Effects of marine protected areas on European lobster (*Homarus gammarus*) in Skagerrak, Norway

Maria Naggum Høydalsvik

Master thesis
Center for Ecological and Evolutionary Synthesis
(CEES)
Department of Biosciences
Faculty of Mathematics and Natural Sciences

UNIVERSITY OF OSLO

18.06.2017

2017

Effects of marine protected areas on European lobster (*Homarus gammarus*) in Skagerrak, Norway

Maria Naggum Høydalsvik

http://www.duo.uio.no/

Print: Reprosentralen, University of Oslo

Abstract

European lobsters (*Homarus gammarus*) have been overfished for decades as it is a highly valued species. Commercial catch per unit of effort (CPUE) in Skagerrak, Norway has decreased to historically low levels in the most recent decades, from over 500 tons year^{-1} in before the 1970s to below 60 tons year^{-1} in 2006. It has also been estimated that the landings caught by recreational fisheries make up over 60% of the total landings of lobsters in the Norwegian Skagerrak region. Recreational catches are not registered and it is therefore difficult to implement effective regulations. The regulations in place are restrictions in number of traps household^{-1}, a minimum landing size (250 mm total length, measured from rostrum to telson) and fishing seasons (1st of October to 30th of November) and it is illegal to land and trade egg bearing females.

As a tool to obtain knowledge and possibly guide use of marine protected areas (MPAs) as a potential conservational tool for European lobster, MPAs were established along the Norwegian Skagerrak coast in September 2006. Marine protected areas are geographical sites were fishing is illegal or very restricted. These MPAs were situated from the basis of the Oslofjord to the south of Norway. In these MPAs only fishing by hook and line is allowed.

To analyze the effects and efficiency of these MPAs, data were obtained by controlled fishing inside the MPAs and in associated control areas (where fishing was allowed). The data runs from 2007 to 2015 and includes information about size, sex and where and when each lobster was caught. To analyze the data both generalized linear mixed models and linear mixed models were used. According to the results, MPAs were successful at protecting lobster. The CPUE was significantly larger in the MPAs compared to the control areas, indicating a larger population density. The mean body size increased rapidly from ~240 mm total length to ~300 mm from the start to the end of the study period in the MPAs, but remained around minimum landing length in the control areas. The sex-ratio of the lobster varied, but showed no clear trend and remained close to 1:1 during the study period. Further effects of the MPAs could include an increase in reproductive output from the MPAs, which could have positive effects both locally and regionally.

Acknowledgements

First I would like to thank my supervisor Asbjørn Vøllestad for excellent advices, feedback and help. I would also like to thank my supervisor Esben Moland Olsen for all help and feedback, Even Moland for help with creating map over the study area and the employees at the Institute of Marine Research in Flødevigen for giving me the opportunity to work with such an exciting project, for collecting and lending me the data about the lobsters, for the opportunity to work in the field, as well as providing information about the project and area.

Secondly, I would like to thank Anders Nielsen, Øystein Langangen, Tom Andersen, Tom Reitan, Ingvild and Solveig for all the help with R and statistics as well as advices on how I could interpret the different results.

Thank you to all my family and friends for support, help, motivation and showing an interest in my work, especially Gabriel, for endless support and help, and Cathrine, Ellen and Solveig.

At last, I would like to thank all my new friends at UiO and room 4317 for making my two years as a master student unforgettable, especially Carina, Mari, Mithila, Petter and Tor. A big thank you to Petter for helping me staying motivated and commenting on my thesis.

Table of Contents

1. Introduction

Marine ecosystems around the globe are under increasing pressure from human impacts, amongst them overharvesting of marine species is one of the most detrimental impacts (Jackson et al., 2001). Overharvesting of marine species, or overfishing, can be defined as the reduction in biomass below the critical level at which the population is able to replenish itself (Beamish, McFarlane, & Benson, 2006). Reported global landings from fisheries have been declining with about 0.7 million tonnes each year since the 1980s and the biomass of predatory fishes have been reduced by two-thirds during the second half of the twentieth century (Pauly et al., 2002). According to the Food and Agriculture Organizations (FAO) analysis in their report "The State of World Fisheries and Aquaculture" (SOFIA) the amount of fish stocks that are harvested sustainably have declined from 90% in 1974 to 68.8% in 2013. They argue that fishery production varies greatly among species; the ten most productive and popular species accounted for 27% of total catches in 2013, and almost all of them are fully fished or overharvested (FAO, 2016). Furthermore, Myers and Worm (2003) argued that industrialized fisheries generally removed as much as 80% of the community biomass within 15 years of fishing. This has further resulted in that the predatory biomass has been reduced to only 10% of pre-industrial levels and that this trend extends globally and could have possible detrimental effect on the ecosystem. Overfishing has also led to collapses of many fish stocks like the Peruvian anchoveta (*Engraulis ringens*) and Canadian cod (*Gadus morhua*) populations (Bundy & Fanning, 2005; Clark, 1977). The European lobster (*Homarus gammarus*) fishery in Skagerrak follows the same trend, where the intense exploitation has been followed by large declines (Sundelöf, Bartolino, Ulmestrand, & Cardinale, 2013).

The total official landings of European lobster in Skagerrak, Norway, have decreased from 500 – 700 tons year^{-1} before the 1970s to 59 tons year $^{-1}$ in 2006 (Pettersen, Moland, Olsen, & Knutsen, 2009), reducing the catch by 88-92%. Due to the low and reduced catches the European lobster was put on the IUCN national red list as "near threatened" in 2006; however, it was removed from the list in 2015 due to uncertainties about population size (Oug, Brattegard, Walseng, & Djursvoll, 2015; Pettersen et al., 2009). In addition to the threats the commercial fisheries pose, recreational fisheries and other unreported catches can have detrimental impacts on vulnerable marine species as well, especially if the total catch is high (Cooke & Cowx, 2004; Young, Foale, & Bellwood, 2014). Recreational catches have the same effects on harvested populations as commercial fishing, in that it reduces biomass and body size and alter the old-age structure, and therefore can have an equally detrimental impact on the target population as commercial fishing (Coleman, Figueira, Ueland, & Crowder, 2004). Recreational catches accounts for over 60% of the total catch of European lobster in the Norwegian Skagerrak; in addition, less than 30% of commercial landings are sold through the legal market and are therefore not properly documented (Kleiven, Olsen, & Volstad, 2012). This makes it difficult to estimate the population size and further establish effective regulations. The regulations that are in effect today are a maximum number of traps household^{-1}, a ban on landing egg-bearing (ovigerous) females, a limited fishing season (1st October to 30th November in Skagerrak) and a minimum landing size (250 mm total length, from rostrum to telson)(Fiskeridirektoratet, 2016).

A minimum landing size is a widespread and classical management regulation for preventing overfishing, ensuring that fish are allowed to grow, mature and spawn at least once before they are harvested (Stergiou, Moutopoulos, & Armenis, 2009). However, this can result in a large proportion of big and old individuals being removed from the population and lead to “longevity overfishing” (Beamish et al., 2006). In marine ecosystems, large and old individuals are usually more productive than younger, smaller individuals and the offspring usually have a higher survival (Berkeley, Chapman, & Sogard, 2004; Moland, Olsen, & Stenseth, 2010). This is also the case for the European lobster; Older, larger individuals have more offspring as well as better quality offspring (Moland et al., 2010). When a female lobster reaches a length of 250 mm, she produces around 8000 eggs, whereas a 370 mm female lobster produces around 32 000 eggs (Moen & Svensen, 2004). Harvesting that target the big ones could therefore lead to reduced long-term productivity and as mentioned above, over 60% of the total lobster harvest in Skagerrak is recreational, which target the big ones especially (Birkeland & Dayton, 2005). Another problem with using minimum landing size for regulating lobster fisheries is that size at maturity is highly variable (Lizárraga-Cubedo, Tuck, Bailey, Pierce, & Kinnear, 2003). For instance, a study on European lobster in Ireland found that over 60% of the commercially harvested lobsters were smaller than the size at 50% maturity and the landings were dominated by lobster smaller than the ones with the most reproductive potential (Tully, Roantree, & Robinson, 2001). Berkeley, Hixon, Larson, and Love (2004) and Gell and Roberts (2003) argue that perhaps the best way to protect a natural old-growth age structure and to combat overfishing, is through establishing marine reserves or marine protected areas.

Marine protected areas (MPAs) are geographical sites where fishing is not allowed or very restricted, creating refuges for targeted species and/or habitats. As an alternative tool for fisheries management and conservation, marine protected areas (MPAs) have gotten more attention over the years (Gubbay, 1995). As they counteract longevity overfishing by protecting the entire population within the MPA, they could also counteract the potential fishery-induced selection towards earlier maturation (Baskett, Levin, Gaines, & Dushoff, 2005). Success of an MPA is a balance between conservation (by increasing population density, biomass, mean body size etc.) and fishery benefits (by spill-over of target species from MPAs to adjacent non-protected areas) (Halpern & Warner, 2003). A comprehensive global study by Lester et al. (2009) shows that MPA-effects include increased population density, biomass, mean body size and species richness. Several other studies document positive effects of MPAs on both biological features of the target species, and adjacent fisheries (Claudet, Pelletier, Jouvenel, Bachet, & Galzin, 2006; Edgar & Stuart-Smith, 2009; Roberts, Bohnsack, Gell, Hawkins, & Goodridge, 2001). Studies focusing on European MPAs have also shown a significant increase in these biological features (Fenberg et al., 2012). Typically, the biological responses to protection are rapid and long-lasting (Halpern & Warner, 2002). Studies show that lobsters, such as the spiny lobster species *Jasus edwardsii* and *Palinurus elephas*, the American lobster (*Homarus americanus*) and European lobster, have all responded positively to the establishment of MPAs, in relation to both conservation of the species and fisheries (Edgar & Barrett, 1999; Goñi, Quetglas, & Reñones, 2006; Kelly, Scott, MacDiarmid, & Babcock, 2000; Moland, Olsen, et al., 2013; Rowe, 2002). In September 2006, three MPAs were established along the Skagerrak coast in Norway. The objective was to obtain knowledge about how a local lobster population would develop within small-scale closures and thereby guide the use of MPAs as a possible conservational tool for this species (Pettersen et al., 2009). An earlier study focusing on these three MPAs have documented positive effects on both body size and population density (Moland, Olsen, et al., 2013). Their degree of spill-over to adjacent areas has also been studied, and it was found that it does happen, but the spill-over is at a low rate (Huserbraten et al., 2013; Thorbjørnsen, 2015).

The aim of this study is to investigate specific effects of the Skagerrak MPAs on the target lobster populations, and evaluate whether or not it could have the desired conservational effects. If MPAs are to be implemented as a mean for future conservation of lobsters, it is important to understand how the MPA are affecting the target population. Specifically, this study focusses on changes in (1) population density, estimated as a catch per unit of effort, (2) mean body size and (3) sex-ratio, since females are semi-protected to due to the ban on harvesting ovigerous individuals. The MPAs, and associated control areas where fishing is allowed, has been monitored for almost a decade, with standardised scientific sampling of catch per unit of effort, body size and sex of lobsters prior to the fishing season.

I hypothesise that when there is no fishing present the population density will increase, the lobsters in the MPA will reach a larger size as they will not be caught when passing the minimum landing size. There is also an expectation that the sex-ratio could become more balanced in the MPAs because of expectations of male lobsters being harvested to a larger degree than females in the fishery.

Specifically, I aim to answer the following questions:

- Is population density, measured as catch per unit of effort, higher in the MPAs compared to in the control areas?
- Are the lobsters larger in size inside the MPAs compared to in the control areas?
- Does the sex-ratio in the MPAs differ compared to in the control area?

2. Materials and methods

2.1 Study area

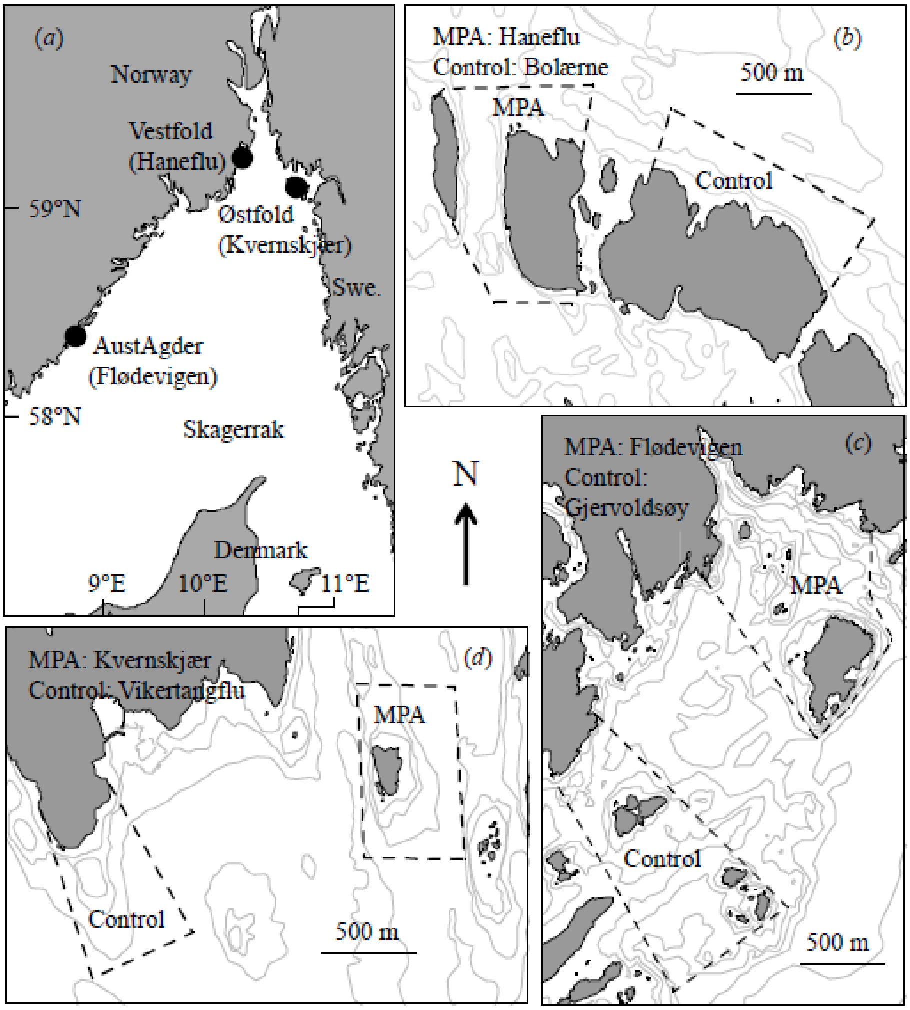


Figure 1: *Map over the MPAs location in Skagerrak, Norway. Clockwise from top: The location of the MPA and control area pairs (a), Vestfold region (b), Aust-Agder region (c) and Østfold region (d) The depth profile in the Vestfold and Østfold regions are 10, 20, 50 m and in the Aust-Agder region it is 5, 10, 20, 30 m.*

The three MPAs in this study (Figure 1) were established in September 2006 by the Ministry of Fisheries and Coastal Affairs. Each MPA has an associated control area that is in close proximity and selected to be as similar as possible to the MPA it is associated with. The aim for establishing these MPAs was to investigate how populations of lobster develop when harvesting is excluded, and they should be in a restricted area (Pettersen et al., 2009). The areas were selected by the following criteria, described by Pettersen et al. (2009): *"(a) have* *an acceptable lobster population, (b) have a habitat suitable to hold a substantial lobster population, (c) be effective to monitor and (d) be supported by local commercial fishers."* The Institute for Marine Research (IMR) conducted surveys to investigate four MPA sites suggested by local fishers and concluded that they were all suitable based on the given biological criteria. Three of these four suggested MPAs are investigated in this study. These MPAs are Flødevigen in Arendal, Haneflu, part of the Bolærne archipelago and Kvernskjær in Hvaler. The areas are protected by regulations given in the law of sea resources which regulates what kind of fishing gear is allowed to use inside these areas (Nærings- og fiskeridepartementet, 2006). All fishing, except line and hook, is prohibited in the MPAs. This ensures that lobster will not be caught, as they are mainly caught by either traps or net. The police and coastguard are responsible for surveillance of the MPAs. All the MPAs harbour typical lobster habitats representative for coastal Skagerrak.

Flødevigen (Figure 1.c) is the largest area, measuring approximately 1 km^2. It is located near the IMR's Flødevigen research station close to Arendal. The MPA covers the entire Flødevigen bay and stretches southeastern, including several small islets and one large island, Ærøya (Moland, Olsen, Andvord, Knutsen, & Stenseth, 2011). It also contains a main gully that stretches from the northwest to the southeast. As described in Huserbraten et al. (2013) most of this MPA is sheltered from the Skagerrak Sea by an archipelago. They further describe that the upper 1 to 5 m are rocky habitat with macro-algae that gradually decrease with the depth. In the southeastern part of the island within the MPA there is a kelp forest which stretches down to 10 – 12 m. The control area that is associated with Flødevigen is Gjervoldsøy.

Haneflu (Figure 1.b), measuring approx. 0,7 km^2 is a part of the Bolærne archipelago situated near the western part of Oslofjord's outlet. The MPA is situated between two islands, Haneflu and Vestre Bolærne. As described in Huserbraten et al. (2013) the MPA is shallow, with a depth of less than 20 m, exluding a few parts where it is deeper. The sediment is mainly hard bottom, with a few larger rocks lying in the slope of each side of the channel between the islands where the MPA is situated. Haneflu has sparse macro-algae. The associated control area is called Bolærne.

Kvernskjær (Figure 1.d) is the smallest MPA, measuring approximately 0,5 km^2. It is a part of the Hvaler archipelago which is situated to the eastern side of the Oslofjor's outlet. It is the most exposed area, as it is not sheltered from the Skagerrak Sea. The location is around a small island with a steep slope and a channel reaching 50 m on the western side. Macro-algae is sparse near the surface in the MPA due to the discharge of freshwater from the river Glomma. However, there is macro-algae present from 5 m to 10 m and a small kelp forest in the southern end (Moland, Olsen, Knutsen, et al., 2011). The associated control area is called Vikertangflu.

2.2 Study species

European lobster is a relatively large and long-lived decapod crustacean, with a maximum estimated longevity of 72 years (Sheehy, Bannister, Wickins, & Shelton, 1999). It is distributed from the north of Norway to Morocco and further east to the Mediterranean Sea (Triantafyllidis et al., 2005). It lives primarily in depths of 50 m and up, but has been found in down to 150m deep (Butler, Cockcroft, MacDiarmid, & Wahle, 2011). The lobster is a primarily nocturnally active animal and prefers to live on rocky substrate, within heaps of stones and in clefts. It feeds primarily on invertebrates, like mussels, snails, polychaetes and sea urchins (Moen & Svensen, 2004). The European lobster does not migrate and generally show a small degree of movement within a geographical area (Smith, Jensen, Collins, & Mattey, 2001).

The lobster undergoes four pelagic larval stages and a juvenile stage before it reaches adult form (Aiken, 1980; Aiken & Waddy, 1980). After they reach adulthood females typically molt biannually and males are thought to molt annually (Sheehy et al., 1999). Timing of reproduction depends on water temperatures, but usually happens in late summer or fall. In general, females are thought to have a 2-year cycle of growth and reproduction. They spawn their eggs and carry them externally between their pleopods until next summer, approximately 11 months, before the eggs hatch. After the eggs hatch, the females molt, and do not carry their eggs externally until spawning again the following fall (Agnalt, Kristiansen, & Jørstad, 2007). According to Phillips and Sastry (1980) hatching time is controlled by temperature and can last from several days to three weeks. The three first larval stages are very different from the adult form, as they are free-swimming and pelagic. The larva begins to seek the bottom in the fourth stage, after spending a few days swimming. In the fifth stage the lobster are completely bottom dwelling, although some swimming has been observed (Phillips & Sastry, 1980). The time spent at the first four stages, varies with temperature and can be between 10 days up to 2 months. Females usually reaches maturity when they are 250 mm total length (TL, from tip of rostrum to end of telson) aged between 4 – 8 years (Sheehy et al., 1999), males can reach maturity at only 180 mm TL (Moen & Svensen, 2004).

2.3 Data collection

The lobsters were captured by the use of standard parlor traps baited with pieces of mackerel (*Scomber scombrus*) and did not have escape vents. Sampling took place from 2004 to 2015, always during the last two weeks of August and the first week of September. This timing ensured that sampling took place before the legal fishing season (1^{st} October to 30^{th} November). In 2004, 20 traps were deployed for three consecutive days (N = 60 trap-nights for each area). In the following years 25 traps were deployed for four executive days (N = 100 trap-nights for each area). From 2006 onwards, 2006 being the last sampling year before the MPAs were implemented, sampling also took place in the control areas close by. I will only analyze data from 2007 onwards, as it was not until the 2007 sampling season that the MPA sites actually acted as MPAs and one could start to measure their effects. Sampling would happen in the control area and in the associated MPA at the same day. The sampling effort was slightly reduced in 2007 and 2010 in Vikertangflu due to severe weather conditions (Moland, Olsen, et al., 2013) (see Table 1). The traps were submerged under water for approximately 24 hours before they were checked for lobster and immediately deployed thereafter. The traps' location was logged using a GPS and they were deployed where it was assumed to be an appropriate habitat for lobster.

Table 1: The total number of European lobster traps deployed and checked each year in each area. The areas are sorted in the different regions, Flødevigen and Gjervoldsøy (Aust-Agder), Haneflu and Bolærne (Østfold) and Kvernskjær and Vikertangflu (Vestfold), with the areas' classification of either marine protected area (MPA) or control area (control). In the MPAs fishing was not allowed and in the control areas fishing by both commercial and recreational fishers was allowed. Some years have lower numbers due to missing traps or severe weather conditions

	Aust-Agder		**Vestfold**		**Østfold**	
	Flødevigen	**Gjervoldsøy**	**Haneflu**	**Bolærne**	**Kvernskjær**	**Vikertangflu**
Year	**MPA**	**Control**	**MPA**	**Control**	**MPA**	**Control**
2007	100	100	100	100	100	75
2008	100	100	100	100	100	100
2009	99	100	100	100	100	100
2010	100	100	100	100	100	75
2011	100	97	100	100	100	100
2012	100	98	99	98	100	100
2013	100	100	100	100	100	98
2014	100	99	99	98	100	100
2015	100	100	100	100	99	97

All lobster caught were tagged using T-bar anchor tags. These were inserted into the ventral muscle between the cephalothorax and the first abdominal segment, to the right side of the midline, to ensure that the tag was not lost during molting (Moland, Olsen, et al., 2013; Moland, Olsen, Knutsen, et al., 2011). The tags are individually numbered and with printed information about the project. When a lobster was recaptured this number was registered. The total length (TotL) of each lobster was measured from the tip of the rostrum to the end of the telson. After that the lobster were sexed, presence of external eggs noted for the females, and each lobster released, often in close proximity to where it was caught. In this study the information about the lobsters' sex and length was used, as well as when and where they were caught. Data on tagged individuals, such as recaptures and tag ID, as well as the data including the presence of external eggs on females were not used.

2.4 Data analyses

2.4.1 Catch per unit of effort

R version 3.3.2 (R Core Team, 2016), with packages lme4 (Bates, Maechler, Bolker, & Walker, 2015) and MASS (Venables & Ripley, 2002) was used to analyze the data. Catch per unit of effort (CPUE) was used to test for the development in number of lobster area^{-1} over time. CPUE was estimated as number of individuals trap^{-1} day^{-1}. Two different models were used to investigate differences between CPUE in MPAs and control areas; one for the entire dataset with all three regions included and one to investigate each region separately. The analysis of the entire dataset was done to investigate the general trend in differences between the MPAs and the control areas over time. The analyses of each region individually were included, since the three different regions were slightly different (difference in macro-algal growth, dominant sediment type and MPA size) and could therefore exhibit different trends.

As the data were non-normally distributed count data, a generalized linear mixed model (GLMM) was used to analyze the effect of status (either control, which was fished both commercially and recreational, or MPA, which was not fished commercially or reactional) and year on CPUE. To find a model with a good fit, I started with a GLMM that had a Poisson-distribution. To test for overdispersion I also ran a GLMM with a negative binomial distribution. The two alternative models were compared by using Bayesian information criterion (BIC) (Aho, Derryberry, & Peterson, 2014), and the model with the better fit (lowest BIC) was selected. The model with a negative binomial distribution gave a better fit (lower BIC by ~47), and was therefore used to analyze further. Number of lobster captured in a given trap a given night (CPUE) was used as response variable. Status of the area and year (as a factor variable) had to be included in the model, as these were the variables that I wanted to investigate, given my hypothesis. To determine whether to include an interaction term between status and year, I ran the model with and without the term. The model with the lowest BIC was selected and I ended up with the one without the interaction effect (BIC values and models in appendix A.1**)**. Status and year were modelled as factors, where status had two levels (MPA or control) and year had nine levels (2007-2015). Region was used a random effect with three levels (Aust-Agder, Vestfold and Østfold):

$$CPUE \sim Status + Year + (1 \mid Region)$$

To test each region separately, both the R-package MASS and basic R was used. Generalized linear models (GLMs) were used as the data in each area were non-normally distributed count data. The same method used to test for overdispersion for all regions combined were used for each area separately. Overdispersion was found in the Vestfold region, but not in the Aust-Agder- and Østfold region. The model analyzing the data from the Vestfold region was a GLM with a negative binomial distribution. A Poisson distribution was used for the models analyzing the data from the Aust-Agder- and the Østfold region. To make the model for each region separately comparable to the model for all regions combined, the same variables were used, excluding the random effect:

$$\text{CPUE} \sim \text{Status} + \text{Year}$$

2.4.2 Mean body size

To analyze for variation in mean body size and how the mean body size distribution varied over time and status I used R-package lme4. As with the CPUE-analyses, I split the analyses in four, one model for all regions combined and three for each region separately. However, the size data was close to normally distributed; therefore the models used were linear models (LMs). The size development for the entire dataset with all three regions combined was analyzed with a linear mixed model (LMM) to include region as a random effect. Several models including different variables and interactions were tested and the model with the lowest BIC-value was selected (BIC values and models in appendix A.2). Mean body size was used as a response variable and status (either MPA or control) and year had to be included, and was a part of all models that were tested. Sex (either male or female), as there could be differences in male and female size, was included in some of them as well as different interaction effects. I ended up with a model that included sex and the interaction between status and year, as well as the necessary variables. Status, year and sex were modelled as factors. Status has two levels (MPA or control), year had nine (2007-2015) and sex had two (male or female). Region was used as a random effect with three levels (Aust-Agder, Vestfold and Østfold):

$$\text{Size} \sim \text{Status} * \text{Year} + \text{Sex} + (1 \mid \text{Region})$$

The models used for each region separately were linear models. I chose to use the same model structure as the model used to test all three region combined to test all three region separately, as I wanted them to be comparable. The models excluded only the random effect:

Size ~ Status * Year + Sex

2.4.4 Sex-ratio

I tested for variation in sex-ratio over time and between areas as harvesting target male and female lobster differently. As with the CPUE and mean body size analyses, four models were run. One model was used for the entire dataset with all three regions included, and three models were used for each of the regions individually. Each lobster was classified as male (1) or female (0). I analyzed the entire dataset using a GLMM with a binomial distribution and region as a random effect. To determine which variables and interaction effects to include, I ran several models. Status (MPA or control), year and region as a random effect had to be included. Size was included to test if there were any difference in sex-ratio depending on size as well as several interactions (BIC values and models in appendix A.3). I ended up with a model that included size, as well as the necessary variables, but no interactions. The proportion of males was used as a response variable. Status and year were modelled as factors, where status had two levels (MPA or control) and year had nine (2007-2015). Size was modelled as a continuous variable. Region was used as a random effect with three levels (Aust-Agder, Vestfold and Østfold):

Proportion of males ~ Status + Year + Size + (1 | Region)

The three models analyzing each region separately was a generalized linear model with a binomial distribution. The same variable as the model testing all region combines were used to make the models comparable, excluding only the random effect:

Proportion of males ~ Status + Year + Size

3. Results

3.1 Catch per unit of effort

3.1.1 All regions

A total of 8628 lobsters were caught (including recaptures) in the six areas during the period 2007 – 2015, with 5181 lobsters captured in the MPAs and 3447 lobsters in the control areas **(**Table 2). Catches in a given year ranged between 33-319 in the areas that are fished both commercially and recreationally (controls) and 60-315 in the MPAs, where fishing is not allowed (MPAs**)**.

In total, CPUE (number of lobster trap^{-1} night^{-1}) varied with time and was on average greater in the MPAs than in the control areas. Figure 2 shows that the trends were relatively similar. Even though CPUE was larger in the MPAs, the CPUE also increased to some extent in the control areas. The variation in CPUE in the MPAs and control areas seem to follow each other, with increases and decreases happening in the same years in both the MPAs and control areas, except in 2015 when they diverge slightly.

The data was analyzed using a generalized linear mixed model. The best model was selected by using the lowest BIC score (appendix A.1). The best model tested CPUE as a response variable with status (MPA or control) and year as factor variables and region as a random effect. According to the model (Table 3; estimates table in appendix B.1) the overall CPUE was significantly greater in the MPAs and there was a significant temporal effect. Because of the geographical differences of the regions, I chose to look at the three different regions separately as well, to investigate possible local trends in more detail. To make the model analyzing general trends comparable to the three individual regions, the same model structure was used excluding only the random effect.

Table 2: Number of lobster captured in the different areas during the years included in my study (2007 – 2015). The areas are sorted in the different regions, Flødevigen and Gjervoldsøy (Aust-Agder), Haneflu and Bolærne (Østfold) and Kvernskjær and Vikertangflu (Vestfold) with the areas' classification of either marine protected area (MPA) or control area (control). In the MPAs fishing was not allowed and in the control areas fishing by both commercial and recreational fishers was allowed. Note: number of traps differs slightly among sites and years (Table 1).

	Aust-Agder		**Vestfold**		**Østfold**		
Year	**Flødevigen MPA**	**Gjervoldsøy Control**	**Haneflu MPA**	**Bolærne Control**	**Kvernskjær MPA**	**Vikertangflu Control**	**Total**
2007	60	33	171	98	162	114	638
2008	95	55	171	78	189	178	766
2009	121	51	297	187	222	245	1123
2010	111	64	315	147	251	198	1086
2011	92	48	180	80	298	319	1017
2012	111	46	279	158	286	277	1157
2013	130	52	269	138	282	239	1110
2014	127	51	203	123	185	171	860
2015	129	43	218	88	227	166	871
Total	976	443	2103	1097	2102	1907	8628

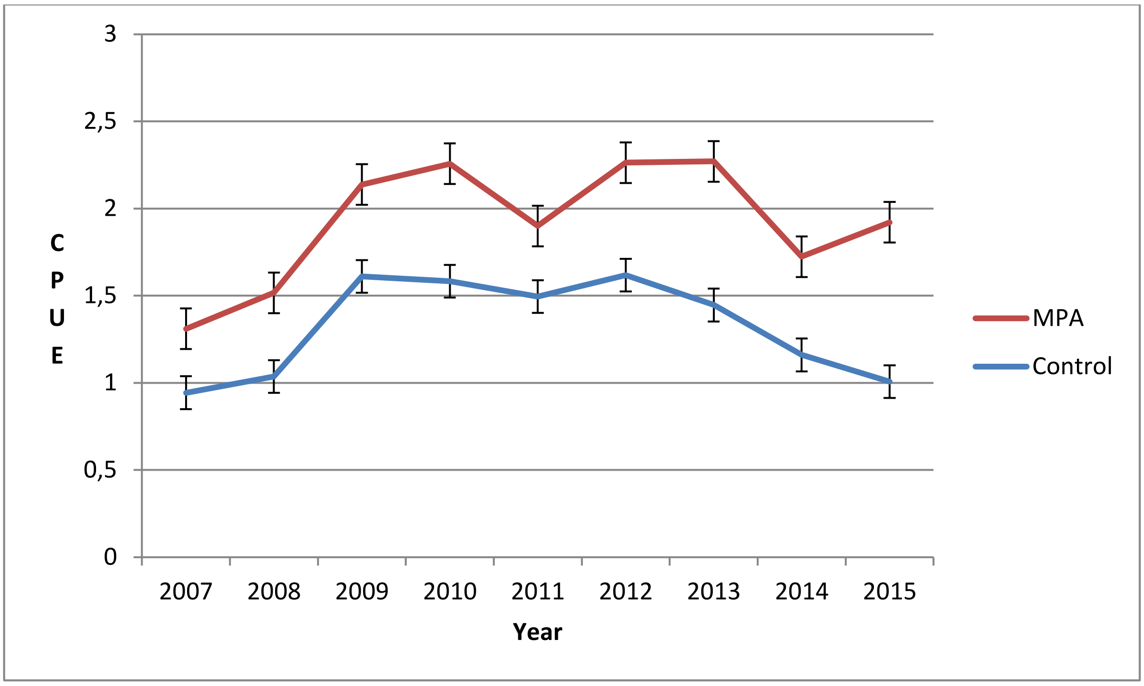


Figure 2: *CPUE of European lobster as the total catch trap^{-1} area^{-1} year^{-1}, and averaged over all the areas and split into "control" or "MPA" based on the status of the areas MPA is marine protected areas where fishing was not allowed and control are areas that fishing both commercially and recreational was allowed. Graph shows observed mean with standard error bars.*

Table 3: Summary statistics of the generalized linear mixed model testing for variation in catch per unit of effort of European lobster with status (MPA vs control area) and time (years) as explanatory variables. Region was used as a random variable in the model, and using a negative-binominal error term. Parameter estimates as given in appendix table B.1.

	DF	Sum sq.	F value	P-value
Status	1	276.91	276.91	**<0.001**
Year	8	238.44	29.81	**<0.001**

3.1.2 Aust-Agder

In the Aust-Agder region a total of 1419 lobster were caught (including recaptures), 976 in the MPA and 443 in the control area (Table 2). Figure 3 shows a two-fold higher catch per unit effort (CPUE) in the initial years from 0.6 – 1.2 lobster trap^{-1} night^{-1}(2007 – 2009, respectively). After 2009, the CPUE decreases, but start to increase again in 2012 and possibly stabilizes at a little above 1.2 lobster trap^{-1} night^{-1} in 2013. In the control area, the CPUE varied less and stayed between 0.4-0.6 lobster trap^{-1} night^{-1}.

The data was analyzed using a generalized linear model, with status (MPA or control) and year as factor variables. According to the model (Table 4; estimates table in appendix B.2) CPUE was significantly larger in the MPA than in the control area and there was a strong significant temporal effect.

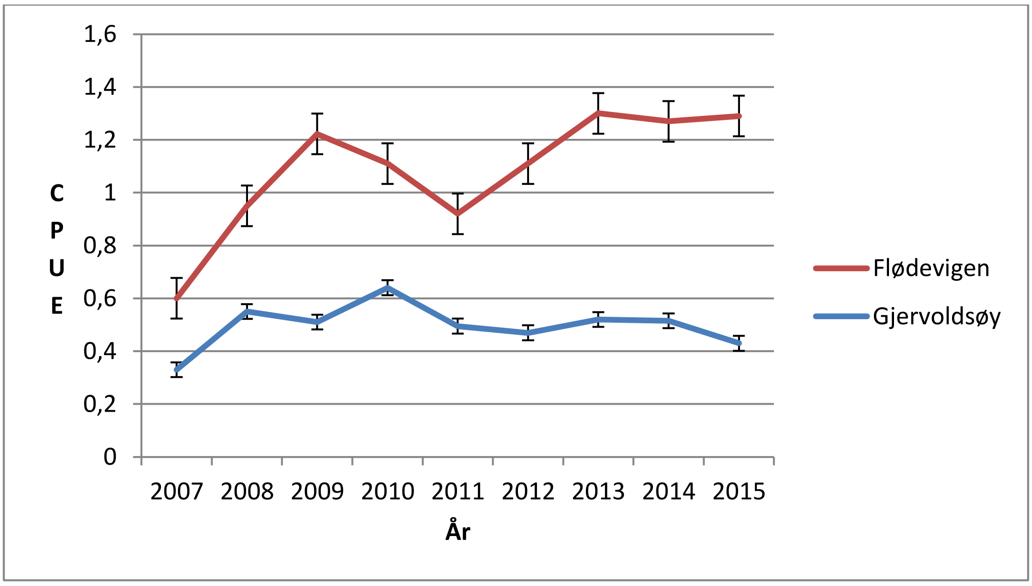


Figure 3: *CPUE as the total catch of European lobster/total effort area^{-1} year^{-1} in the Aust-Agder region, split into MPA (Flødevigen) and control area (Gjervoldsøy) MPA is a marine protected area where fishing was not allowed and control are areas that fishing both commercially and recreational was allowed.. Graph shows observed mean with standard error bars.*

Table 4: Summary statistics for the generalized linear mixed model testing for variation in catch per unit of effort of European lobster with status (MPA vs control area) and time (years) as explanatory variables in the Aust-Agder region. A negative-binominal error term was used. Significant p – values are in bold.

	DF	Sum sq.	F-Value	P-value
Status	1	156.69	193.97	< **0.001**
Year	8	31.60	4.88	**<0.001**

3.1.3 Vestfold

In the Vestfold region a total of 2103 lobster were caught in the MPA (Haneflu) and 1097 lobster were caught in the control area (Bolærne), including recaptures (Table 2). The CPUE in both the MPA and control area shows similar development, but the MPA has a larger CPUE than the control areas during all years. The CPUE is highest in 2010 in the MPA and in

2009 in the control. There is a large year-to-year variation both in the MPA and the control area, but there is no clear trend other than the CPUE being larger in the MPA. The MPA and the control diverge a bit towards the end (2015), where the MPA shows an increase in CPUE while the CPUE in the control decreases (Figure 4).

As with Aust-Agder, a generalized linear model was used to analyze the data, the same model structure was used. The model (Table 5, see appendix B.3 for estimates) shows that CPUE was significantly larger in the MPA compared to the control. Further there was a highly significant temporal effect, where some years show a larger CPUE.

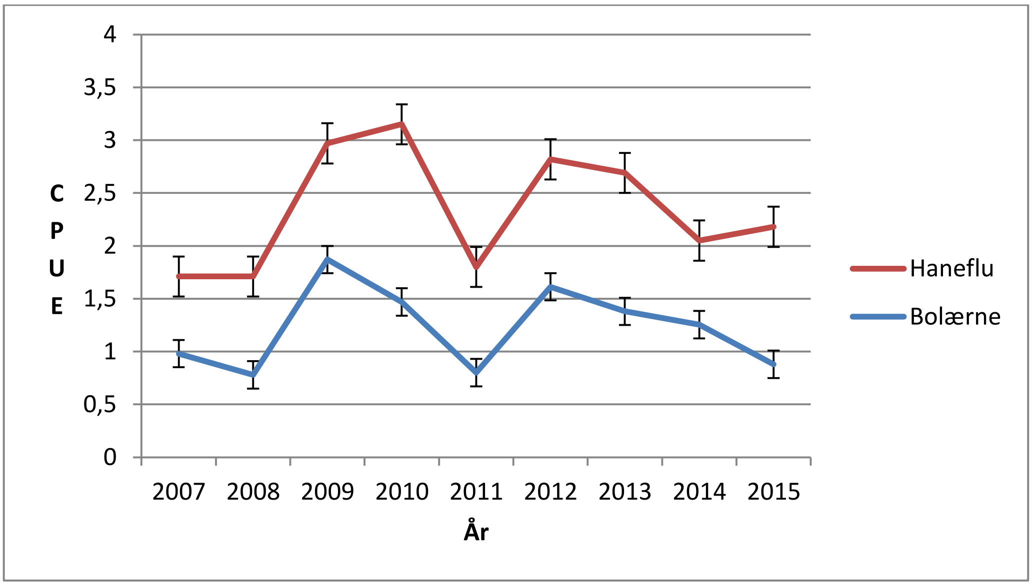


Figure 4: *CPUE as the total catch of European lobster/total effort area^{-1} year^{-1} in the Vestfold region, split into MPA (Haneflu) and control area (Bolærne) MPA is a marine protected area where fishing was not allowed and control are areas that fishing both commercially and recreational was allowed.. Graph shows observed mean with standard error bars.*

Table 5: Summary statistics for the generalized linear mixed model testing for variation in catch per unit of effort of European lobster with status (MPA vs control) and time (years) as explanatory variables in the Vestfold region. A negative-binominal error term was used. Significant p-values are in bold.

	DF	Sum sq.	F-value	P-value
Status	1	560	267.42	**<0.001**
Year	8	347	20.73	**<0.001**

3.1.4 Østfold

In the Østfold region a total of 2102 lobster were caught in the MPA (Kvernskjær) and a total of 1907 lobster were caught in the control area (Vikertangflu), including recaptures. The CPUE in this region differs from the rest of the regions as there was almost no difference in development over time between the MPA and the control area. There was an increase in the CPUE in both areas up to 2011 when the CPUE decreases again and continued to do so, except for 2015 when the CPUE increased slightly in the MPA (Figure 5).

To analyze the data for this region, a generalized linear model was used with the same structure as the two other regions. According to the model (Table 6; estimates table in appendix B.4) there was no significant effect of status, but a strong temporal effect, where some of the years show a significant larger CPUE.

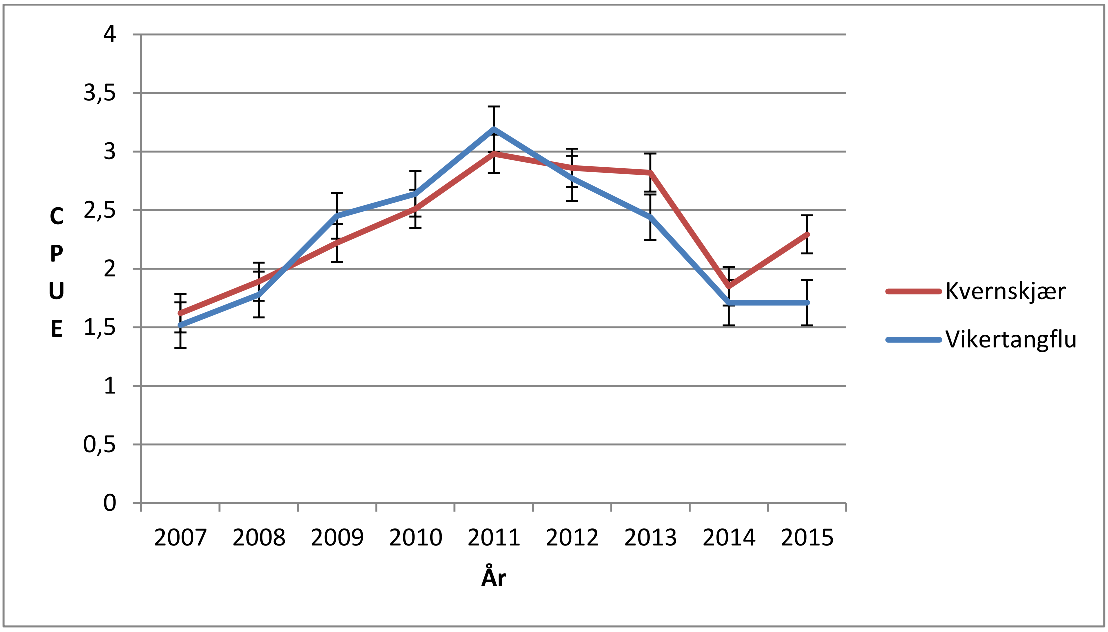


Figure 5: *CPUE as the total catch of European lobster/total effort area^{-1} year^{-1} in the Østfold region, split into MPA (Kvernskjær) and control area (Vikertangflu) MPA is a marine protected area where fishing was not allowed and control are areas that fishing both commercially and recreational was allowed.. Graph shows observed mean with standard error bars.*

Table 6: Summary statistics for the generalized linear mixed model testing for variation in catch per unit of effort of European lobster with status (MPA vs control) and time (years) as explanatory variables in the Østfold region. A negative-binominal error term was used. Significant p-value is in bold.

	DF	Sum sq.	F-value	P-value
Status	1	3	1.3	0.3
Year	8	418	24.4	**<0.001**

3.2 Mean body size

3.2.1 All regions

A total of 8627 lobster (5181 in the MPA, 3446 in the control areas, including recaptures) were measured and used for analyses. The lobster showed a generally quick response in development in mean body size in all areas (Figure 6). The mean body size of lobster in the control areas were generally below minimum landing size (240 mm before 2009, 250 mm after 2009), whereas the mean body size of lobster in the MPAs tended to increase with time.

To analyze the data a linear mixed model was used. The best model was selected using the lowest BIC scores (appendix A.2). The best model tested mean body size as a response variable with status (MPA or control), year as a factor variable, sex (male or female) and the interaction between status and year. According to the model there was a strong effect of status, where it was estimated that lobster are generally larger in the MPAs (Table 7; estimates in appendix B.5). Further there was also an effect of year and an effect of the interaction between status and year, where the estimates are increasing with year. The analysis also shows a significant effect of sex, where males generally were larger than females.

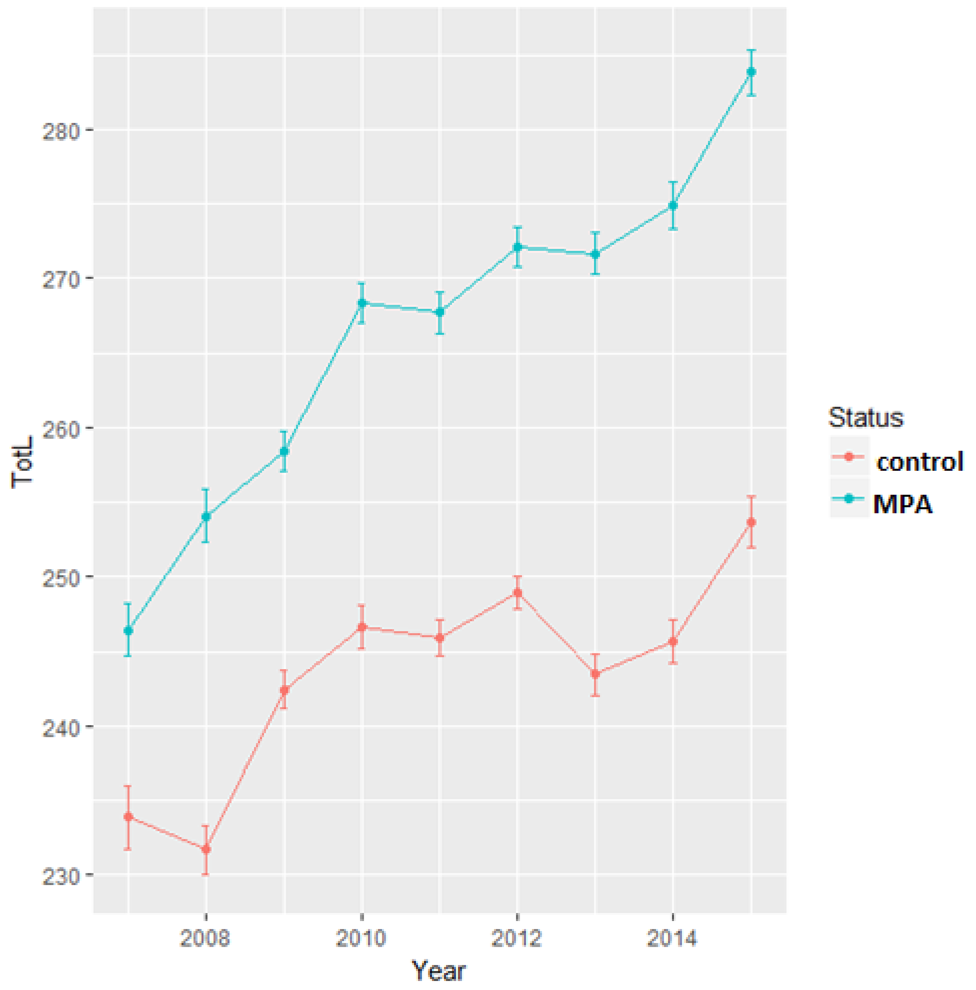


Figure 6: *Temporal variation in mean body size (± standard error) of European lobster captured in the marine protected areas (MPA) (blue-green) and the tree control areas (control) (red).In the MPAs fishing was not allowed. In the control areas fishing both commercially and recreation was allowed. The y-axis shows total length (TotL) in mm. The graph shows the observed mean, averaged over all the three areas.*

Table 7: The statistics summary over the linear mixed model testing for mean body size with status (MPA vs control), time (years), sex (male/female) and the interaction between year and status as explanatory variables. Region was used as a random variable. Significant p-values in bold.

	DF	**Sum sq.**	**F-value**	**P-value**
Status	1	1038666	1004.8	**<0.001**
Year	8	573010	69.2	**<0.001**
Sex	1	55454	53.6	**<0.001**
Status: Year	8	53921	6.5	**<0.001**

3.2.2 Aust-Agder, Vestfold and Østfold

The development in mean body size of lobster in the three different regions follows the same overall trend as all the regions combined. The mean body size relatively quickly increases in the MPAs and fluctuates around minimum landing size in the controls (Figure 7). There was a clear trend of the mean body size getting larger over time in the MPAs. Each separate region has more year-to-year variation than all the three regions combined. In the controls the mean body size varied more among regions, with a possible weak increasing trend in Aust-Agder and Vestfold, where the last measurement is 260 mm in both places. The mean body size of lobster in the control area in Østfold tends to stay below 250 mm and varied less.

These three areas were tested separately with linear models. The models have the same structure as the model analyzing all regions combined only excluding the random effect. The models have status (MPAs or controls), year and sex (male or female) as factor variables and included the interaction between status and year. According to the models there was a strong effect of status and year in all regions (Table 8). However, in Østfold the mean body size estimate for MPAs were lower than the two other regions and not significant (estimates in appendix B.6-B.8). There was a strong interaction effect in Østfold, but not in the other two regions (Table 8). However, the mean body size estimates for the interaction effect were significant in both Aust-Agder and Østfold and are increasing with years. Males were significantly larger in all regions.

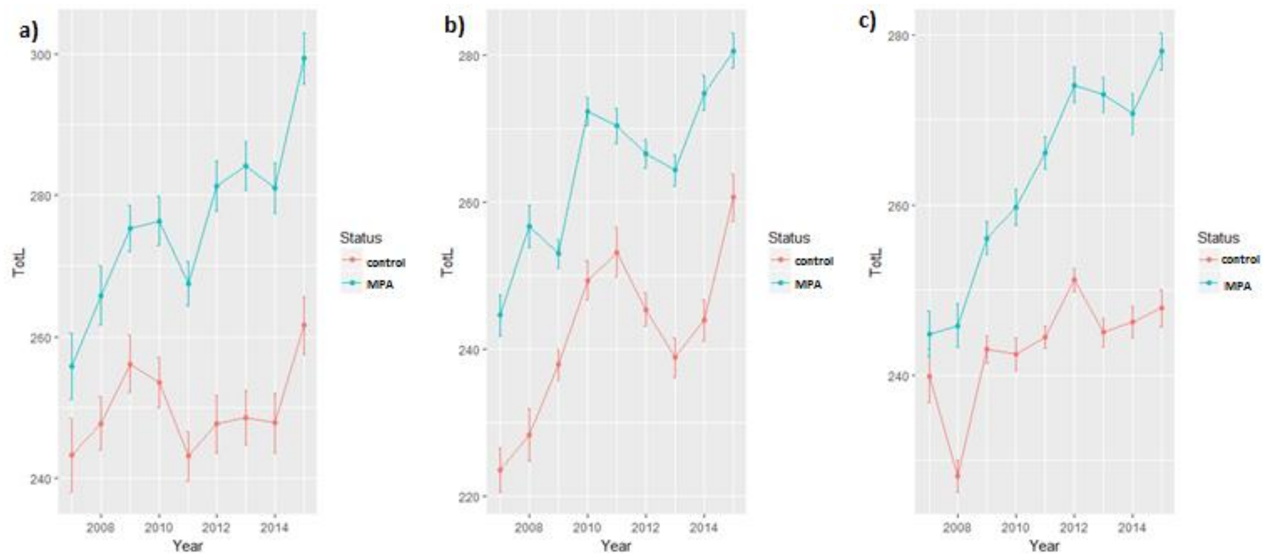


Figure 7: *Temporal variation in mean body size (± standard error) of European lobster captured in the three different regions in the three marine protected areas (MPA) (blue-green) and the three control areas (control) (red). Each figure shows the temporal variation in one of the regions, from left: Aust-Agder (a), Vestfold (b) and Østfold (c). The y-axis shows total length (TotL) in mm and the x-axis shows years Note the differences in scale on the y-axis for all the three figures.*

Table 8: The statistics summary over the linear model testing for body size with status (MPA vs control), time (years, as a factor variable), sex (male/female) and the interaction between year and status as explanatory variables for all three regions. Significant p-values are in bold.

Aust-Agder	**DF**	**Sum sq.**	**F-value**	**p-value**
Status	1	241964	194.46	**<0.001**
Year	8	114429	11.50	**<0.001**
Sex	1	11885	9.55	**0.002**
Status: Year	8	19360	1.94	0.05
Vestfold				
Status	1	378422	348.04	**<0.001**
Year	8	307161	35.31	**<0.001**
Sex	1	24217	22.27	**<0.001**
Status: Year	8	16246	1.87	0.06
Østfold				
Status	1	429733	483.58	**<0.001**
Year	8	267709	37.66	**<0.001**
Sex	1	16311	18.35	**<0.001**
Status: Year	8	43637	6.14	**<0.001**

3.3 Sex-ratio

3.3.1 All regions

A total of 4497 males and 4131 females were caught over the study period, including recaptures. A total of 2711 males and 2470 females were caught in the MPAs. A total of 1786 males and 1661 females were caught in the control areas. The proportion of females and males in the areas remained relatively similar throughout the study period in both MPA and control areas (Figure 8).

The data was tested using a generalized linear mixed model. The best model was selected based on the lowest BIC values (model selection in appendix A.3). The best model tested proportion of males as a response variable with status (MPA or control) and year as factor variables and body size as a continuous variable, with region as a random effect. There was a significant effect of body size and year (Table 9), but no large significant overall effect of MPAs on the proportion of males. There is a weakly significant estimate of the MPAs, which suggest that the sex-ratio become slightly more females biased in MPAs (table in appendix B.9). The estimates also suggest that with increasing size, the sex-ratio becomes more male biased.

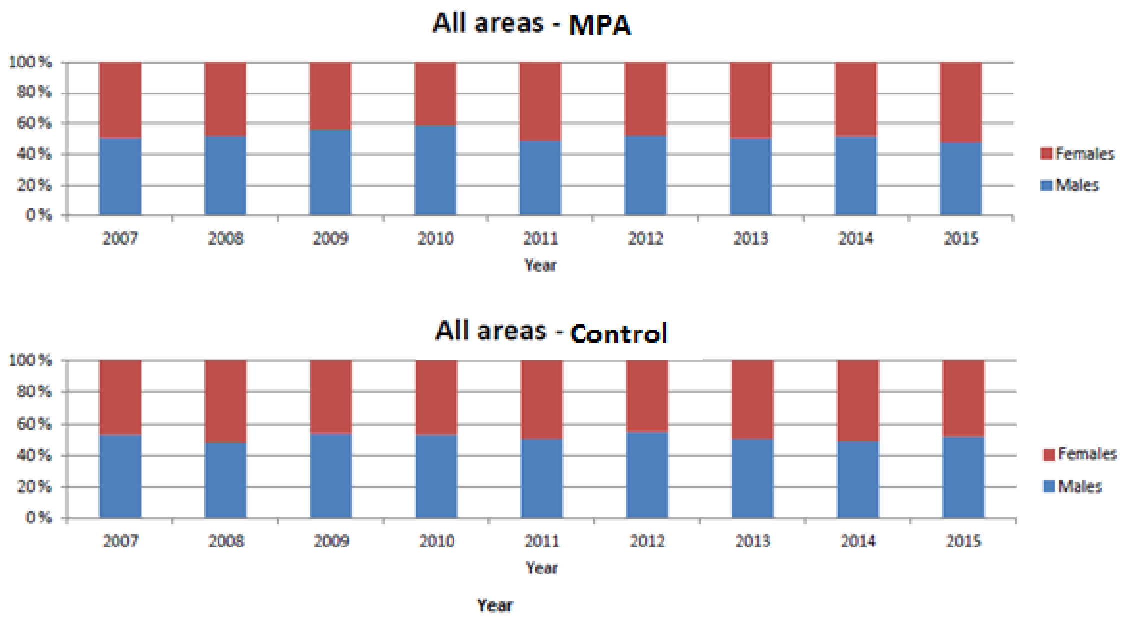


Figure 8: *Temporal variation in the proportion of male (blue) and female (red) lobster in the three marine protected areas (MPA) and the three control areas (control).In the MPAs no fishing was allowed, in the control areas fishing both commercially and recreational was allowed. Y-axis shows percentages of males and females. The x-axis shows years.*

Table 9: The statistical summary of the generalized linear mixed model testing proportion of males with status (MPA vs control), time (years) and body size as explanatory variables. Region was used as a random variable and the model used a binomial error term. Significant p-values in bold.

	DF	Sum sq.	F-value	P-value
Status	1	0.0231	0.0231	0.88
Year	8	18.6089	2.3261	**0.02**
Body size	1	51.982	51.9821	<**0.001**

3.3.2 Aust-Agder, Vestfold and Østfold

The total number of male and female lobster caught in the different areas is summarized in Table 10. In the three different regions the sex-ratio varied a bit more amongst year than in the areas combined. There was generally somewhat more males in the Vestfold region, where they account for 50% or more during most of the study period (Sex-ratio figures in appendix C.1-C.3). The three regions were tested separately with generalized linear models, with the same structure as the model analyzing the three regions combined excluding only the random effect. These models tested proportion of males as a response variable with status (MPA or control) and year as factor variables and body size as a continuous variable. The effect of body size was significant in all three regions. Year was only significant in the Vestfold region (Table 11). According to the estimates (Table B.10-B12 in appendix) the sex-ratio becomes slightly female biased in Vestfold, but there were no significant estimates of MPA in the two other regions. In Vestfold there was also significant estimates that indicates the sex-ratio becomes more female biased from 2012 onwards. The estimates also indicate that with increasing size the sex-ratio becomes more male biased, which is the trend in all regions.

Table 10: The total number of males and females caught, all years summarized and divided into each region and the status within a given region.

	Males Control	Males MPA	Females Control	Females MPA
Aust-Agder	220	488	223	488
Vestfold	624	1141	473	962
Østfold	942	1082	965	1020

Table 11: The statistical summary of the generalized linear model testing proportion of males with status (MPA vs control), time (years) and the interaction between status and year as explanatory variables. Aust-Agder, Vestfold and Østfold are the three regions included in this study. A binomial error term was used. Significant p-values in bold.

Aust-Agder	**DF**	**Sum sq.**	**F-value**	**P-value**
Status	1	0.0	0.03	0.87
Year	8	3.3	1.66	0.10
Body size	1	2.4	9.50	**0.002**
Vestfold				
Status	1	0.5	2.07	0.15
Year	8	7.2	3.70	**<0.001**
Body size	1	5.4	22.23	**<0.001**
Østfold				
Status	1	0.5	1.819	0.18
Year	8	3.7	1.843	0.06
Body size	1	4.5	18.17	**<0.001**

4. Discussion

Overfishing is a huge problem for the European lobster population in Skagerrak. The regulations in place include a minimum landing size (250 mm, measured from rostrum to telson) and a ban on landing ovigerous female lobster. Because of the use of minimum landing size, the big ones have been targeted, leaving a less productive part of the population back. Regulation also seemed to favor female lobster, because of the ban on landing ovigerous females. The regulations were not effective enough, and MPAs were established to obtain knowledge and guide the use of MPAs as a possible conservational tool for lobster in Skagerrak. This study was done to elucidate the effects of MPAs on populations of European lobster in Skagerrak, specifically the effects on population density, mean body size and sex-ratio.

As expected the catch per unit of effort (CPUE) in the MPAs was significantly larger than in the control areas. CPUE was used as an indicator of population density. The overall trends in the MPAs, even though the CPUE is significantly larger in the MPAs, follow the large year-to-year variation in the control areas almost identically. The mean body size of the lobster increased in all of the MPAs as expected but stayed around the minimum landing size in the control areas. The sex-ratio of lobster in the MPAs and control areas was relatively balanced from the start of the study period and stayed relatively balanced during the entire study period. Thus, there was no overall effect of MPAs on the sex-ratio, and if there is an effect of MPAs it is surprising that the proportion of males is reduced. The observed effects of MPAs on population density and mean body size could result in a greater reproductive output. Larger females have a greater fecundity and the larger lobster population will produce more offspring as a larger population will have a larger spawning population as well. Because lobster have pelagic larvae, some of the recruits produced in the MPAs will drift to adjacent areas, possibly replenishing areas that are overfished. There is also a possibility of a spill-over effect by adults and juveniles to adjacent areas because of density dependent dispersal. Overall the MPAs did have positive effects on the populations residing in the MPAs by increasing the population and their mean body size.

4.1 Catch per unit of effort

The general trend of CPUE inside the MPAs being significantly larger than the CPUE in the control areas, matches earlier studies done on the same MPAs and on another MPA in Skagerrak (Moland, Olsen, et al., 2013; Moland, Ulmestrand, Olsen, & Stenseth, 2013). The larger CPUE in the MPA is interpreted as a larger population density (Hoskin, Coleman, von Carlshausen, & Davis, 2011). When MPAs are established, direct effects, such as an increase in population density could develop within 1 – 5 years (Babcock et al., 2010), as shown here, where CPUE is larger from the beginning of the study period. At the beginning of the study period, the lobsters in the MPA had been illegal to land since 1st of December 2005 (due to the ending of the fishing season in 2005). An increase in population density has been reported by many studies done on MPAs (Kelly et al., 2000; Moland, Ulmestrand, et al., 2013; Rowe, 2002; Cole, Ayling, & Creese, 1990)

Although the population density is larger in the MPAs than outside, the population does not continue to increase during the study period (2007 – 2015). There is a large year-to-year variation, but nothing indicating that the population is increasing other than in the initial years. Rather it seems like the population is stabilizing at a higher level. As the population and mean body size of lobster is getting larger and larger inside the reserve, the space for each individual lobster is getting smaller. The larger lobster are more successful as they are able to win more fights (Karnofsky, Atema, & Elgin, 1989), and could possibly be killing and/or driving smaller lobster away. Especially large males are dominant and will try to clear shelters close to its' own shelter of other males (Karnofsky & Price, 1989). Territorial behaviors in large female lobster have also been observed, especially close to molting (Ennis, 1984). In the MPAs were the percentage of large lobster is increasing, the smaller ones may seek territories with a smaller density of large lobster. Density-dependent interactions have been found for other organisms, such as reef-fish, in which aggression was more intense inside the reserve and that the larger fish chased away the smaller fish, forcing them to relocate outside the reserve (Abesamis & Russ, 2005). However, the studies focusing on spill-over from the MPAs has only proven a limited spill-over and no net spill-over (Huserbraten et al., 2013; Thorbjørnsen, 2015). These studies have primarily received data about spill-over from recapture and tagging data, as well as data from fishers. This means that a lobster needs to be captured and then recaptured in the control area or caught by fishers for it to be registered as spill-over. Many lobsters which have not been recaptured or captured will emigrate to all the adjacent areas, not just the control areas or areas used by fishers. This means that the entire emigrating population will not be registered and the spill-over could therefore be larger than previously thought. Other studies have shown spill-over from MPAs, but shows that the lobsters do not wander far from the MPAs (Goñi et al., 2006) and spill-over is highest when the preferred habitat continues across the MPA boarder (Goñi et al., 2008).

The year-to-year variation addressed earlier follow the same pattern both in the MPAs and the control areas. The ups and downs of CPUE in the MPAs are almost the same as in the control areas. These similarities could be the result of year-to-year variation in catchability of lobster or harvesting efficiency due to weather conditions or other environmental factors. Severe weather conditions could affect the harvesting efficiency and low temperatures have shown to reduce lobster catchability (McLeese & Wilder, 1958). In lower temperatures the lobster is less active. A study showed that the American lobsters were not active during winter when temperatures were low and that activity increased when the temperatures increased during spring/summer (Ennis, 1984). Because lobster actively need to seek the traps themselves, varying temperatures could affect the CPUE.

The Østfold region stood out by being the only region in which the MPA did not have a CPUE larger than in the control area. In fact, the CPUE increases during the first half of the study period in both areas simultaneously and decreases towards the end of the study period. The MPA in Østfold was also the only MPA in which the CPUE was larger in the control area than in the MPA before MPA establishment (Moland, Olsen, et al., 2013), possibly indicating that the habitat is more favorable for lobsters in the control area. Østfold also has the smallest MPA in this study. If the control area do have more favorable habitat, the reason for the increase in both the MPA and control area could be spill-over from the MPA to the control area.

4.2 Mean body size

When fishing mortality is greatly reduced, as in MPAs, it is expected that the lobsters will increase in size as they are allowed to live longer and grow; and as expected, the lobsters in the MPAs are generally increasing in mean body size over the years, in contrast to the control area in which the mean body size remained around minimum landing size. This is the case for all the regions and the result matches the results from an earlier study done on the same MPAs (Moland, Olsen, et al., 2013). Their results showed a 13% increase in mean body size in the MPAs, and a negligible increase in the control areas, compared to my general findings of a 13.2% increase in mean body size from the start to end of study period, and an increase of 7.8% in control areas (Figure 6). Although there is a general 7.8% increase in mean body size in the control areas, the mean body size in 2015 (the end of the study period) was very close to the minimum landing size (254 mm, minimum landing size is 250 mm). This increase could therefore be result of the change in regulation from a minimum landing size of 240 mm to 250 mm in 2008, as it is after 2008 the increase is visible on Figure 6 (Moland, Olsen, et al., 2013). The trend is the same in all regions, with a bit more variation in the control areas when looking at each region separately. All three regions show a rapid increase in mean body size in the MPAs. Other studies, from all over the world, also show a significant increase in mean body size in MPAs (Edgar & Barrett, 1999; Kelly, Scott, MacDiarmid, & Babcock, 2000; Lester et al., 2009).

Studies show that the increased mean body size of females leads to an increased reproductive output (MacDiarmid, 1989). Fecundity in a female European lobster increases greatly with size (Tully et al., 2001). A 370 mm lobster produces approximately 32 000 eggs, in contrast to a 250 mm produces approximately 8000 eggs (Moen & Svensen, 2004). Díaz, Mallol, Parma, and Goñi (2011) found that the reproductive output of lobster in a Mediterranean MPA increased 600% within twenty years of protection. They also found that it was mostly due to the larger size of the females, rather than abundance that the reproductive output increased. Even though the MPA only was 18% of the lobster habitat in the region, it accounted for 80% of the regional egg production. Mature females also became 20 times more abundant and the egg production per unit area was 30 times greater in the MPA. The increase in reproductive output could have both local and regional effects depending on the current water movement and temperature. The European lobster larva is pelagic for 10 days – 2 months (depending on temperature) during which they will drift to other areas (Phillips & Sastry, 1980). The most sheltered regions will have a smaller scale of drift out to other regional areas, whereas in the more exposed regions the larvae could potentially drift along the entire Skagerrak coast, as it takes approximately two weeks for the upper water masses to move along the entire Skagerrak coast, depending on season (Danielssen et al., 1997). Díaz et al. (2011) argues that the increased reproduction has a far greater benefit to adjacent areas than the spill-over of adult lobster. The significance of large males in relation to reproduction is unknown. However, large females do prefer large males, and will seek the largest males pre-mating (Karnofsky & Price, 1989).

4.3 Sex-ratio

The results show that the sex-ratio of males and females are close to 1:1 in all regions in both MPAs and controls. This is unexpected due to the regulations that seemed to be targeting males more than females as there is a ban on landing ovigerous females. The models show that MPAs do not have a large significant effect on the sex-ratio (Table 9 and 11), confirming the visible lack of trends in Figure 8 above and Figure C.1-C.3 in appendix. An explaining factor could be that male lobsters are in general more catchable (Moland, Ulmestrand, et al., 2013), creating a bias towards males and the figures could show that there is a 1:1 ratio of males and females, when in reality there are more females. However, if this was the only explanation, one would expect to see more than 50% males at the end of the study period in the MPAs, which there is not. There are, in fact, relatively fewer males towards the end of the study period in the MPAs.

Some of the models estimated a weak but significant decrease in the proportion of males in the MPAs (all three regions combined and Vestfold, appendix B.9 and B.11). The estimates of the MPAs were negative (bias towards females) in all the models, but were only significant in the Vestfold region and in all regions combined. The possible decrease in the proportion of males in MPAs could be connected to the significant increase in the proportion of larger males in the MPAs. The larger proportion of big males was evident in all the models and body size was the strongest effect on sex-ratio measured. Lobsters are in general aggressive and territorial, and males even more so (Karnofsky & Price, 1989). When looking at shelter use in American lobster (*Homarus americanus*), O'Neill and Cobb (1979) found that the dominance is often by large male lobster. As an effect to the percentage of large males in the population, the smaller ones could possibly be emigrating to areas where the percentage of large males is lower, i.e. in non-protected areas. A study on European spiny lobster (*Palinurus elephas*) also found that there were generally more females in the MPA (Goñi, Reñones, & Quetglas, 2002). Another study showed that the percentage of males emigrating from MPAs were higher than the percentage of females emigrating (Goñi, Hilborn, Díaz, Mallol, & Adlerstein, 2010). Thorbjørnsen (2015) also found that there were more large females immigrating to the MPAs than males, which could affect the sex-ratio as well.

4.4 Effects of MPAs

In summary, the MPAs were successful at protecting lobster. The population density increased and so did the mean body size of the lobster. These two increases could possibly result in an increase in recruitment, not only to the MPAs, but also to adjacent areas due to larval drift. These larvae can drift along the entire Skagerrak coast within two weeks and by that replenish other areas as well. The spill-over detected in previous studies is limited, but the stabilizing trends in population density could indicate that lobsters are emigrating. The lobster emigrating can rebuild stocks outside the MPAs, although the likelihood of them being caught when above minimum landing size is high (Wiig, Moland, Haugen, & Olsen, 2013). The increased reproduction in the MPAs arguably will benefit the fished areas more than the potential effects of spill-over, as seen in Díaz et al. (2011) study were 80% of all egg production in the region was from the MPAs. Grüss, Kaplan, Guénette, Roberts, and Botsford (2011) argued that home range is critical for the conservational success for any target species, as a home range that is of a much larger size than the MPA contributes to too much movement outside the MPAs and reducing the protection value. However, Moland, Olsen, Andvord, et al. (2011) found that lobsters within the Skagerrak region have home ranges that are within the limits of the MPAs, meaning that protection of lobster is still efficient, even with small MPAs.

5. Conclusion

In conclusion, the MPAs did have the desired conservational effects. The MPAs successfully protected the lobster and that resulted in an increase in population density and an increase in body size. The sex-ratio was not affected by protection as it was close to 1:1 from the beginning of the study period. The MPAs did not have any noteworthy further effect on the sex-ratio, and if so the effect is that it becomes a slightly smaller proportion of males in the MPAs.

Population density, measured as catch per unit of effort, did not increase continually, but seemed to stabilize at some point. There was a great year-to-year variation which could indicate influences from other factors not investigated in this study, such as temperature and weather condition. The population density was significantly larger in the MPAs than in the control areas for two of the three studied areas. In the third MPA the CPUE was similar to that observed in the control area. The third MPA stood out from the beginning by being the only MPA in which the CPUE was larger in the control area before MPA establishment.

Mean body size increased rapidly in all MPAs, but stayed around minimum landing size (250 mm) in the control areas, with some year-to-year variation. This was the trend for all the three regions. The increase in mean body size of female lobster could influence how many eggs they produce and increase the reproductive output of the MPAs. The increased reproductive output could have both a local and regional effect, as the lobster larvae is pelagic and will drift with the currents while in a pelagic stage.

I did not find any large effects of MPAs on the sex-ratio of lobster, except a weak tendency for the proportion of males to decrease in the MPAs towards the end of my study. This could reflect some aspects of male behavior and dominance.

Overall, the MPAs work as a refuge for the overfished populations of European lobster in Skagerrak and spill-over, though only a limited degree is detected, could also benefit the fisheries. MPAs could also function as a possible nursery zone, where many of the eggs hatched in the MPAs will drift to other areas and hopefully increase population density of overfished areas.

Future studies may cast some light over other factors affecting the lobster populations in Skagerrak. I would suggest starting by investigating survival of recaptured lobster within

MPAs and the associated control areas and compare to see if survival is mirroring the CPUE variations. If not, the CPUE variations may be due to variation in catchability and not due to survival in MPAs. Survival could also shed some light on whether lobster within the MPA is more resilient to environmental factors. Another aspect of MPAs that is not investigated in this study is differences in size and the number of ovigerous females. It is a general idea that harvesting is inducing selection towards earlier maturation. Calculating size at maturation within MPAs and the associated control areas could potentially tell something about whether or not MPAs are counteracting this effect.

References

Abesamis, R. A., & Russ, G. R. (2005). Density-dependent spillover from a marine reserve: Long-term evidence. *Ecological Applications, 15*(5), 1798-1812.

Agnalt, A.-L., Kristiansen, T. S., & Jørstad, K. E. (2007). Growth, reproductive cycle, and movement of berried European lobsters (*Homarus gammarus*) in a local stock off southwestern Norway. *Ices Journal of Marine Science, 64*(2), 288-297.

Aho, K., Derryberry, D., & Peterson, T. (2014). Model selection for ecologists: the worldviews of AIC and BIC. *Ecology, 95*(3), 631-636.

Aiken, D. E. (1980). Molting and growth. In J. S. Cobb & B. F. Phillips (Eds.), *The biology and management of lobsters. Volume 1. physiology and behaviour* (pp. 115 - 118). New York: Academic Press.

Aiken, D. E., & Waddy, S. L. (1980). Reproductive biology. In J. S. Cobb & B. F. Phillips (Eds.), *The biology and management of lobsters. Volume 1. Physiology and behaviour* (pp. 252 - 261). New York: Academic Press.

Babcock, R. C., Shears, N. T., Alcala, A. C., Barrett, N. S., Edgar, G. J., Lafferty, K. D., . . . Russ, G. R. (2010). Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *Proceedings of the National Academy of Sciences, 107*(43), 18256-18261.

Baskett, M. L., Levin, S. A., Gaines, S. D., & Dushoff, J. (2005). Marine reserve design and the evolution of size at maturation in harvested fish. *Ecological Applications, 15*(3), 882-901.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using {lme4}. *Journal of Statistical Software, 67*(1), 1-48.

Beamish, R. J., McFarlane, G. A., & Benson, A. (2006). Longevity overfishing. *Progress in Oceanography, 68*(2–4), 289-302.

Berkeley, S. A., Chapman, C., & Sogard, S. M. (2004). Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology, 85*(5), 1258-1264.

Berkeley, S. A., Hixon, M. A., Larson, R. J., & Love, M. S. (2004). Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries, 29*(8), 23-32.

Birkeland, C., & Dayton, P. K. (2005). The importance in fishery management of leaving the big ones. *Trends in Ecology & Evolution, 20*(7), 356-358.

Bundy, A., & Fanning, L. P. (2005). Can Atlantic cod (*Gadus morhua*) recover? Exploring trophic explanations for the non-recovery of the cod stock on the eastern Scotian Shelf, Canada. *Canadian Journal of Fisheries and Aquatic Sciences, 62*(7), 1474-1489.

Butler, M., Cockcroft, A., MacDiarmid, A., & Wahle, R. (2011). *Homarus gammarus*. *The IUCN Red List of Threatened Species 2011: e.T169955A69905303.* Retrieved from http://www.iucnredlist.org/details/169955/0

Clark, W. (1977). The lessons of the Peruvian anchoveta fishery. *California Cooperative Oceanic Fisheries Investigations Reports, 19*, 57-63.

Claudet, J., Pelletier, D., Jouvenel, J. Y., Bachet, F., & Galzin, R. (2006). Assessing the effects of marine protected area (MPA) on a reef fish assemblage in a northwestern Mediterranean marine reserve: Identifying community-based indicators. *Biological Conservation, 130*(3), 349-369.

Cole, R. G., Ayling, T. M., & Creese, R. G. (1990). Effects of marine reserve protection at Goat Island, northern New Zealand. *New Zealand Journal of Marine and Freshwater Research, 24*(2), 197-210.

Coleman, F. C., Figueira, W. F., Ueland, J. S., & Crowder, L. B. (2004). The impact of United States recreational fisheries on marine fish populations. *Science, 305*(5692), 1958-1960.

Cooke, S. J., & Cowx, I. G. (2004). The role of recreational fishing in global fish crises. *BioScience, 54*(9), 857-859.

Danielssen, D. S., Edler, L., Fonselius, S., Hernroth, L., Ostrowski, M., Svendsen, E., & Talpsepp, L. (1997). Oceanographic variability in the Skagerrak and Northern Kattegat, May–June, 1990. *Ices Journal of Marine Science, 54*(5), 753-773.

Díaz, D., Mallol, S., Parma, A. M., & Goñi, R. (2011). Decadal trend in lobster reproductive output from a temperate marine protected area. *Marine Ecology Progress Series, 433*, 149-157.

Edgar, G. J., & Barrett, N. S. (1999). Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. *Journal of Experimental Marine Biology and Ecology, 242*(1), 107-144.

Edgar, G. J., & Stuart-Smith, R. D. (2009). Ecological effects of marine protected areas on rocky reef communities—a continental-scale analysis. *Marine Ecology Progress Series, 388*, 51-62.

Ennis, G. P. (1984). Territorial behavior of the American lobster *Homarus americanus*. *Transactions of the American Fisheries Society, 113*(3), 330-335.

FAO. (2016). *The state of world fisheries and aquaculture 2016. Contributing to food security and nutrition for all.* Rome.

Fenberg, P. B., Caselle, J. E., Claudet, J., Clemence, M., Gaines, S. D., Garcia-Charton, J. A., . . . Sorensen, T. K. (2012). The science of European marine reserves: Status, efficacy, and future needs. *Marine Policy, 36*(5), 1012-1021.

Fiskeridirektoratet. (2016). Strenge regler for hummerfiske. Retrieved from http://www.fiskeridir.no/Fritidsfiske/Noen-utvalgte-arter/Hummer

Gell, F. R., & Roberts, C. M. (2003). Benefits beyond boundaries: the fishery effects of marine reserves. *Trends in Ecology & Evolution, 18*(9), 448-455.

Goñi, R., Adlerstein, S., Alvarez-Berastegui, D., Forcada, A., Reñones, O., Criquet, G., . . . Planes, S. (2008). Spillover from six western Mediterranean marine protected areas: evidence from artisanal fisheries. *Marine Ecology Progress Series, 366*, 159-174.

Goñi, R., Hilborn, R., Díaz, D., Mallol, S., & Adlerstein, S. (2010). Net contribution of spillover from a marine reserve to fishery catches. *Marine Ecology Progress Series, 400*, 233-243.

Goñi, R., Quetglas, A., & Reñones, O. (2006). Spillover of spiny lobsters *Palinurus elephas* from a marine reserve to an adjoining fishery. *Marine Ecology Progress Series, 308*, 207-219.

Goñi, R., Reñones, O., & Quetglas, A. (2002). Dynamics of a protected western Mediterranean population of the European spiny lobster *Palinurus elephas* (Fabricius, 1787) assessed by trap surveys. *Marine and Freshwater Research, 52*(8), 1577-1587.

Grüss, A., Kaplan, D. M., Guénette, S., Roberts, C. M., & Botsford, L. W. (2011). Consequences of adult and juvenile movement for marine protected areas. *Biological Conservation, 144*(2), 692-702.

Gubbay, S. (1995). Marine protected areas — past, present and future. In S. Gubbay (Ed.), *Marine Protected Areas: Principles and techniques for management* (pp. 1-14). Dordrecht: Springer Netherlands.

Halpern, B. S., & Warner, R. R. (2002). Marine reserves have rapid and lasting effects. *Ecology Letters, 5*(3), 361-366.

Halpern, B. S., & Warner, R. R. (2003). Matching marine reserve design to reserve objectives. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 270*(1527), 1871-1878.

Hoskin, M. G., Coleman, R. A., von Carlshausen, E., & Davis, C. M. (2011). Variable population responses by large decapod crustaceans to the establishment of a temperate marine no-take zone. *Canadian Journal of Fisheries and Aquatic Sciences, 68*(2), 185-200.

Huserbraten, M. B. O., Moland, E., Knutsen, H., Olsen, E. M., Andre, C., & Stenseth, N. C. (2013). Conservation, spillover and gene flow within a network of northern European marine protected areas. *Plos One, 8*(9): e73388. doi:10.1371/journal.pone.0073388

Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., . . . Warner, R. R. (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science, 293*(5530), 629-637.

Karnofsky, E. B., Atema, J., & Elgin, R. H. (1989). Field observations of social behavior, shelter use, and foraging in the lobster, *Homarus americanus*. *The Biological Bulletin, 176*(3), 239-246.

Karnofsky, E. B., & Price, H. J. (1989). Dominance, territoriality and mating in the lobster, *Homarus americanus*: A mesocosm study. *Marine Behaviour and Physiology, 15*(2), 101-121.

Kelly, S., Scott, D., MacDiarmid, A. B., & Babcock, R. C. (2000). Spiny lobster, *Jasus edwardsii*, recovery in New Zealand marine reserves. *Biological Conservation, 92*(3), 359-369.

Kleiven, A. R., Olsen, E. M., & Volstad, J. H. (2012). Total catch of a red-listed marine species is an order of magnitude higher than official data. *Plos One, 7*(2): e31216. doi:10.1371/journal.pone.0031216

Lester, S. E., Halpern, B. S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B. I., Gaines, S. D., . . . Warner, R. R. (2009). Biological effects within no-take marine reserves: a global synthesis. *Marine Ecology Progress Series, 384*, 33-46.

Lizárraga-Cubedo, H. A., Tuck, I., Bailey, N., Pierce, G. J., & Kinnear, J. A. M. (2003). Comparisons of size at maturity and fecundity of two Scottish populations of the European lobster, *Homarus gammarus*. *Fisheries Research, 65*(1–3), 137-152.

MacDiarmid, A. B. (1989). Size at onset of maturity and size-dependent reproductive output of female and male spiny lobsters *Jasus edwardsii* (Hutton) (Decapoda, Palinuridae) in northern New Zealand. *Journal of Experimental Marine Biology and Ecology, 127*(3), 229-243.

McLeese, D. W., & Wilder, D. G. (1958). The activity and catchability of the Lobster (*Homarus americanus*) in relation to temperature. *Journal of the Fisheries Research Board of Canada, 15*(6), 1345-1354.

Moen, F. E., & Svensen, E. (2004). *Homarus gammarus* - Common lobster. In F. E. Moen & E. Svensen (Eds.), *Marine fish & invertebrates of Northern Europe* (pp. 240 - 242). Essex: AquaPress.

Moland, E., Olsen, E. M., Andvord, K., Knutsen, J. A., & Stenseth, N. C. (2011). Home range of European lobster (*Homarus gammarus*) in a marine reserve: implications for future reserve design. *Canadian Journal of Fisheries and Aquatic Sciences, 68*(7), 1197-1210.

Moland, E., Olsen, E. M., Knutsen, H., Garrigou, P., Espeland, S. H., Kleiven, A. R., . . . Knutsen, J. A. (2013). Lobster and cod benefit from small-scale northern marine protected areas: inference from an empirical before - after control-impact study. *Proceedings of the Royal Society Biological Sciences, 280*(1754). doi:http://dx.doi.org/10.1098/rspb.2012.2679

Moland, E., Olsen, E. M., Knutsen, H., Knutsen, J. A., Enersen, S. E., Andre, C., & Stenseth, N. C. (2011). Activity patterns of wild European lobster *Homarus gammarus* in coastal marine reserves: implications for future reserve design. *Marine Ecology Progress Series, 429*, 197-207.

Moland, E., Olsen, E. M., & Stenseth, N. C. (2010). Maternal influences on offspring size variation and viability in wild European lobster *Homarus gammarus*. *Marine Ecology Progress Series, 400*, 165-173.

Moland, E., Ulmestrand, M., Olsen, E. M., & Stenseth, N. C. (2013). Long-term decrease in sex-specific natural mortality of European lobster within a marine protected area. *Marine Ecology Progress Series, 491*, 153-164.

Myers, R. A., & Worm, B. (2003). Rapid worldwide depletion of predatory fish communities. *Nature, 423*(6937), 280-283.

Nærings- og fiskeridepartementet. (2006). Forskrift om fredningsområder for hummer. Retrieved from https://lovdata.no/dokument/SF/forskrift/2006-07-06-883

O'Neill, D. J., & Cobb, J. S. (1979). Some factors influencing the outcome of shelter competition in lobsters (*Homarus americanus*). *Marine Behaviour and Physiology, 6*(1), 33-45.

Oug, E., Brattegard, T., Walseng, B., & Djursvoll, P. (2015). Krepsdyr (Crustacea). Norsk rødliste for arter 2015. Artsdatabanken. Retrieved from http://www.artsdatabanken.no/Rodliste/Artsgruppene/Krepsdyr

Pauly, D., Christensen, V., Guenette, S., Pitcher, T. J., Sumaila, U. R., Walters, C. J., . . . Zeller, D. (2002). Towards sustainability in world fisheries. *Nature, 418*(6898), 689-695.

Pettersen, A. R., Moland, E., Olsen, E. M., & Knutsen, J. A. (2009). Lobster reserves in coastal Skagerrak - An integrated analysis of the implementation process. In E. Moksness, E. Dahl, & J. G. Støttrup (Eds.), *Integrated Coastal Zone Management* (pp. 178-186). Oxford: Wiley.

Phillips, B. F., & Sastry, A. N. (1980). Larval ecology. In J. S. Cobb & B. F. Phillips (Eds.), *The biology and management of lobsters. Volume 2. ecology and management* (pp. 12 - 15). New York: Academic Press.

R Core Team. (2016). R: A language and environment for statistical computing. (Version R version 3.3.2 "Sincere Pumpkin Patch"). Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Roberts, C. M., Bohnsack, J. A., Gell, F., Hawkins, J. P., & Goodridge, R. (2001). Effects of marine reserves on adjacent fisheries. *Science, 294*(5548), 1920-1923.

Rowe, S. (2002). Population parameters of American lobster inside and outside no-take reserves in Bonavista Bay, Newfoundland. *Fisheries Research, 56*(2), 167-175.

Sheehy, M. R. J., Bannister, R. C. A., Wickins, J. F., & Shelton, P. M. J. (1999). New perspectives on the growth and longevity of the European lobster (*Homarus gammarus*). *Canadian Journal of Fisheries and Aquatic Sciences, 56*(10), 1904-1915.

Smith, I., Jensen, A., Collins, K., & Mattey, E. (2001). Movement of wild European lobsters *Homarus gammarus* in natural habitat. *Marine Ecology Progress Series, 222*, 177-186.

Stergiou, K. I., Moutopoulos, D. K., & Armenis, G. (2009). Perish legally and ecologically: The ineffectiveness of the minimum landing sizes in the Mediterranean Sea. *Fisheries Management and Ecology, 16*(5), 368-375.

Sundelöf, A., Bartolino, V., Ulmestrand, M., & Cardinale, M. (2013). Multi-annual fluctuations in reconstructed historical time-series of a European lobster (*Homarus gammarus*) population disappear at increased exploitation levels. *Plos One, 8*(4), e58160. doi:10.1371/journal.pone.0058160

Thorbjørnsen, S. H. (2015). *Movement dynamics and individual characteristics of European lobster (Homarus gammarus) tagged inside and outside Skagerrak lobster reserves.* (Master of Science Master thesis), University of Bergen.

Triantafyllidis, A., Apostolidis, A. P., Katsares, V., Kelly, E., Mercer, J., Hughes, M., . . . Triantaphyllidis, C. (2005). Mitochondrial DNA variation in the European lobster (*Homarus gammarus*) throughout the range. *Marine Biology, 146*(2), 223-235.

Tully, O., Roantree, V., & Robinson, M. (2001). Maturity, fecundity and reproductive potential of the European lobster (*Homarus gammarus*) in Ireland. *Journal of the Marine Biological Association of the United Kingdom, 81*(01), 61-68.

Venables, W. N., & Ripley, B. D. (2002). *Modern Applied Statistics with S* (4th ed.). New York: Springer.

Wiig, J. R., Moland, E., Haugen, T. O., & Olsen, E. M. (2013). Spatially structured interactions between lobsters and lobster fishers in a coastal habitat: fine-scale behaviour and survival estimated from acoustic telemetry. *Canadian Journal of Fisheries and Aquatic Sciences, 70*(10), 1468-1476.

Young, M. A. L., Foale, S., & Bellwood, D. R. (2014). Impacts of recreational fishing in Australia: historical declines, self-regulation and evidence of an early warning system. *Environmental Conservation, 41*(4), 350-356.

Appendix A: Model selection

Table A.1: The BIC-values for the different models tested to analyze CPUE for the entire dataset. The one in bold is the best model, and used to analyze further.

Model	BIC-value
CPUE ~ Status + Year + (1 | Region)	**16523.49**
CPUE ~ Status * Year + (1 | Region)	16570.22

Table A.2: The BIC-values for the different models tested to analyze mean body size (MBS) for the entire dataset. The one in bold is the best model, and used to analyze further.

Model	BIC-value
MBS ~ Status + Year + (1 | Region)	84545.84
MBS ~ Status * Year + (1 | Region)	84537.84
MBS ~ Status + Year + Sex + (1 | Region)	84491.78
MBS ~ Status * Year + Sex + (1 | Region)	**84483.10**
MBS ~ Status + Year * Sex + (1 | Region)	84520.49
MBS ~ Status * Year * Sex + (1 | Region)	84540.09
MBS ~ Status * Sex + Year + (1 | Region)	84497.99

Table A.3: The BIC-values for all the models tested to analyze proportion of males (PoM) for the entire dataset. The one in bold is the best model, and used to analyze further.

Model	BIC-value
PoM ~ Status + Year + (1 | Region)	12015.77
PoM ~ Status * Year + (1 | Region)	12080.44
PoM ~ Status + Year + Body size + (1 | Region)	**11969.69**
PoM ~ Status * Year + Body size +(1 | Region)	12033.71
PoM ~ Status + Year * Body size + (1 | Region)	12025.48
PoM ~ Status * Year * Body size + (1 | Region)	12163.66

Appendix B: Estimates

CPUE

Table B.1: The estimates for the generalized linear mixed model used to test catch per unit effort (CPUE) of lobster of the entire dataset with the three regions combined. CPUE was tested with status (MPA or control) and year (as a factor variable) as explanatory variables. Region was used as a random effect and a negative binomial distribution was used. Significant p-values (<0.05) are in bold.

	Estimates	Std. error	z-value	p-value
Intercept	-0.19	0.27	-0.73	0.46
Status MPA	0.39	0.02	16.74	**<0.001**
2008	0.14	0.06	2.44	**0.01**
2009	0.52	0.05	10.04	**<0.001**
2010	0.53	0.05	10.21	**<0.001**
2011	0.42	0.05	7.87	**<0.001**
2012	0.55	0.05	10.71	**<0.001**
2013	0.51	0.05	9.79	**<0.001**
2014	0.26	0.05	4.78	**<0.001**
2015	0.27	0.05	4.99	**<0.001**

Table B.2: The estimates for the generalized linear model used to test catch per unit effort (CPUE) of lobster in the Aust-Agder region. CPUE was tested with status (MPA or control) and year (as a factor variable) as explanatory variables. A Poisson distribution was used. Significant p-values (<0.05) are in bold.

	Estimates	Std. error	z-value	p-value
Intercept	-1.23	0.11	-11.13	**<0.001**
Status MPA	0.79	0.06	13.73	**<0.001**
2008	0.48	0.13	3.62	**<0.001**
2009	0.62	0.13	4.93	**<0.001**
2010	0.63	0.13	4.93	**<0.001**
2011	0.41	0.13	3.07	**0.002**
2012	0.53	0.13	4.05	**<0.001**
2013	0.67	0.13	5.27	**<0.001**
2014	0.65	0.13	5.10	**<0.001**
2015	0.61	0.13	4.78	**<0.001**

Table B.3: The estimates for the generalized linear model used to test catch per unit effort (CPUE) of lobster in the Vestfold region. CPUE was tested with status (MPA or control) and year (as a factor variable) as explanatory variables. A negative binomial distribution was used. Significant p-values (<0.05) are in bold.

	Estimates	Std. error	z-value	p-value
Intercept	-0.08	0.07	-1.14	0.25
Status MPA	0.65	0.04	16.30	**<0.001**
2008	-0.08	0.09	-0.90	0.37
2009	0.59	0.08	7.21	**<0.001**
2010	0.54	0.08	6.50	**<0.001**
2011	-0.04	0.09	-0.40	0.68
2012	0.50	0.08	6.02	**<0.001**
2013	0.41	0.08	4.89	**<0.001**
2014	0.21	0.09	2.36	**0.02**
2015	0.12	0.09	1.38	0.17

Table B.4: The estimates for the generalized linear model used to test catch per unit effort (CPUE) of lobster in the Østfold region. CPUE was tested against status (MPA or control) and year (as a factor variable) as explanatory variables. A Poisson distribution was used. Significant p-values (<0.05) are in bold.

	Estimates	Std. error	z-value	p-value
Intercept	0.043	0.06	6.87	**<0.001**
Status MPA	0.04	0.03	1.27	0.20
2008	0.15	0.08	1.94	0.05
2009	0.39	0.08	5.17	**<0.001**
2010	0.49	0.08	6.36	**<0.001**
2011	0.67	0.07	9.30	**<0.001**
2012	0.58	0.07	7.92	**<0.001**
2013	0.51	0.07	6.91	**<0.001**
2014	0.12	0.08	1.54	0.12
2015	0.24	0.08	2.06	**0.002**

Mean body size

Table B.5: The estimates for the linear mixed model used to test the mean body size of the lobster of the entire dataset with the three regions combined. Mean body size was tested with status (MPA or control), year as a factor variable, sex (male or female) and the interaction between status and year as explanatory variables. Region was used as a random effect. Significant p-values (<0.05) are in bold.

	Estimate	Std. error	t-value	p-value
Intercept	233.33	4.24	55.05	**<0.001**
Status MPA	12.52	2.62	4.78	**0.001**
2008	-2.41	2.75	-0.88	0.38
2009	8.86	2.52	3.51	**<0.001**
2010	12.55	2.60	4.83	**<0.001**
2011	12.46	2.56	4.86	**<0.001**
2012	15.40	2.52	6.10	**<0.001**
2013	9.87	2.58	3.83	**<0.001**
2014	11.87	2.69	4.42	**<0.001**
2015	19.72	2.78	7.10	**<0.001**
Male	5.11	0.69	7.35	**<0.001**
MPA: 2008	9.35	3.53	2.65	**0.008**
MPA: 2009	2.39	3.26	0.73	0.46
MPA: 2010	8.79	3.30	2.66	**0.008**
MPA: 2011	8.74	3.32	2.64	**0.008**
MPA: 2012	10.11	3.25	3.11	**0.002**
MPA: 2013	14.95	3.28	4.55	**<0.001**
MPA: 2014	15.47	3.44	4.49	**<0.001**
MPA: 2015	16.99	3.48	4.87	**<0.001**

Table B.6: The estimates for the linear model used to test the mean body size of the lobster of the Aust-Agder region. Mean body size was tested with status (MPA or control), year as a factor variable, sex (male or female) and the interaction between status and year as explanatory variables. Significant p-values (<0.05) are in bold.

	Estimate	**Std. error**	**t-value**	**p-value**
Intercept	231.24	2.10	109.93	**<0.001**
Status MPA	12.70	2.64	4.82	**<0.001**
2008	-1.93	2.77	-0.70	0.49
2009	8.54	2.54	3.36	**<0.001**
2010	12.80	2.62	4.89	**<0.001**
2011	12.18	2.58	4.73	**<0.001**
2012	14.99	2.54	5.90	**<0.001**
2013	9.73	2.60	3.75	**<0.001**
2014	12.02	2.71	4.44	**<0.001**
2015	19.85	2.80	7.10	**<0.001**
Male	4.95	0.70	7.07	**<0.001**
MPA: 2008	9.49	3.56	2.67	**0.008**
MPA: 2009	3.10	3.28	0.95	0.34
MPA: 2010	8.68	3.33	2.61	**0.009**
MPA: 2011	9.14	3.34	2.74	**0.006**
MPA: 2012	10.65	3.27	3.26	**0.001**
MPA: 2013	15.51	3.31	4.69	**<0.001**
MPA: 2014	16.36	3.47	4.71	**<0.001**
MPA: 2015	17.65	3.51	5.03	**<0.001**

Table B.7: The estimates for the linear model used to test the mean body size of the lobster of the Vestfold region. Mean body size was tested with status (MPA or control), year as a factor variable, sex (male or female) and the interaction between status and year as explanatory variables. Significant p-values (<0.05) are in bold.

	Estimates	**Std. error**	**t-value**	**p-value**
Intercept	220.48	3.40	64.88	**<0.001**
Status MPA	21.01	4.18	5.03	**<0.001**
2008	4.43	5.00	0.89	0.38
2009	13.98	4.11	3.40	**<0.001**
2010	25.55	4.30	5.94	**<0.001**
2011	29.63	4.97	5.96	**<0.001**
2012	21.91	4.24	5.17	**<0.001**
2013	15.57	4.36	3.57	**<0.001**
2014	20.63	4.47	4.62	**<0.001**
2015	37.03	4.84	7.65	**<0.001**
Male	5.53	1.18	4.69	**<0.001**
MPA: 2008	7.83	6.15	1.27	0.20
MPA: 2009	-5.52	5.19	-1.06	0.29
MPA: 2010	1.64	5.32	0.31	0.76
MPA: 2011	-3.94	6.09	-0.65	0.52
MPA: 2012	0.37	5.31	0.07	0.94
MPA: 2013	4.58	5.42	0.85	0.40
MPA: 2014	9.92	5.63	1.76	0.08
MPA: 2015	-0.59	5.90	-0.10	0.92

Table B.8: The estimates for the linear model used to test the mean body size of the lobster of the Østfold region. Mean body size was tested with status (MPA or control), year as a factor variable, sex (male or female) and the interaction between status and year as explanatory variables. Significant p-values (<0.05) are in bold.

	Estimates	**Std. error**	**t-value**	**p-value**
Intercept	233.67	3.13	74.54	**<0.001**
Status MPA	5.13	3.64	1.41	0.16
2008	-11.30	3.58	-3.16	**0.002**
2009	3.25	3.38	0.96	0.34
2010	2.48	3.50	0.71	0.48
2011	4.71	3.25	1.45	0.15
2012	11.09	3.32	3.34	**<0.001**
2013	5.15	3.39	1.52	0.13
2014	6.43	3.60	1.78	0.07
2015	7.93	3.63	2.19	**0.03**
Male	4.14	0.94	4.39	**<0.001**
MPA: 2008	12.18	4.79	2.54	**0.01**
MPA: 2009	7.52	4.58	1.64	0.10
MPA: 2010	11.98	4.62	2.59	**0.01**
MPA: 2011	16.50	4.36	3.78	**<0.001**
MPA: 2012	17.88	4.43	4.04	**<0.001**
MPA: 2013	22.65	4.49	5.05	**<0.001**
MPA: 2014	19.22	4.83	3.98	**<0.001**
MPA: 2015	25.20	4.75	5.31	**<0.001**

Sex-ratio

Table B.9: The estimates for the generalized linear mixed model used to test the sex-ratio of the lobster of the entire dataset. Proportion of males was tested with status (MPA or control), year as a factor variable and body size as explanatory variables. Region was used as a random effect. A binomial distribution was used. Significant p-values (<0.05) are in bold.

	Estimate	Std. Error	z-value	p-value
Intercept	-1.08	0.19	-5.80	**<0.001**
Status MPA	-0.09	0.05	-2.07	**0.04**
2008	-0.05	0.11	-0.45	0.7
2009	0.09	0.10	0.90	0.37
2010	0.11	0.10	1.115	0.26
2011	-0.14	0.10	-1.33	0.18
2012	-0.03	0.10	-0.28	0.78
2013	-0.13	0.10	-1.25	0.21
2014	-0.14	0.11	-1.29	0.20
2015	-0.22	0.11	-2.095	**0.04**
Body size	0.005	<0.001	7.2	**<0.001**

Table B.10: The estimates for the generalized linear model used to test the sex-ratio of the lobster of the Aust-Agder region. Proportion of males was tested with status (MPA or control), year as a factor variable and body size as explanatory variables. A binomial distribution was used. Significant p-values (<0.05) are in bold.

	Estimate	Std. error	z-value	p-value
Intercept	-1.30	0.42	-3.08	**0.002**
Status MPA	-0.12	0.12	-0.94	0.35
2008	0.43	0.27	1.60	0.11
2009	0.26	0.26	0.99	0.32
2010	-0.17	0.26	-0.67	0.51
2011	-0.09	0.27	-0.32	0.75
2012	0.38	0.27	1.43	0.15
2013	0.10	0.26	0.38	0.71
2014	0.13	0.26	0.51	0.61
2015	-0.07	0.27	-0.25	0.80
Body size	0.004	0.001	3.07	**0.002**

Table B.11: The estimates for the generalized linear model used to test the sex-ratio of the lobster of the Vestfold region. Proportion of males was tested with status (MPA or control), year as a factor variable and body size as explanatory variables. A binomial distribution was used. Significant p-values (<0.05) are in bold.

	Estimate	Std. error	z-value	p-value
intercept	-0.79	0.28	-2.87	**0.004**
Status MPA	-0.23	0.08	-2.82	**0.005**
2008	-0.08	0.18	-0.44	0.66
2009	-0.01	0.15	-0.06	0.96
2010	0.16	0.16	1.01	0.32
2011	-0.13	0.18	-0.73	0.47
2012	-0.3	0.16	-1.97	**0.048**
2013	-0.40	0.16	-2.53	**0.01**
2014	-0.38	0.17	-2.25	**0.02**
2015	-0.43	0.17	-2.48	**0.01**
Body size	0.01	0.001	4.69	**<0.001**

Table B.12: The estimates for the generalized linear model used to test the sex-ratio of the lobster of the Østfold region. Proportion of males was tested with status (MPA or control), year as a factor variable and body size as explanatory variables. A binomial distribution was used. Significant p-values (<0.05) are in bold.

	Estimate	Std. error	z-value	p-value
intercept	-1.15	0.28	-4.17	**<0.001**
Status MPA	-0.008	0.07	-0.12	0.90
2008	-0.16	0.16	-1.03	0.31
2009	0.14	0.15	0.92	0.36
2010	0.19	0.15	1.24	0.21
2011	-0.08	0.15	-0.54	0.59
2012	0.11	0.15	0.72	0.47
2013	0.05	0.15	0.35	0.72
2014	-0.004	0.16	-0.03	0.98
2015	0.07	0.16	-0.46	0.64
Body size	0.005	0.001	4.25	**<0.001**

Appendix C: Sex-ratio figures

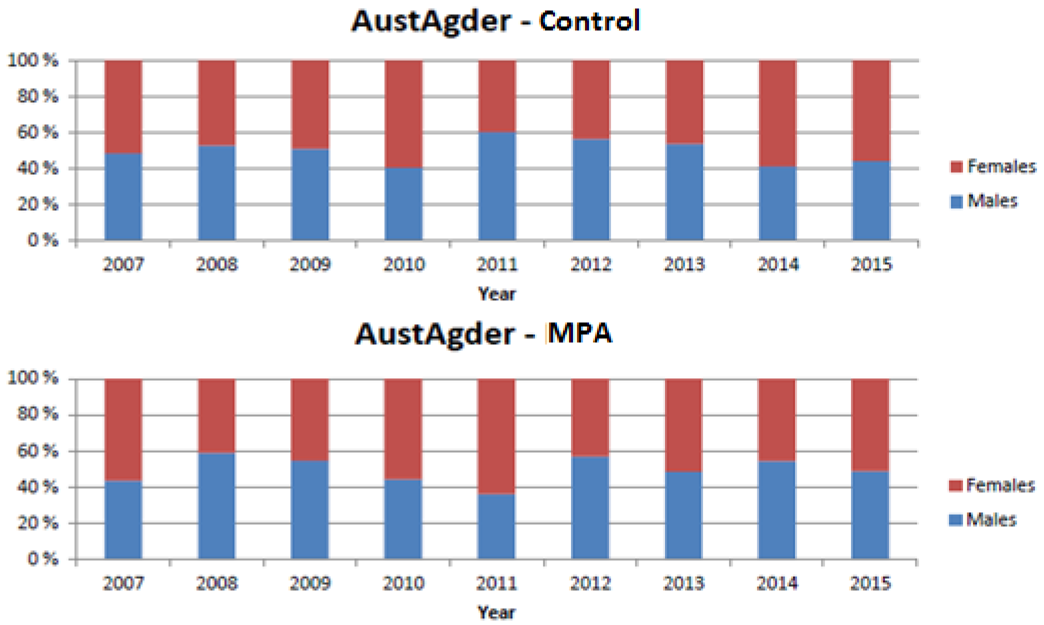
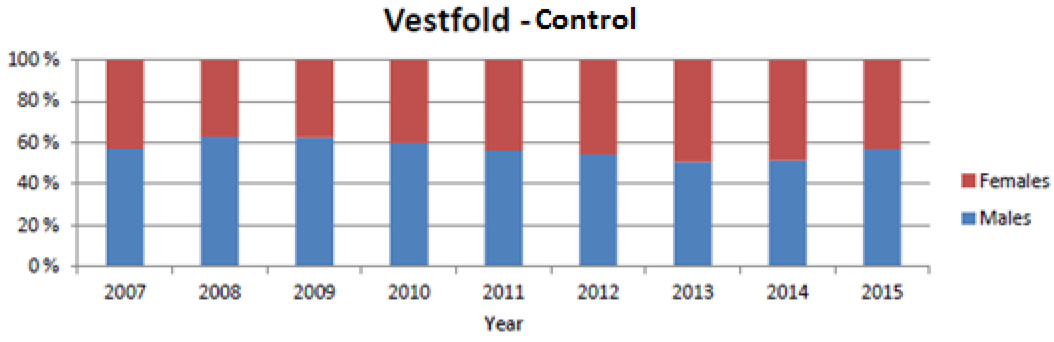


Figure C.1: *Temporal variation in the proportion of male (blue) and female (red) lobster in the marine protected area (MPA) and the control area (control) in the Aust-Agder region. In the MPA no fishing was allowed, in the control area fishing both commercially and recreational was allowed. Y-axis shows percentages of males and females. The x-axis shows years.*



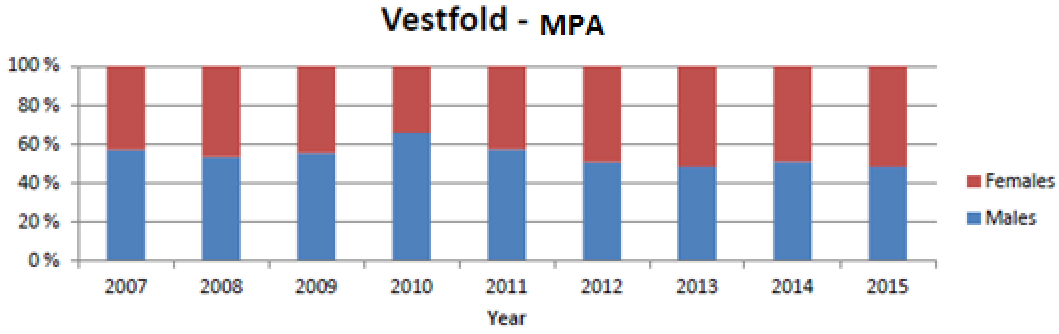


Figure C.2: *Temporal variation in the proportion of male (blue) and female (red) lobster in the marine protected area (MPA) and the control area (control) in the Vestfold region. In the MPA no fishing was allowed, in the control area fishing both commercially and recreational was allowed. Y-axis shows percentages of males and females. The x-axis shows years.*

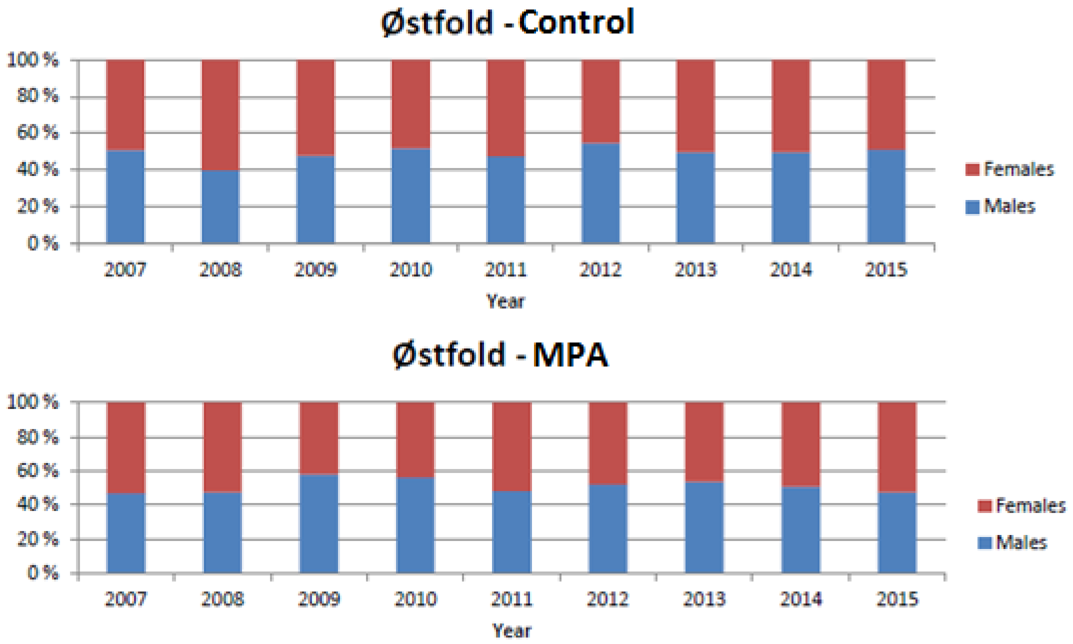


Figure C.3: *Temporal variation in the proportion of male (blue) and female (red) lobster in the marine protected area (MPA) and the control area (control) in the Østfold region. In the MPA no fishing was allowed, in the control area fishing both commercially and recreational was allowed. Y-axis shows percentages of males and females. The x-axis shows years.*