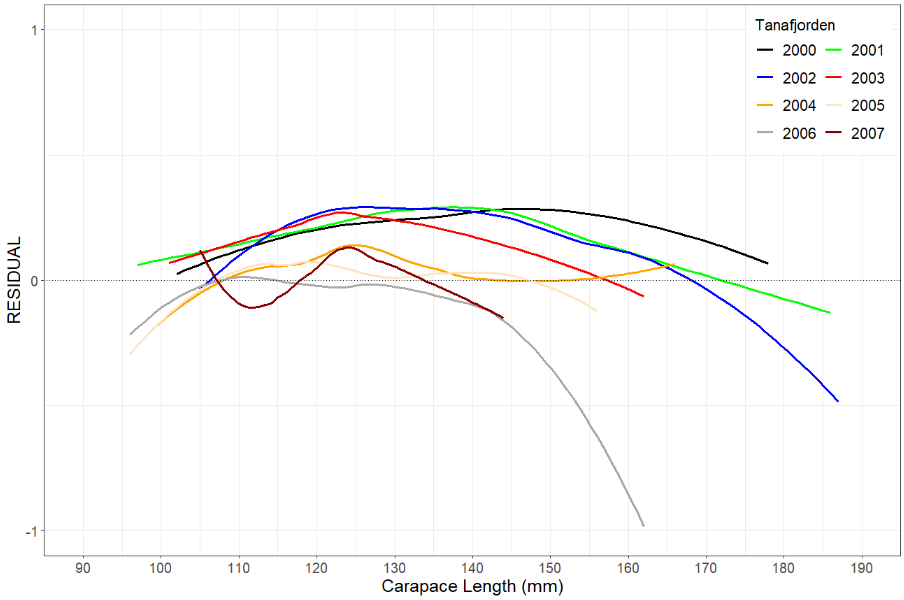
The commonality seen in almost every regression model of the correlation between dry roe mass and CL except for Varangerfjorden and Porsangerfjorden is that the residuals for the regression tends to pull the loess slope downwards among smaller and larger crabs whilst the line being close to 0 in the middle values of CL (Appendix 26– 29). The opposite can be seen for Varangerfjorden 2022 showing curvature looking like a "W" (Appendix 27). Porsangerfjorden 2022 also show an inconsistent curve compared to the other fjords (Appendix 26).



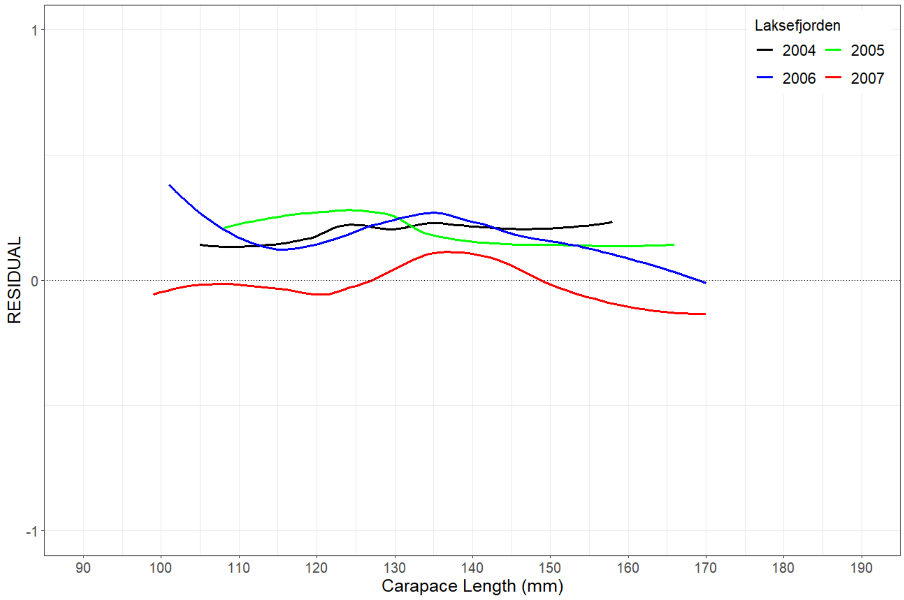
Appendix 26. Loess regression lines for the residuals from the reproductive investment as a function of CL log linear regression model plotted against carapace length for all data within fjords.



Appendix 27. Loess regression lines for residual vs Carapace length. Residual values from the ln linear regression model between dry weight roe and Carapace length for each year within Varangerfjorden.



Appendix 28. Loess regression lines for residual vs Carapace length. Residual values from the ln linear regression model between dry weight roe and Carapace length for each year within Tanafjorden



Appendix 29. Loess regression lines for residual vs Carapace length. Residual values from the ln linear regression model between dry weight roe and Carapace length for each year within Laksefjorden