Norwegian University of Life Sciences

Master's thesis 2025 30 ECTS
Faculty of Environmental Sciences and Natural Resource Management

Can Small Marine Protected Areas Benefit the European Lobster (*Homarus gammarus*) in the Oslofjord?

Emilie Nyenget Løvberg
Teacher Education in Natural Sciences

Acknowledgements

This master thesis marks the end of my five-year study at NMBU and I'm proud to call myself "Lektor i realfag". There are several people I would like to thank that has made this possible.

A big thanks to my two supervisors, Stein and Thrond, for your expertise and enthusiasm on lobsters in the Oslofjord. Thank you, Stein, for answering all my questions, having an eye for details and your quick responses. Thank you, Thrond, for your great help through the statistics which I found frustrating at times. Couldn't have asked for a better lobster duo! Thank you to Marinreperatørene for letting me use your data, answering my questions and having good conversations. This thesis is a part of "SITRAP – tverrfaglig masterprosjekt Oslofjorden 3.0".

I want to thank "Lektordamene" for good laughs, great conversations and five years together at NMBU. These five years would not have been the same if it weren't for you!

Lastly in want to thank friends and family for your support through all my years in Ås.

Norges miljø- og biovitenskapelige universitet

Emilie Nyenget Løvberg

May 2025

Abstract

Marine protected areas (MPAs) have demonstrated their effectiveness as a conservation tool. The red listed European lobster, *Homarus gammarus*, has been under great pressure in the Oslofjord, due to extensive harvest. Therefore, two MPAs designated for lobsters were established to help restore the population. However, these MPAs are relatively small, and their ecological effects are not well documented due to their recent establishment (i.e. 2017 and 2021). Using a "before-after control-impact" study approach (BACI), lobsters from the two MPAs in the Oslofjord, Drøbak and the Inner Fjord, were surveyed. Catch per unit effort (CPUE) was calculated and total length and sex were recorded. The study revealed that the MPAs had a positive effect on both CPUE and total length. CPUE approximately doubled in Drøbak two years post-protection, and lobsters had an average increase of 2 cm in both areas. Before protection the Inner Fjord had a higher proportion of females while Drøbak had a higher proportion of males. After protection, the Inner Fjord had an increase of males, while the proportion of males remained stable in Drøbak. The results indicate that small MPAs have a positive effect on CPUE and total length but also highlight differences in sex ratio between MPAs.

Sammendrag

Marine verneområder (MPA-er) har vist seg å være et effektivt verktøy for bevaring. Den rødlistede Europeiske hummeren, *Homarus gammarus*, har vært utsatt for stort press i Oslofjorden på grunn av omfattende fangst. På bakgrunn av dette ble to verneområder for hummer opprettet for å bidra til å gjenoppbygge bestanden. Disse verneområdene er imidlertid relativt små, og deres økologiske effekter er ikke godt dokumentert på grunn av deres nylige etablering (hhv. 2017 og 2021). Ved bruk av en «before-after control-impact» studie (BACI), ble hummer fra disse to verneområdene i Oslofjorden, Drøbak og Indre Fjord, undersøkt. Fangst per innsatsenhet (CPUE) ble beregnet, og totallengde samt kjønn registrert. Studien viser at verneområdene hadde en positiv effekt på både CPUE og totallengde. CPUE omtrent doblet seg i Drøbak to år etter innføringen av vern, og hummerne hadde en gjennomsnittlig økning på 2 cm i begge områder. Før vernet hadde Indre Fjord en høyere andel hunnhummer, mens Drøbak hadde en høyere andel hannhummer. Etter vernet økte andelen hannhummer i Indre Fjord, mens kjønnsfordelingen forble stabil i Drøbak. Resultatene indikerer at selv små verneområder kan gi positiv effekt på totallengde og CPUE, samtidig som de avdekket forskjeller i kjønnssammensetningen mellom verneområdene.

Table of content

1 Introduction

The ecological condition of the Oslofjord is experiencing significant pressure. Currently, 1.6 million people live across the 26 municipalities adjacent to the fjord. Historically the Oslofjord was considered the most species-rich fjord in Norway (Miljødirektoratet, 2023, 2024). As of 2024, the Oslofjord was home to 83 marine-associated species classified as threatened on the Norwegian red list (Miljødirektoratet, 2024). Due to anthropogenic stress, the Oslofjord also contains the threatened habitat eelgrass, which is an important habitat for juvenile cod and crustaceans (Institute of Marine Research, 2024; Miljødirektoratet, 2024). The Norwegian Water Regulation classify the ecological state of the Inner Oslofjord as moderate (Miljødirektoratet, 2024). Major threats includes overfishing and bottom trawling (Miljødirektoratet, 2024). Several marine areas have been established for the protection of cod (*Gadus morhua*) and European lobster (*Homarus gammarus*).

Marine protected areas (MPAs) were implemented in the Norwegian Naturmangfoldloven in 2009 § 39 and have been demonstrated to be an effective conservation tool (Fernández-Chacón et al., 2021). The laws purpose is to protect marine areas that are representative, vulnerable, distinctive or threatened underwater habitats along the coast and in territorial waters (Miljødirektoratet, 2025). When established, the purpose and restrictions of the MPAs need to be specified and whether it applies to the bottom, the water column, the surface or a combination of these three categories. The MPAs described in this study are designated lobster protected areas. The lobster is a heavily exploited species and may therefore respond quickly to protection (Lester et al., 2009). However, the response in areas with smaller populations could be relatively slower (Sánchez Lizaso et al., 2002). Due to the reduction in population size, the European lobster (henceforth termed lobster) was considered vulnerable on the Norwegian red list in 2021 after being categorized as least concern in 2015 (Tandberg et al., 2021). The Norwegian government has developed an action plan for the Oslofjord, which include a requirement that each municipality establish one marine protected area designated for lobster conservation before 2026 (Klima- og miljødepartementet, 2021).

MPAs have been shown to have a positive impact on total length and an overall increase in catch per unit effort (CPUE) both inside and outside the MPAs (Fernández-Chacón et al., 2021; Knutsen et al., 2022; Moland et al., 2013a; Moland et al., 2013b; Thorbjørnsen et al., 2018). Since lobster size and reproductive potential are positively related (Campbell & Robinson, 1983), MPAs may contribute to a further increase in population size. Marine protected areas vary in size and organisms respond differently to protection. Larger MPAs are more efficient in protecting whole ecosystems compared to smaller MPAs ('Aulani Wilhelm et al., 2014). However, previous studies have shown that even small MPAs may have a higher CPUE of lobsters compared to control areas and therefore have a positive effect on protection (Moland et al., 2013a; Sørdalen et al., 2022).

Lobsters have a relatively small home range, commonly moving less than 1 km (Agnalt et al., 2007; Rowe, 2001). Despite their limited mobility, small MPAs may not achieve the intended protection of lobsters as lobsters can move across the boundaries (Kellner et al., 2007). A challenge for small MPAs is their vulnerability to human-related stressors which reduces the effective size of the protected area, also known as the edge effect (Ohayon et al., 2021). Larger MPAs, on the other hand, are more likely to cover the natural range of lobsters, reducing the risk of lobsters moving out of the MPAs and into areas where they can get harvested. As the size of an MPA increases, the relative influence of edge effect declines. The influence of surrounding fished areas can extend approximately as much as 1 km into the MPA (Ohayon et al., 2021). This effect is reflected in the sharp decline in CPUE observed near MPA boundaries (Goñi et al., 2006), indicating a high fishing pressure that contributes to the edge effect.

Marine protected areas could also benefit adjacent areas due to spillover effects. The abundance of lobster is highest inside the core of the MPAs which can lead to intraspecific competition for shelters and large lobsters migrate to avoid competition (Steneck, 2006; Thorbjørnsen et al., 2018). The CPUE typically decreases gradually from the center of the MPA and up to 4 km from the reserve boundary, except from a sharp decline at the border (Goñi et al., 2006; Ohayon et al., 2021). This suggests that the protected areas may also benefit areas that are adjacent to the MPAs.

Intensive harvest pressure could lead to an alteration in sex ratio. Sex-biased fisheries may occur when males are larger and fisheries are size-selective, or when regulations protect females with external roe, as for the European lobster (Iacchei et al., 2005; Ogburn, 2019; Skud, 1969). In the last decade, there has been a substantial decrease of male lobsters in Norway, especially males exceeding 30 cm (Kleiven et al., 2017) Since the harvest regulations protect females with external roe, this has resulted in a female-dominated sex ratio for lobsters over 30 cm (Kleiven et al., 2017). Moreover, males with a large crusher claw relative to body size are more likely to get caught in traps as they take more risk (Moland et al., 2019), which could lead to a further alteration in sex ratio.

This study consisted of two study areas, Drøbak and the Inner Fjord. The two MPAs are relatively small, 0.85 km^2 and 2.05 km^2, respectively. The overall aim for this study was to compare the effects of these two recently established (i.e. the Inner Fjord in 2017 and Drøbak in 2021) lobster marine protected areas.

Specifically, I:

1) Compared catch per unit effort between the two MPAs and control areas, starting prior to the establishment of the protected areas. I predicted that the CPUE would increase more in Inner Fjord than Drøbak, given the MPA in the Inner Fjord is larger.
2) Examined the size distribution of lobsters in both MPAs and control areas, predicting that the effect of MPA on lobster size would be stronger in the larger and more effective MPA in the Inner Fjord compared to the smaller MPA in Drøbak.
3) Compared the sex ratio between the two MPAs and control areas and whether it had changed since their establishment. I predicted that prior to protection there would be more females, as they are not allowed to harvest every second year when carrying external roe. Over time there would be a larger increase of the proportion of males in the Inner Fjord compared to Drøbak due to its larger protected area.

Figure 1: Lobster caught in Drøbak 31.08.24.

2 Materials and methods

2.1 Area description

The study was conducted in two areas. The study area in Drøbak had one marine protected area, Jetéen, and two control areas, Askholmene and Biologen (Figure 2). The study area in the Inner Fjord comprised one marine protected area, Nesodden, and one control area, Snarøya (Figure 3).

Jetéen is a man-made wall below the ocean surface. It stretches from Oscarsborg fortress to Sætre in Asker municipality, and it is approximately 1.5 km long. It was built in 1874 - 1879 to prevent military ships entering the Oslofjord from the west (Hammer & Berg, 2024). The construction, made up of boulders, is 4 m wide at the top and stretches down to depths of 20 m. Today there are two openings in the wall for smaller boats to pass. The area along Jetéen in Drøbak was designated a MPA in 2021 and is a no-take zone for lobsters. The MPA is 0.85 km^2 (Fiskedirektoratet, n.d.). The control area, Biologen, is a narrow area stretching from Badeparken to south of Lehmannsbrygga in Drøbak. The second control area lies around Askholmene, between Håøya and the mainland (Figure 2).

The second area, Nesoddtangen, was established as a MPA in 2017. This was the first marine protected area in the Inner Oslofjord. The MPA is 2.05 km^2 (Fiskedirektoratet, n.d.). The control area lies between Nesoddtangen and Snarøya and stretches along the southeast part of Snarøya. The control area is approximately 0.5 km^2 (Figure 3).

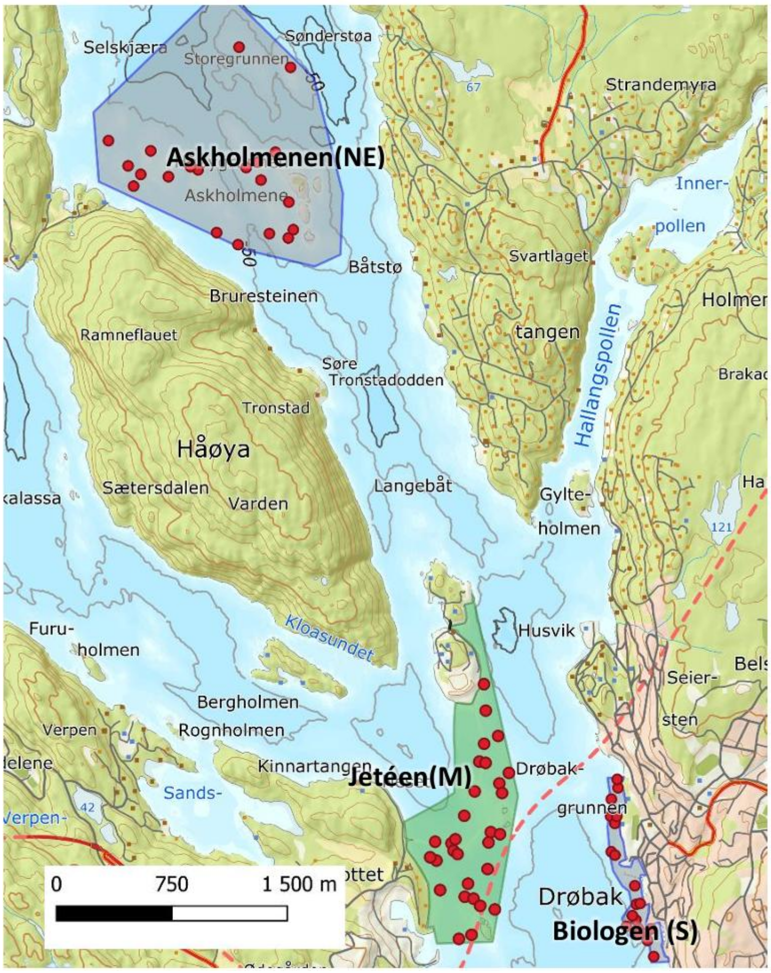

Figure 2: Area description for Drøbak with traps (red circles). Control areas are: Askholmene (NE) and Biologen (S). While Jetéen (M) is the MPA. Map source: (Haugen et al., 2023).

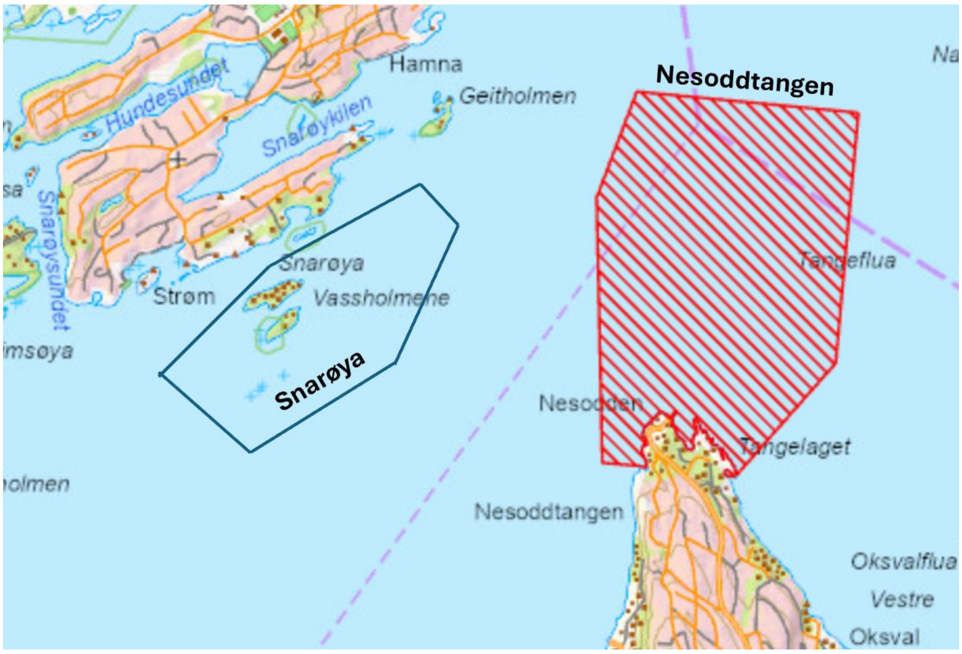

Figure 3: Area description of the Inner Oslofjord. Snarøya is the control area, Nesoddtangen is the MPA marked in red. Map from: (Fiskedirektoratet, n.d.).

2.2 Study species and harvest regulations

The European lobster is found along the coast from the Mediterranean Sea to Lofoten in Norway. This species typically inhabits shallow waters at depths of 5 - 40 m (Tandberg et al., 2021). Their preferred habitat consists of rocks and boulders where they can hide (Institute of Marine Research, 2022). Lobsters can get up to approximately 50 cm in total length and weigh 8 kg (Institute of Marine Research, 2022). Their estimated lifespan is 42 – 72 years and females become sexually mature between 9 – 11 years (Sheehy et al., 1999).

Lobsters only come together for mating purposes. When copulating the male gives the female packages of sperm (Institute of Marine Research, 2022). The female carries her unfertilized eggs for a year. Upon spawning the eggs are released and undergo fertilization when passing the sperm packages in the oviducts (Institute of Marine Research, 2022). The fertilized eggs attach to the setae of the swimmerettes, beneath the abdomen, for another 9 - 11 months (Agnalt et al., 2007). When hatched the planktonic larvae has a pelagic phase. The larvae will moult four times, before they seek the bottom in the fifth stage (Incze & Wahle, 1991). The early benthic juvenile stage, 4 – 20 mm carapace length, remains poorly understood, as individuals within this size range has never been observed in the wild. The scarcity of such findings represents a significant knowledge gap of the European lobster (Institute of Marine Research, 2022). Lack of knowledge also limits our understanding of the specific habitats utilized by lobsters during this critical development stage.

Regulations on lobster protected areas went into effect in 2006 (Forskrift om fredningsområder for hummer, 2006). These areas are no-take zones for lobster. However, it is allowed to fish in these protected areas with handlines, fishing rods, jigging, trolling lines and purse seines from Sweden to Vestland (Forskrift om fredningsområder for hummer, 2006§1). Outside the protected areas, Norwegian law states that it is not allowed to harvest lobster smaller than 25 cm and larger than 32 cm (between Sweden and Vestland County, there is no maximum length restriction from Rogaland and further north). In addition it is illegal to harvest lobster with external roe (Forskrift om høsting av hummer, 2021§8,§9,§10). The annual lobster harvest between Sweden and Vestland starts the 1st of October and ends 30th of November, while the harvest north of Vestland ends 31st of December. From 1st of January to 1st of October it is illegal to store lobster in the sea (Fiskedirektoratet, n.d.).

2.3 Methods

The data collection is part of a bigger research project and methods used for data collection in Drøbak were the same as described in Haugen et al. (2023).

A BACI (before-after, control-impact) design as described in Haugen et al. (2023), was used in this study. A Before-after-control-impact (BACI) analysis offers a robust and simple tool to analyze the effects of MPAs (Kerr et al., 2019; Sciberras et al., 2013). However, a limitation with the BACI design is that the “before” and “after” are binary which can mask important patterns over time. Another limitation with BACI for evaluating MPAs is that there are no true comparable controls, because it is a natural experiment (Kerr et al., 2019). Neither the control areas nor protected areas can exclude influence from pollution, which furthermore could affect how the results are interpreted.

The first lobster traps (“skotteteiner” in Norwegian) in Drøbak were set in September 2020 to get before and after data for the conservation area. Jetéen was made a MPA in 2021. Since 2021 there has been data collected in August-September and December each year, before and after the annual lobstering season (Figure 4). Traps were distributed randomly using QGIS’s vector tool in two depth layers, strata: 3-15 m and 15-30 m in each area. Each of the three areas in Drøbak had 20 traps in the same location every year. From September 2022 additional 10 traps were added to Jetéen (Figure 4). The randomization- and stratification routines used to position the traps are the same as used previously by The Institute of Marine Research (Espeland et al., 2014). Each data collection period was conducted over five days in Drøbak. Every 24 hours the traps were emptied and baited with fresh mackerel. Lobster total length and sex were recorded. All lobsters were measured on their backs from the rostrum to the tip of the central tail fan. The abundance of lobster was measured as CPUE. CPUE was calculated as the amount of lobster per trap per 24 hours.

In the Inner Fjord the data collection was conducted over a period of nine days each September, starting in 2017. The lobster traps were baited with fresh mackerel every 24 hours. Both the MPA and control area were equipped with 15 traps each (Figure 4). The parameters recorded were total length (cm), sex and CPUE was calculated. When the traps were distributed the first year, they were distributed in areas with perceived lobster habitat. The traps were set in the same location each year. Depth measurements were conducted in 2017, with all traps deployed at depths between 6 and 20 meters.

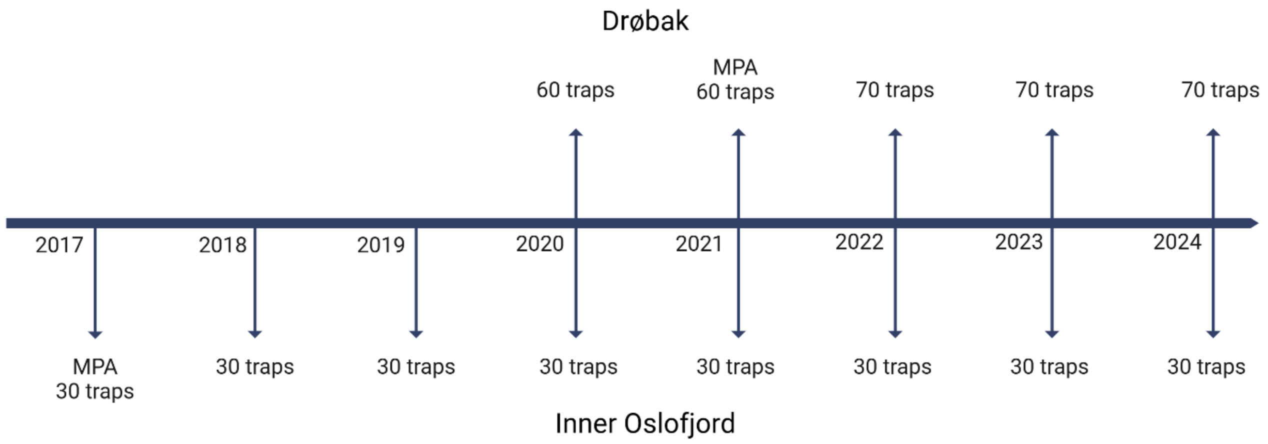

Figure 4: Timeline for Drøbak and Inner Oslofjord, when MPAs where established and the number of traps in each area.

Sampling was conducted during August-September, before the legal trapping season opening October 1st. This resulted in two years of before-data in Drøbak and one year in the Inner Fjord (Figure 4). Year zero in the results refers to the year the MPAs were established (i.e. 2017 and 2021, Figure 4).

2.4 Statistical analysis

All analysis were performed using R Statistical Software 4.4.1 (2024-06.14 ucrt) (R Development Core Team, 2024).

The mean catch per unit effort (CPUE) was used as an indicator for abundance of lobster in this study. The response variable, CPUE, was log-transformed using the log1p function. Multiple linear models were fitted, including study year, sex, area (Drøbak vs. Inner Fjord) and control/impact. Control/impact, area and sex were used as binomial predicter variables, while study year was a categorical predicter variable. Predictions were back-transformed from log-space for interpretability. To evaluate change in size distribution, a set of linear models were fitted using total length (cm) as a continuous response variable. To assess the effect of MPAs on sex ratio, a generalized linear model with a binomial error distribution was fitted. The response variable was sex. The predicter variables were control/impact, before/after, study year and area. Lobsters that were reported as NA were excluded from the analysis in RStudio, this concerned 15 lobsters caught in the Inner Fjord.

Model selection was based on Akaike's Information Criterion (AIC) following procedures described in Zuur et al. (2009). AIC was used for model selection in all three analyses: CPUE, size distribution and sex ratio.

ChatGPT-4 Turbo was used as a tool to help with coding in RStudio and interpreting the data. In addition, it was used for language assistance; providing synonyms, linking words and structural help for paragraphs (OpenAI, 2025).

3 Results

3.1 Catch per unit effort

The number of lobsters caught were generally higher in Drøbak than in the Inner Fjord. The last three years in Drøbak show an increased CPUE, starting one year post protection (Figure 5). The immediate effect of protection was less in the Inner Fjord (Figure 5 & 6).

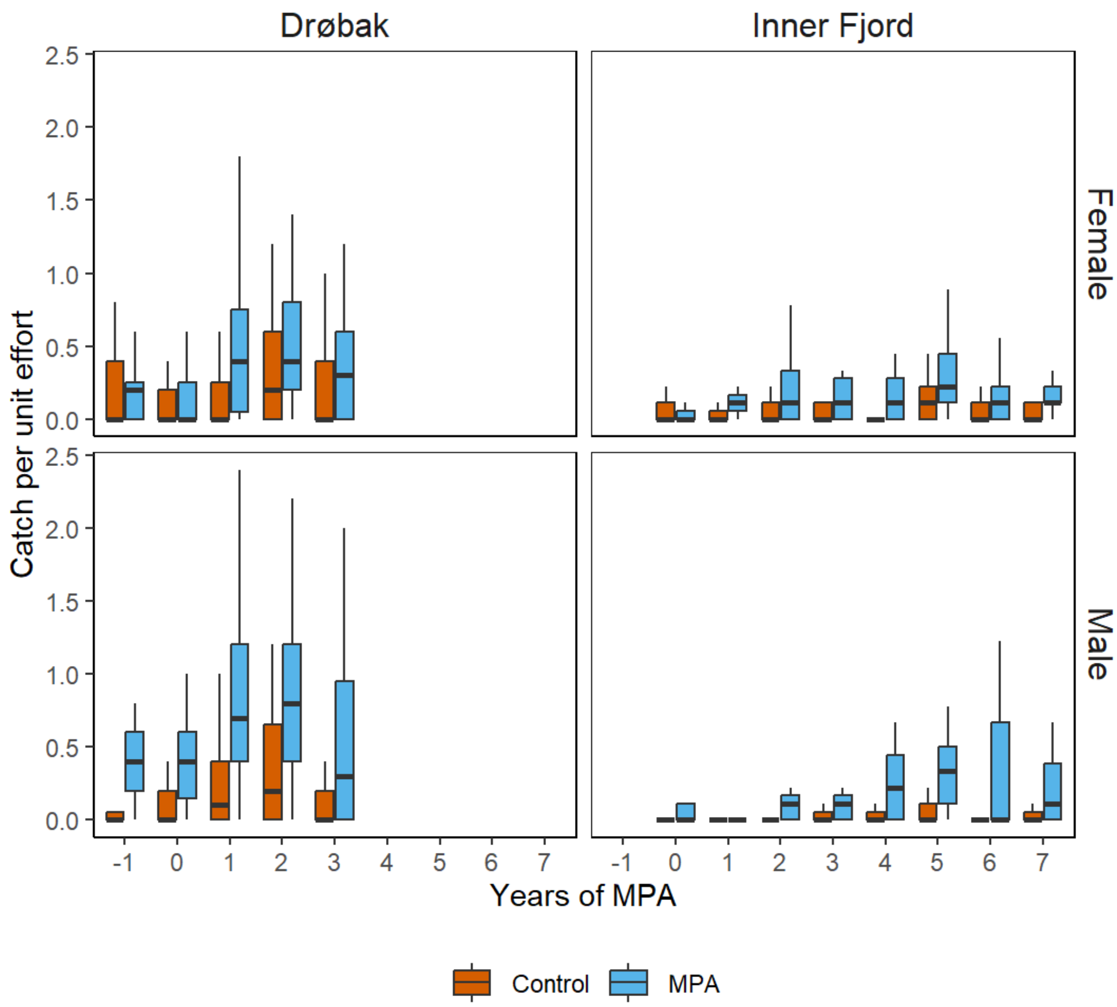

Figure 5: Box plot showing catch per unit effort (lobster/trap/24 hour) for males and females in marine protected areas (MPAs) and control areas in Drøbak and the Inner Fjord for all study years (i.e. 2020 – 2024 in Drøbak and 2017 – 2024 in the Inner Fjord). Zero is the year MPAs were established, all data are from August-September, prior to the legal trapping season (October-November) in control areas.

The best candidate model (Table 1) for CPUE (74% support) included:

CPUE ~ SY + Sex + Area + CoIm + SY:Sex + SY:Area + Sex:Area + SY:CoIm + Sex:CoIm + Area:CoIm + Sex:Area:CoIm

Table 1: Candidate models with AIC model selection with catch per unit effort as the response variable. CoIm: Control/Impact, Area: Inner Fjord and Drøbak, SY: Study year.

Model	K	AICc	ΔAICc	AICcWt	LL
SY+Sex+Area+CoIm+SY:Sex+SY:Area+Sex:Area+SY:CoIm+Sex:CoIm+Area:CoIm+Sex:Area:CoIm	27	-35.62	0.00	0.74	45.62
SY+Sex+Area+CoIm+SY:Sex+SY:Area+Sex:Area+SY:CoIm+Sex:CoIm+Area:CoIm+SY:Area:CoIm+Sex:Area:CoIm	30	-32.80	2.82	0.18	47.40
SY+Sex*Area*CoIm	14	-30.75	4.87	0.06	29.60
SY+Sex+Area+CoIm+SY:Sex+SY:Area+Sex:Area+SY:CoIm+Sex:CoIm+Area:CoIm+SY:Sex:Area+SY:Area:CoIm+Sex:Area:CoIm	33	-27.94	7.68	0.02	48.18
SY+Sex+Area+CoIm+SY:Sex+SY:Area+Sex:Area+SY:CoIm+Sex:CoIm+Area:CoIm+SY:Sex:Area+SY:Sex:CoIm+SY:Area:CoIm+Sex:Area:CoIm	38	-19.18	16.43	0.00	49.20
SY*Area+CoIm*Sex	14	-17.73	17.89	0.00	23.09
SY*CoIm*Area+Sex	22	-15.64	19.97	0.00	30.36
SY*Sex*Area*CoIm	41	-13.37	22.24	0.00	49.56
SY+Sex+Area*CoIm	11	-10.90	24.71	0.00	16.59
SY*Sex+Area*CoIm	16	-4.39	31.23	0.00	18.48
SY+Sex+Area+CoIm	10	-2.27	33.34	0.00	11.25
SY*Sex*Area+CoIm	22	-2.08	33.53	0.00	23.58
SY*CoIm+Sex+Area	15	0.00	35.61	0.00	15.26
SY*Sex+Area+CoIm	15	4.26	39.87	0.00	13.12

CPUE was higher in Drøbak compared with the Inner Fjord (Table 2, Figure 6, Appendix A.1). CPUE increased in the MPA in Drøbak compared with before the MPA establishment (Figure 6). The second year in Drøbak had the highest CPUE in the MPA compared with control areas (Figure 6). Males had a higher CPUE in the MPA in Drøbak before the protection and responded more positively to protection than females. In the Inner Fjord the difference in CPUE between the MPA and control area was smaller overall than in Drøbak (Figure 6). However, males showed an increase in the MPA the final year (Figure 6). The multiple R-squared for the model was 0.26, indicating that 26% of the variation in the response was accounted for by the predictors.

Table 2: Parameter estimates for the best fitted model for CPUE (see Table 1): SY + Sex + Area + CoIm + SY:Sex + SY:Area + Sex:Area + SY:CoIm + Sex:CoIm + Area:CoIm + Sex:Area:CoIm. SY: Study years, CoIm: Control/Impact, IF: Inner Fjord. Anova test with backwards elimination. The model R-square = 0.26.

Parameter estimates			**Likelihood ratio test statistics**				
Term	Estimate	SE	Effect	Df	Sum Sq	F value	P
Intercept	0.15	0.03	SY	5	2.58	9.42	< 0.001
SY0	-0.03	0.05	Sex	1	0.26	4.70	< 0.05
SY1	0.03	0.05	Area	1	5.71	104.28	< 0.001
SY2	0.09	0.05	CoIm	1	5.55	101.42	< 0.001
SY3	0.03	0.05	SY:Sex	5	0.21	0.78	0.56
SY4	-0.09	0.05	SY:Area	3	0.65	3.98	< 0.01
Sex[M]	-0.06	0.04	Sex:Area	1	0.44	8.02	< 0.01
Area[IF]	-0.06	0.05	SY:CoIm	5	0.57	2.01	< 0.1
CoIm[Impact]	0.04	0.05	Sex:CoIm	1	0.76	13.82	< 0.001
SY0:Sex[M]	0.07	0.06	Area:CoIm	1	0.73	13.41	< 0.001
SY1:Sex[M]	0.06	0.06	Sex:Area:CoIm	1	0.43	7.88	< 0.01
SY2:Sex[M]	0.08	0.06					
SY3:Sex[M]	0.00	0.06					
SY4:Sex[M]	0.16	0.08					
SY0:Area[IF]	0.01	0.05					
SY1:Area[IF]	-0.09	0.05					
SY2:Area[IF]	-0.15	0.05					
SY3:Area[IF]	NA	NA					
SY4:Area[IF]	NA	NA					
Sex[M]:Area[IF]	-0.03	0.05					
SY0:CoIm[Impact]	-0.01	0.06					
SY1:CoIm[Impact]	0.12	0.06					
SY2:CoIm[Impact]	0.11	0.06					
SY3:CoIm[Impact]	0.06	0.06					
SY4:CoIm[Impact]	0.16	0.08					
Sex[M]:CoIm[Impact]	0.17	0.04					
Area[IF]:CoIm[Impact]	-0.04	0.05					
Sex[M]:Area[IF]:CoIm[Impact]	-0.18	0.07					

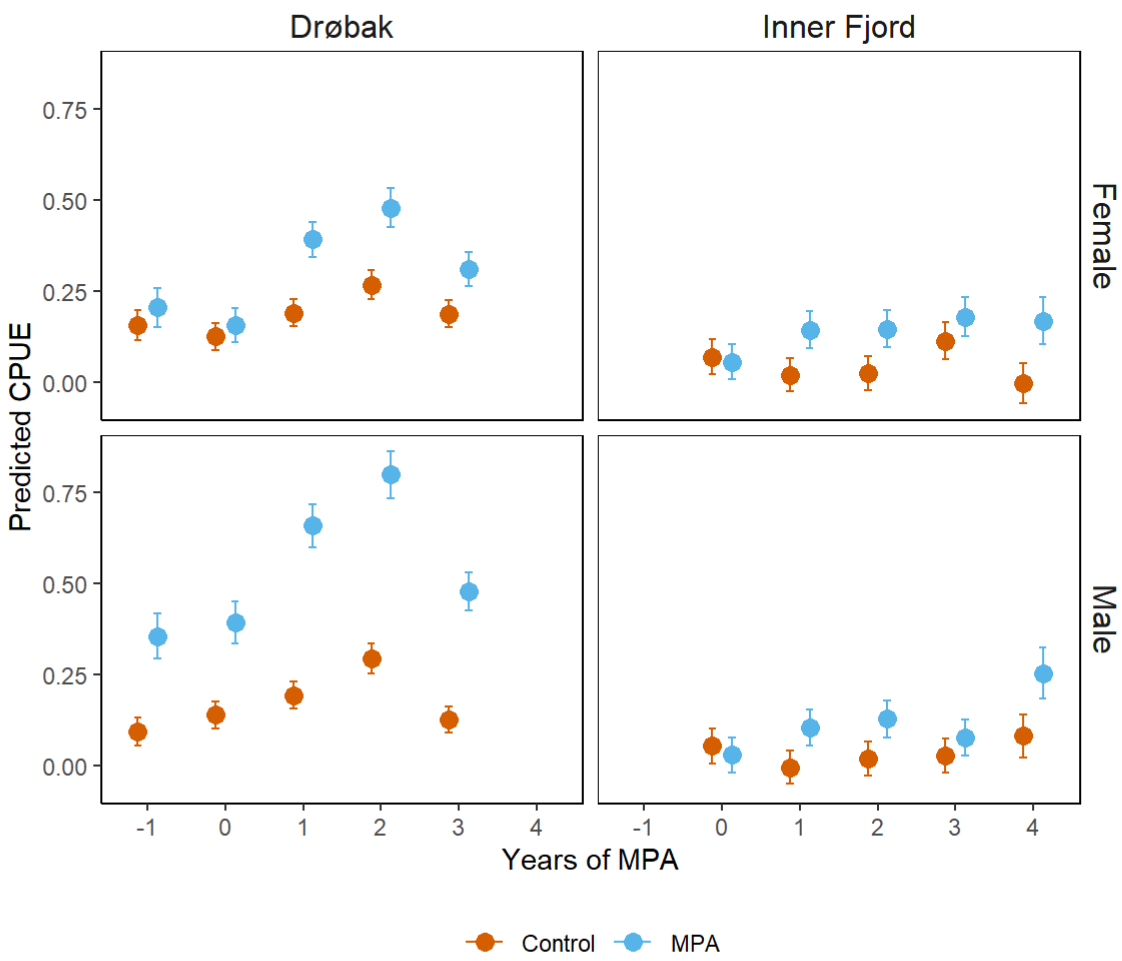

Figure 6: Point estimates with standard error (SE) of CPUE (lobster/trap/24 hour) for males and females over five years in Drøbak and in the Inner Fjord. Year zero is the year MPAs were established.

3.2 Size distribution

The size distribution in the control areas were relatively stable for both sexes in Drøbak and the Inner Fjord (Figure 7). In Drøbak both males and females were smaller in the control area compared to MPA the last year (Figure 8).

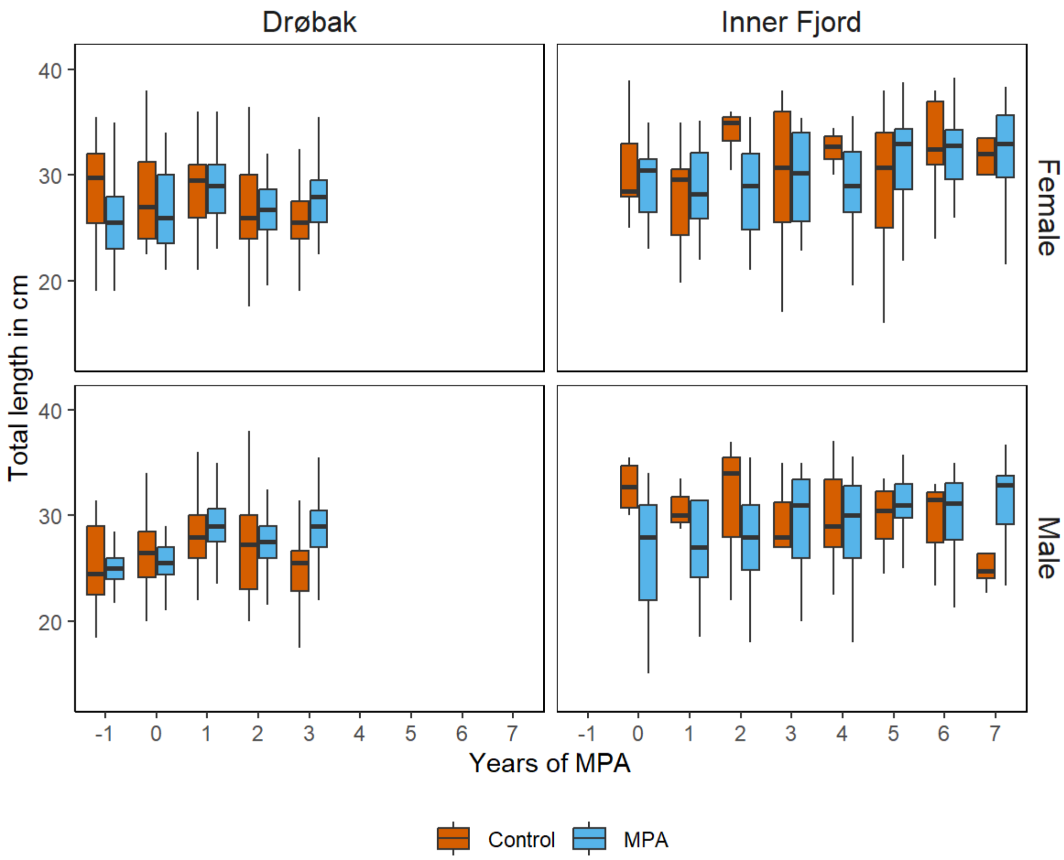

Figure 7: Box plot showing total length in Drøbak and the Inner Fjord for all study years (i.e. 2020 - 2024 in Drøbak and 2017 – 2024 for the Inner Fjord) separated by area and sex. Year zero is the year MPA was established, all data are from August-September, prior to the legal trapping season (October-November) in control areas.

The best candidate model (Table 3) for lobster length (100% support) included:

Total length ~ Study Year * Control Impact * Area + Sex.

Table 3: Candidate models with AIC model selection with total length in cm as the response variable. SY: Study year, CoIm: Control/Impact, Area: Inner Fjord and Drøbak.

Model	K	AICc	Δ AICc	AICcWt	Cum.Wt	LL
SY*CoIm*Area+Sex	22	8408.82	0.00	1.00	1.00	-4182.07
SY*CoIm*Area*Sex	41	8420.23	11.41	0.00	1.00	-4167.94
SY*CoIm+Area+Sex	15	8425.31	16.50	0.00	1.00	-4197.49
SY*CoIm+Area*Sex	16	8426.74	17.92	0.00	1.00	-4197.19
SY*Area	11	8444.20	35.38	0.00	1.00	-4211.01

SY+CoIm*Area+Sex	11	8447.98	39.17	0.00	1.00	-4212.90
SY*CoIm+Sex	14	8448.00	39.18	0.00	1.00	-4209.86
SY*CoIm	13	8449.49	40.67	0.00	1.00	-4211.62
SY+CoIm*Area+Sex	14	8450.34	41.53	0.00	1.00	-4211.03
SY*CoIm*Sex	25	8450.93	42.11	0.00	1.00	-4200.02
SY+Area	8	8452.46	43.64	0.00	1.00	-4218.18
SY+CoIm+Area+Sex	10	8454.93	46.11	0.00	1.00	-4217.39
SY+CoIm+Sex	9	8476.59	46.11	0.00	1.00	-4229.24
SY+Coim	8	8478.17	69.35	0.00	1.00	-4231.04

Lobsters in Drøbak were generally smaller, -3.26 cm (± 1.07 SE), than the lobsters in the Inner Fjord (Table 4). The difference in size between MPA and control areas were smaller in Drøbak compared to the Inner Fjord (Table 4, Figure 8).

Table 4: Parameter estimates for best model fitted: ~ Study year * Control/Impact * Area + Sex. SY: Study year, CoIm: Control/Impact. Anova test with backwards elimination. The response variable was total length in cm. The model R-square = 0.11.

Parameter estimates			**Likelihood ratio test statistics**				
Term	Estimate	SE	Effect	Df	Sum Sq	F value	P
Intercept	30.49	1.19	SY	5	1167.8	15.21	< 0.001
SY0	0.97	1.76	CoIm	1	16.1	1.05	0.31
SY1	-2.01	1.63	Area	1	417.5	27.19	< 0.001
SY2	2.51	1.71	Sex	1	19.0	1.23	0.27
SY3	-1.69	0.62	SY:CoIm	5	622.2	8.11	< 0.001
SY4	0.25	1.68	SY:Area	3	242.2	5.26	< 0.01
CoIm[Impact]	-3.63	1.44	CoIm:Area	1	155.6	10.14	< 0.01
Area[Drøbak]	-3.26	1.07					
Sex[F]	0.28	0.21					
SY0:CoIm[Impact]	0.20	2.11					
SY1:CoIm[Impact]	3.29	1.98					
SY2:CoIm[Impact]	-1.25	2.01					
SY3:CoIm[Impact]	4.19	0.84					
SY4:CoIm[Impact]	2.23	1.93					
SY0:Area[Drøbak]	-1.05	1.75					
SY1:Area[Drøbak]	3.54	1.61					
SY2:Area[Drøbak]	-2.88	1.67					
SY3:Area[Drøbak]	NA	NA					
SY4:Area[Drøbak]	NA	NA					
CoIm[Impact]:Area[Drøbak]	1.68	1.25					
SY0:CoIm[Impact]:Area[Drøbak]	0.64	2.11					
SY1:CoIm[Impact]:Area[Drøbak]	-1.11	1.91					
SY2:CoIm[Impact]:Area[Drøbak]	3.21	1.92					
SY3:CoIm[Impact]:Area[Drøbak]	NA	NA					
SY4:CoIm[Impact]:Area[Drøbak]	NA	NA					

Before the protection, lobsters inside the MPAs were smaller in Drøbak and the Inner Fjord compared to their respective control areas (Figure 8, Appendix A.2). Total lobster length increased post-protection in the MPA in Drøbak for both males and females, while it decreased in the control areas (Figure 8). In the Inner Fjord lobsters showed an increase in size in the MPA (Figure 8). Lobsters in the control area varied in size for both sexes, probably due to a small sample size in the Inner Fjord. However, lobsters in the control area were generally bigger than the lobsters inside the MPA in the Inner Fjord (Figure 8).

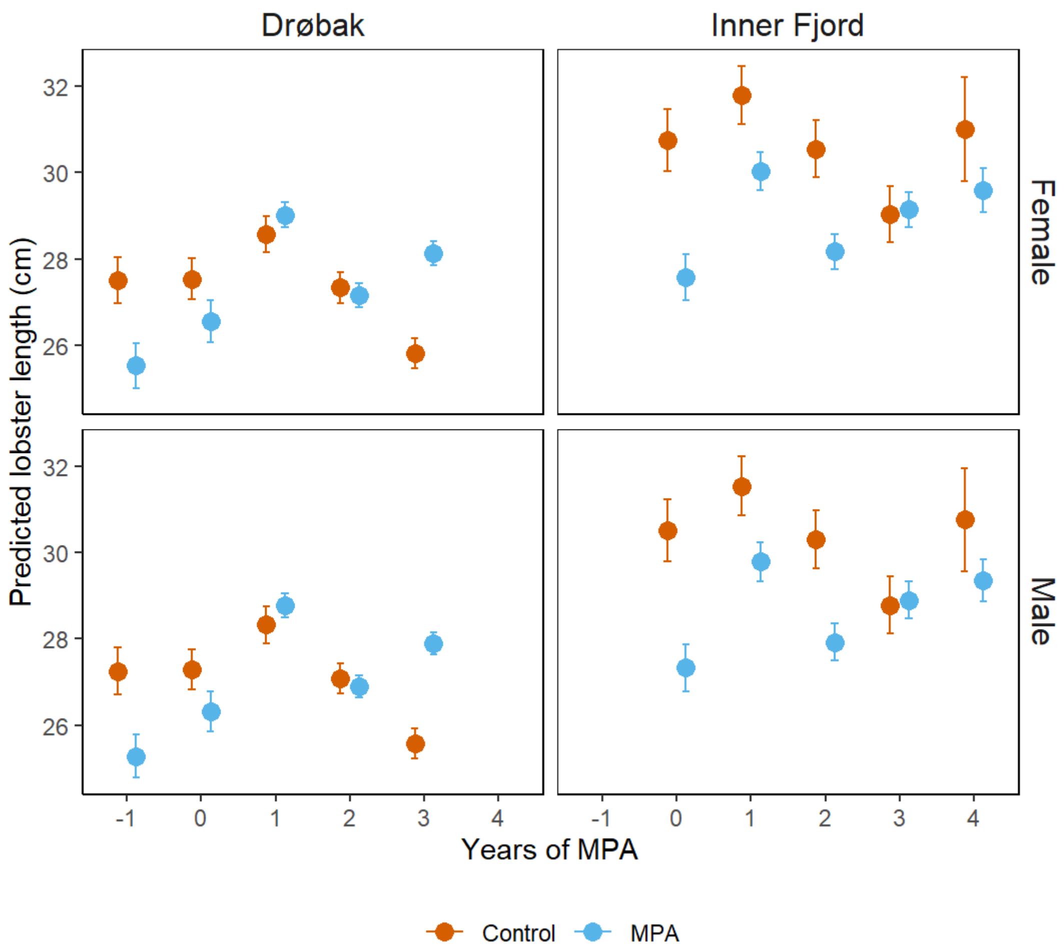

Figure 8: Point estimates with standard error (SE) for total length (cm) for males and females over five years in Drøbak and the Inner Fjord. Year zero refers to the year marine protected areas were established.

3.3 Sex ratio

Drøbak had a higher proportion of males in the MPA all years (Figure 9). The Inner Fjord had an increase of males in the MPA the last four years (Figure 9). The control areas in Drøbak had an overall even distribution of the two sexes, with a slight majority of females the first and final year (Figure 9).

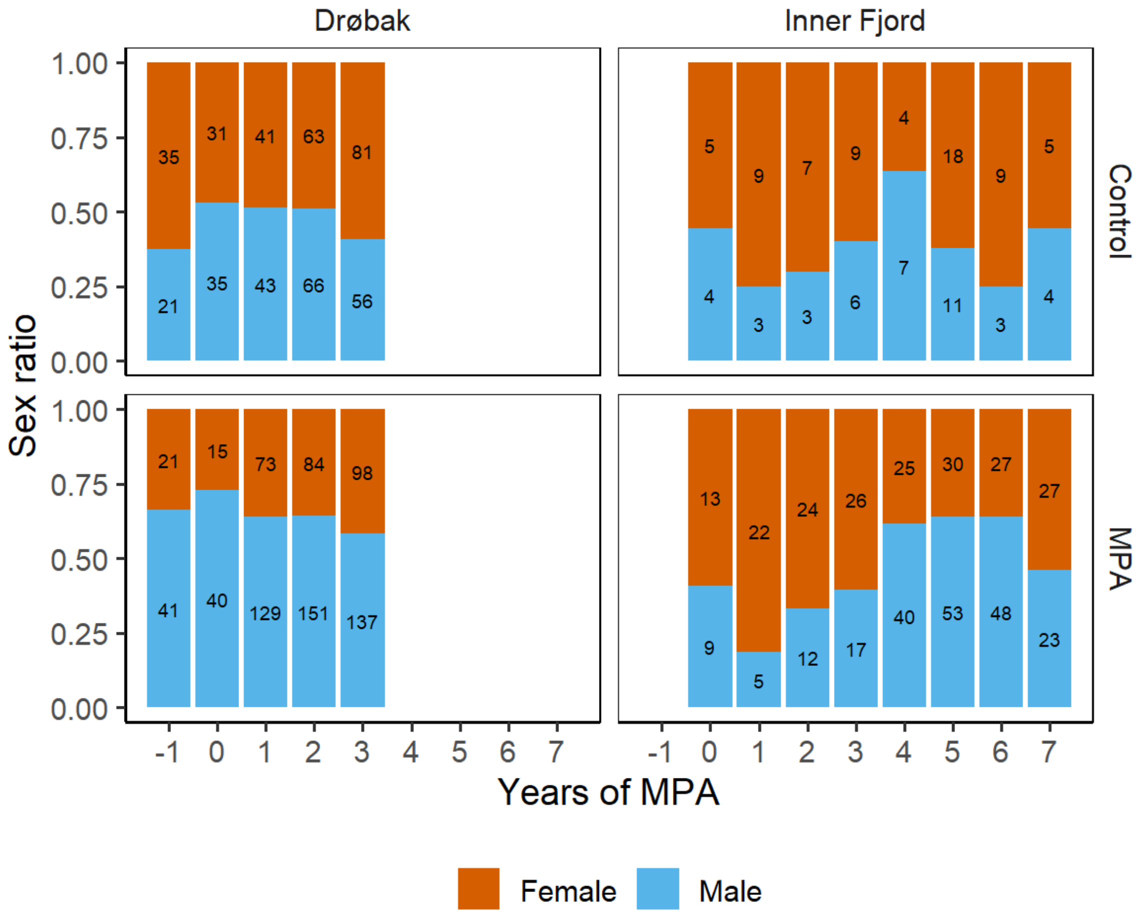

Figure 9: Sex ratio in Drøbak and the Inner Fjord for all study years (i.e. 2020 – 2024 in Drøbak and 2017 – 2024 in the Inner Fjord). Numbers inside the bars represent total catch. Year zero is the year MPA was established, all data are from August-September, prior to the legal trapping season (October-November) in control areas.

The best candidate model (Table 5) for sex (100 % support) included:

Sex ~ StudyYear + Control impact * Area

Table 5: Candidate models with AIC model selection with sex as the response variable. SY= Study year, CoIm = Control/Impact, Area = Inner Fjord and Drøbak, BA = Before/after.

Model	K	AICc	Δ AICc	AICcWt	Cum.Wt	LL
SY+CoIm*Area	9	2025.73	0.00	1.00	1.00	-1003.80
SY*CoIm*Area	20	2038.72	12.99	0.00	1.00	-999.08
CoIm*Area	4	2039.93	14.21	0.00	1.00	-1015.95
CoIm+Area	3	2040.73	15.00	0.00	1.00	-1017.35
BA+CoIm*Area	5	2041.27	15.54	0.00	1.00	-1015.62
BA+CoIm+Area	4	2042.14	16.41	0.00	1.00	-1017.05
BA*CoIm+Area	5	2042.99	17.27	0.00	1.00	-1016.48
BA*CoIm*Area	8	2045.58	19.85	0.00	1.00	-1014.74
BA+CoIm	3	2063.33	37.60	0.00	1.00	-1028.66
BA*CoIm	4	2064.23	38.50	0.00	1.00	-1028.10

The MPA in Drøbak had a consistently higher proportion of males compared with control areas while there was no apparent difference between MPA and control area in the Inner Fjord (Table 6, Figure 10, Appendix A.3). Following protection, Drøbak had a decrease of males both in control areas and MPA while the proportion of males had a marked increase in both areas in the Inner Fjord the fourth year (Figure 10).

Table 6: Parameter estimates for best model fitted: ~ Study year + CoIm * Area. Anova test with backwards elimination, with sex as the response variable. SY: Study year, CoIm: Control/Impact.

Parameter estimates			**Likelihood ratio test statistics**				
Term	Estimate	SE	Effect	Df	Deviance	Resid. Df	P
Intercept	-0.78	0.35	SY	5	6.53	1505	0.26
SY0	0.46	0.25	CoIm	1	23.21	1504	< 0.001
SY1	0.12	0.22	Area	1	39.87	1503	< 0.001
SY2	0.20	0,21	CoIm:Area	1	4.66	1502	< 0.05
SY3	-0.04	0.21					
SY4	1.31	0.21					
CoIm [Impact]	-0.06	0.32					
Area [Drøbak]	0.52	0.30					
CoIm[Impact]:Area[Drøbak]	0.74	0.34					

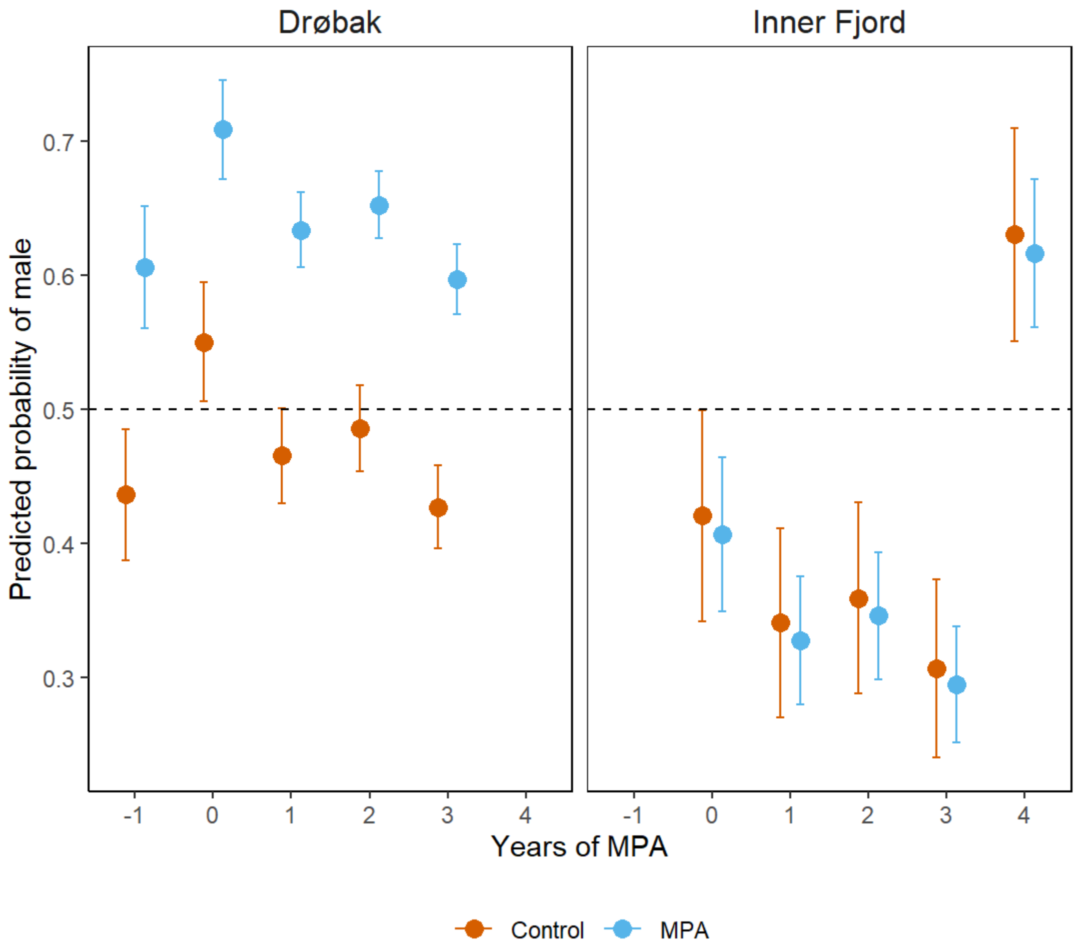

Figure 10: Point estimates with standard error (SE) for proportion of males and females separated by Drøbak and the Inner Fjord. The black, stapled line represents a 50% sex ratio. Year zero is the MPA establishment.

4 Discussion

4.1 Catch per unit effort

Results indicate an increase in catch per unit effort within the marine protected areas in Drøbak and the Inner Fjord. This is consistent with previous findings, as MPAs have shown to be an effective tool for the protection of lobsters (Fernández-Chacón et al., 2021; Knutsen et al., 2022; Moland et al., 2013a). In Drøbak, mean CPUE showed a substantial post-protection increase, indicating a strong initial response to MPA establishment. The abundance of lobsters approximately doubled between the year of MPA establishment and the second year (from ~ 0.4 to ~ 0.8 CPUE for males and ~ 0.2 to ~ 0.5 CPUE for females). Previous studies have also shown that heavily exploited species with relative high population growth rates may respond quickly to protection (Lester et al., 2009). The comparatively lower total catch in the Inner Fjord may contribute to a slower response of the protection (Sánchez Lizaso et al., 2002), however, a small increase was observed.

The two MPAs are relatively small, Drøbak covering 0.85 km^2 and the Inner Fjord 2.05 km^2. The edge effect, known as the degradation of the effective size of the protected area, could have a substantial impact on size limited MPAs (Kellner et al., 2007; Ohayon et al., 2021). For lobsters this effect may extend approximately 400 m into the MPAs (Ohayon et al., 2021). If the MPA is too small, this edge effect may span the entire area, thereby limiting its protective function. However, previous studies have also found that even small MPAs may have a considerable higher CPUE compared to control areas (Moland et al., 2013a; Sørdalen et al., 2022).

The initial prediction that the Inner Fjord would exhibit a greater increase in CPUE compared to Drøbak due to its larger protected area was not supported by the results. Although the MPA in Inner Fjord was larger in size, Drøbak had the largest increase in CPUE. Lobsters are relatively stationary, 77 - 95% of lobsters move less than 1000 m, and are therefore less exposed to threats outside reserve borders (Agnalt et al., 2007; Rowe, 2001). Therefore, larger MPAs would be expected to be more effective in lobster protection. However, the total catch in the Inner Fjord was considerably lower than in Drøbak, which can explain the slow initial response in CPUE. Furthermore, the MPA in Drøbak, Jetéen, which is made up of rocks and boulders makes a suitable habitat for lobsters and could potentially support a higher density (Institute of Marine Research, 2022).

The small increase in CPUE in the control areas in Drøbak could indicate that these areas also benefit from protection. This could be linked to the spillover-effect (Goñi et al., 2006), however, a capture-mark-recapture study in Drøbak found that lobsters did not migrate beyond their marking locations, suggesting limited movement outside the protected area (Haugen et al., 2024). The small variation in control areas in Drøbak could potentially be explained by larvae recruitment from other regions, as planktonic larvae undergo four pelagic phases, during the first two phases they drift with ocean currents (Haugen et al., 2024). Or, favorable environmental conditions in certain years may have contributed to the development of particularly strong recruitment (Haugen et al., 2024). Higher lobster density within the MPAs can lead to intraspecific competition for shelters and especially large lobsters may migrate to avoid competition (Steneck, 2006; Thorbjørnsen et al., 2018). The migration of large lobsters is thought to result from the high energetic cost of competition, where the effort required to fight for shelter is outweighed by the benefits of securing shelter another place (Steneck, 2006). Lobster density is expected to be highest within the MPAs and decline gradually with increasing distance from the MPA boundary (Goñi et al., 2006; Kleiven et al., 2019). However, Goñi et al. (2006) also reported a sharp decline in CPUE on the border of the MPA, indicating a high fishing pressure. These findings suggest that while MPAs can enhance local populations and contribute to adjacent areas, the small variation in CPUE in control areas in Drøbak is more likely due to certain strong years of hatching and survival of lobster larvae due to environmental conditions.

Catch per unit effort is not necessarily a good measure for the actual population size. Factors as temperature and climate could affect the catchability of lobsters (Sundelöf et al., 2013). Especially high temperatures are linked to an increase in CPUE (Matic´-Skoko et al., 2022; Sheehy & Bannister, 2002). However, the two MPAs lie close, approximately 25 km apart, and would be equally affected by such changes. Furthermore, lobsters are exposed to ghost traps (Miljødirektoratet, 2024), which could also influence the catch rate. Since control areas are open for harvest, a greater occurrence of ghost traps is expected in these areas. Even with preventive measures in place, ghost traps remain a problem.

The traps in the Inner Fjord were intentionally not placed in areas with a history of no catch, whereas in Drøbak, trap placement was randomized using QGIS. This difference in methodology may have influenced the results, potentially leading to an overestimation of catch rates in the Inner Fjord compared to Drøbak, due to their nonrandom placements of traps. Nevertheless, the low CPUE in the Inner Fjord may also suggest more illegal harvest than in Drøbak due to the high population of people in the Inner Oslofjord. Although this would only be speculations. The BACI design was used in both study areas and offers a simple and robust design. It is a useful tool to interpret contrasts between MPA and control areas and changes before-and-after implementation (Kerr et al., 2019).

4.2 Size distribution

The prediction that the Inner Fjord would have a larger increase in body size compared with Drøbak was not supported by the results. The two MPAs had an increase in lobster length of approximately 2 cm for both sexes from before the protection to the final year. Compared to control, lobsters were larger in the MPA In Drøbak the final year. Previous studies have shown that MPAs have a positive impact on lobsters' size compared to control areas (Moland et al., 2013a; Moland et al., 2013b; Thorbjørnsen et al., 2018). Similar results were reported in Fernández-Chacón et al. (2020) where survival was lower and lobsters typically smaller in areas open to harvest. Several studies suggest the increase in body size inside the MPAs are due to the absence of harvest and the reduction in size- and growth-selective fishing (Kleiven et al., 2017; Lester et al., 2009; Sørdalen et al., 2022). Moreover, lobsters with higher feeding rates grow faster and are more likely to get caught in traps in the harvested areas, however, these lobsters are protected inside the MPA (Sørdalen et al., 2022). Before the protection, lobsters in the MPAs were initially smaller than in the control areas for both areas and lobsters in Drøbak were approximately 2 cm smaller than in the Inner Fjord. These patterns suggest that the areas designated as MPAs were subject to relatively high fishing pressure prior to protection.

As previously indicated, fishing pressure tends to increase outside the MPAs (Kleiven et al., 2019), which furthermore would impact the mean size of lobsters in harvested areas. In the coming years, it would be expected that the average total length in harvested areas will continue to increase as the effects of the maximum (32 cm) size regulations become more pronounced over time. A study done by the Institute of Marine Research show that minimum size regulation (22 cm until 2008 and 25 cm from 2008) had a small positive effect on total length (Kleiven et al., 2017). However, the traps rarely catch lobsters smaller than 22 cm (Haugen et al., 2024), thus the effect of the minimum size regulation is not yet documented. Furthermore, the increased fishing pressure in the exploited areas might undermine the expected growth in size.

Males tend to be larger in MPAs compared to control areas, indicating that males grow faster than females in protected areas (Sørdalen et al., 2018). Furthermore, females molt more frequently and grow more during each molt in the MPA compared to control areas (Sørdalen et al., 2022). Contrary to the findings in this study where size differences between males and females were not observed. Temporal trends may become more pronounced as the duration of the protection increases.

Females have been reported to mate with larger males inside the MPAs (Sørdalen et al., 2018). In addition, a sexual selection on males' body and claw size were stronger inside the protected area. As commercial fisheries favor larger lobsters, a weakening of sexual selection will likely accelerate fisheries' induced evolution towards smaller body size (Sørdalen et al., 2018). However, the maximum size regulations protect lobsters exceeding 32 cm, but the extent of illegal harvest is unknown. Moreover, since lobster size is positively correlated with reproductive potential for both sexes (Campbell & Robinson, 1983), continued growth is likely to contribute to a further increase in population size and at first a decrease in total length due to higher recruitment inside the MPAs.

4.3 Sex ratio

The initial prediction that there would be a larger increase of males in the Inner Fjord MPA compared to Drøbak was supported by the results. However, the prediction that both areas would have a higher proportion of females prior to protection was not observed. Drøbak had a higher proportion of males and the Inner Fjord a higher proportion of females before the MPA establishment. Current harvest regulations protect females with external roe, which is usually every other year, making females more likely to be spared from harvest than males (Agnalt et al., 2007). This would result in a female skewed sex ratio, as shown in the Inner Fjord. Although initial differences in sex ratio existed between the two areas, the change over time was similar in both control areas and MPAs in Drøbak and the Inner Fjord. These findings were unexpected as fisheries influence the sex ratio for lobsters (Iacchei et al., 2005; Ogburn, 2019; Skud, 1969). Previous studies indicate that the proportion of males should decrease in harvested areas (Jury et al., 2019; Koepper et al., 2021). Furthermore, males with a large crusher claw relative to body size are more likely to get caught in traps as these lobsters take more risk, which again would favor females (Moland et al., 2019; Moland et al., 2013b). A lower proportion of males was therefore anticipated in the control areas.

The two areas, Drøbak and the Inner Fjord, showed a pronounced difference in sex ratio. Given the notably lower total catch in the Inner Fjord (250 individuals) compared to Drøbak (1261 individuals), it is reason to believe that the fishing pressure was higher in the Inner Fjord before the protection. The high fishing pressure disfavoring males could be one reason for the difference in sex ratio observed between the two areas (Moland et al., 2019; Moland et al., 2013b). The response to protection could be slower in areas with smaller populations (Sánchez Lizaso et al., 2002), thus, the effects in the Inner Fjord may still be emerging, despite the high proportion of males observed the final year. However, there could be other factors not accounted for in this study that could affect the sex ratio as differences in the benthic zone.

The Institute of Marine Research reported that there has been a substantial decrease in males over 30 cm since 2010 in harvested areas (Kleiven et al., 2017). In the same period, the proportion of females with external roe has increased, due to protection when carrying roe and the minimum harvest regulation. This results in an uneven sex ratio, especially for lobsters exceeding 30 cm (Kleiven et al., 2017). However, the results from this study detected no difference in size distribution in either the MPAs or control areas regarding sex. Sørdalen et al. (2018) found that males grow faster under protection, increasing the likelihood that larger males migrate out of the MPAs and potentially get caught in traps. However, the probability of catching male lobster in the Inner Fjord increased in the protected area and the control area, indicating that the protection had the same effect on male survival in both areas.

5 Conclusion

This study shows that lobsters may benefit from small marine protected areas. The lobsters had an increase in total length and CPUE in Drøbak and the Inner Fjord. These findings are supported by several studies (Fernández-Chacón et al., 2021; Knutsen et al., 2022; Moland et al., 2013a; Moland et al., 2013b; Thorbjørnsen et al., 2018). The lobster is heavily exploited despite harvest regulations, which lead to a quick response when protected. In the Drøbak MPA, covering an area of only 0.85 m^2, CPUE for both males and females was double its pre-protection level. Smaller MPAs are easier to manage compared to larger MPAs and are less exposed to illegal harvest ('Aulani Wilhelm et al., 2014). The Inner Fjord had the expected development in sex ratio with an increase of the relative number of males in the MPA, unlike Drøbak where the proportion of males remained relatively constant in both the MPA and in control area. This study supports the establishment of marine protected areas designated for lobsters in the Oslofjord, for further increase in recruitment.

6 References

'Aulani Wilhelm, T., Sheppard, C. R. C., Sheppard, A. L. S., Gaymer, C. F., Parks, J., Wagner, D., & Lewis, N. a. (2014). Large marine protected areas – advantages and challenges of going big. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *24*(S2), 24-30. https://doi.org/10.1002/aqc.2499

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. https://doi.org/10.1093/icesjms/fsl020

Campbell, A., & Robinson, D. G. (1983). Reproductive Potential of Three American Lobster (*Homarus americanus*) Stocks in the Canadian Maritimes. *Canadian Journal of Fisheries and Aquatic Sciences*, *40*(11). https://doi.org/10.1139/f83-225

Espeland, S. H., Kleiven, A. R., Moland, E., & Knutsen, J. A. (2014). *Aktiv forvaltning av marine ressurser - lokalt tiplasset forvaltning* (Rapport fra havforskningen, Issue. https://www.hi.no/hi/nettrapporter/rapport-fra-havforskningen/2014/34-2014_aktiv_forvaltning_arsrapport_2014

Fernández-Chacón, A., Buttay, L., Moland, E., Knutsen, H., & Olsen, E. M. (2021). Demographic responses to protection from harvesting in a long-lived marine species *Biological Conservation 257*. https://doi.org/10.1016/j.biocon.2021.109094

Fernández-Chacón, A., Villegas-Ríos, D., Moland, E., Baskett, M. L., Olsen, E. M., & Carlson, S. M. (2020). Protected areas buffer against harvest selection and rebuild phenotypic complexity. *Ecological applications*, *30*(5). https://doi.org/10.1002/eap.2108

Fiskedirektoratet. (n.d.). *Fredningstider og -område for hummar*. Retrieved 8. April from https://www.fiskeridir.no/Fritidsfiske/Artar/Hummarfiske/Fredings-og-bevaringsomraade

Forskrift om fredningsområder for hummer. (2006). (LOV-2008-06-06-37-§16). Lovdata. https://lovdata.no/dokument/SF/forskrift/2006-07-06-883

Forskrift om høsting av hummer. (2021). (LOV-2008-06-06-37-§16). Lovdata. https://lovdata.no/dokument/SF/forskrift/2021-12-23-3890?q=hummer

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*. https://doi.org/10.3354/meps308207

Hammer, E., & Berg, O. F. (2024). Oscarsborg festning In *Store norske leksikon*.

Haugen, T. O., Colman, J. E., Chavarie, L., Hove, K., Lemmens, L., & Moe, S. R. (2024). *Torsk og hummer i indre Oslofjord: Effekter av vernetiltak pr 2023* (MINA fagrapport 99). https://static02.nmbu.no/mina/publikasjoner/mina_fagrapport/pdf/mif99.pdf

Haugen, T. O., Colman, J. E., & Moe, S. R. (2023). *Torsk og hummer i indre Oslofjord: Effekter av vernetiltak* (MINA fagrapport 83). https://static02.nmbu.no/mina/publikasjoner/mina_fagrapport/pdf/mif83.pdf

Iacchei, M., Robinson, P., & Miller, K. A. (2005). Direct impacts of commercial and recreational fishing on spiny lobster, *Panulirus interruptus*, populations at Santa Catalina Island, California, United States. *New Zealand Journal of Marine and Freshwater Research*, *39*(6). https://doi.org/10.1080/00288330.2005.9517386

Incze, L. S., & Wahle, R. A. (1991). Recruitment from pelagic to early benthic phase in lobsters *Homarus americanus**. *Marine Ecology Progress Series 79*, 77-87. https://doi.org/10.3354/meps079077

Institute of Marine Research. (2022). *Lobster - European* Retrieved 17. February from https://www.hi.no/en/hi/temasider/species/lobster-european

Institute of Marine Research. (2024). *Tema: Ålegras*. Retrieved 6. May from https://www.hi.no/hi/temasider/arter/alegras
Jury, S. H., Pugh, T. L., Henninger, H., Carloni, J. T., & Watson, W. H. (2019). Patterns and possible causes of skewed sex ratios in American lobster (*Homarus americanus*) populations. *Invertebrate Reproduction & Development*, *63*(3). https://doi.org/10.1080/07924259.2019.1595184
Kellner, J. B., Tetreault, I., Gaines, S. D., & Nisbet, R. M. (2007). FISHING THE LINE NEAR MARINE RESERVES IN SINGLE AND MULTISPECIES FISHERIES. *Ecological applications*, *17*(4). https://doi.org/10.1890/05-1845
Kerr, L. A., Kritzer, J. P., & Cadrin, S. X. (2019). Strengths and limitations of before-after-control-impact analysis for testing the effects of marine protected areas on managed populations. *ICES Journal of Marine Science*, *76*(4). https://doi.org/10.1093/icesjms/fsz014
Kleiven, A. R., Moland, E., Sørdalen, T. K., Espeland, S. H., & van der Meeren, G. I. (2017). *Evaluering av effekten av forvaltningstiltak på hummer og forslag til tiltak* (Rapport fra Havforskningen nr.15-2017). https://www.hi.no/hi/nettrapporter/rapport-fra-havforskningen/2017/15-2017_hummerrapport_ark
Kleiven, P. J. N., Espeland, S. H., Olsen, E. M., Abesamis, R., Moland, E., & Kleiven, A. R. (2019). Fishing pressure impacts the abundance gradient of European lobsters across the borders of a newly established marine protected area. *Proceedings Of The Royal Society B*, *286*(1894). https://doi.org/10.1098/rspb.2018.2455
Klima- og miljødepartementet. (2021). *Helhetlig tiltaksplan for en ren og rik Oslofjord med et aktivt friluftsliv*. Retrieved from https://www.regjeringen.no/no/dokumenter/helhetlig-tiltaksplan-for-en-ren-og-rik-oslofjord-med-et-aktivt-friluftsliv/id2842258/
Knutsen, J. A., Kleiven, A. R., Olsen, E. M., Knutsen, H., Espeland, S. H., Sørdalen, T. K., Thorbjørnsen, S. H., Hutchings, J. A., Fernández-Chacón, A., Huserbråten, M., Villegas-Ríos, D., Halvorsen, K. T., Nillos Kleiven, P. J., Langeland, T. K., & Moland, E. (2022). Lobster reserves as a management tool in coastal waters: Two decades of experience in Norway. *Marine Policy*, *136*. https://doi.org/10.1016/j.marpol.2021.104908
Koepper, S., Revie, C. W., Stryhn, H., Clark, K. F., Scott-Tibbetts, S., & Thakur, K. K. (2021). Spatial and temporal patterns in the sex ratio of American lobsters (*Homarus americanus*) in southwestern Nova Scotia, Canada. *Scientific Reports*, *11*. https://doi.org/10.1038/s41598-021-03233-8
Lester, S. E., Halpern, B., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B., Gaines, S. D., Airmamè, S., & Warner, R. (2009). Biological effects within no-take marine reserves: a global synthesis. *Marine Ecology Progress Series*, *384*. https://doi.org/10.3354/meps08029
Matic´-Skoko, S., Pavicˇic´, M., Sˇ epic´, J., Janekovic´, I., Vrdoljak, D., Vilibic´, I., Staglicˇic´, N., Sˇ egvic´-Bubic´, T., & Vujevic´, A. (2022). Impacts of Sea Bottom Temperature on CPUE of European Lobster *Homarus gammarus* (Linnaeus, 1758; Decapoda, Nephropidae) in the Eastern Adriatic Sea. *Frontiers in Marine Science*, *9*. https://doi.org/10.3389/fmars.2022.891197
Miljødirektoratet. (2023). *Gjennomføring av helheltlig tiltaksplan for Oslofjorden: Rapport for året 2022-2023* (Rapport M-2591). https://www.miljodirektoratet.no/publikasjoner/2023/november-2023/gjennomforing-av-helhetlig-tiltaksplan-for-oslofjorden-2022-2023/
Miljødirektoratet. (2024). *Tilstandsrapport for Oslofjorden* (Rapport M-2885). https://www.miljodirektoratet.no/publikasjoner/2025/januar-2025/tilstandsrapport-for-oslofjorden/

Miljødirektoratet. (2025). *Marint vern*. Retrieved 14. February from https://www.miljodirektoratet.no/ansvarsomrader/vernet-natur/marint-vern/

Moland, E., Carlson, S. M., Villegas-Ríos, D., Wiig, J. R., & Olsen, E. M. (2019). Harvest selection on multiple traits in the wild revealed by aquatic animal telemetry. *Ecology and Evolution 9*(11). https://doi.org/10.1002/ece3.5224

Moland, E., Olsen, E. M., Knutsen, H., Garrigou, P., Espeland, S. H., Kleiven, A. R., Knutsen, J. A., & Knutsen, C. A. (2013a). 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 B*, *280*(1754). https://doi.org/10.1098/rspb.2012.2679

Moland, E., Ulmestrand, M., Olsen, E. M., & Stenseth, N. C. (2013b). Long-term decrease in sex-specific natural mortality of European lobster within a marine protected area. *Marine Ecology Progress Series*, *491*. https://doi.org/10.3354/meps10459

Ogburn, M. B. (2019). The effects of sex-biased fisheries on crustacean sex ratios and reproductive output *Invertebrate Reproduction & Development*, *63*(3). https://doi.org/10.1080/07924259.2019.1612787

Ohayon, S., Granot, I., & Belmaker, J. (2021). A meta-analysis reveals edge effects within marine protected areas. *Nature Ecology & Evolution 5*. https://doi.org/10.1038/s41559-021-01502-3

OpenAI. (2025). *ChatGPT (Mar 14 version)*. In https://chat.openai.com/

R Development Core Team. (2024). *RStudio: Intergrated Development Environment for R*. In (Version 2024.12.0.467) https://www.R-project.org/

Rowe, S. (2001). Movement and harvesting mortality of American lobsters (*Homarus americanus*) tagged inside and outside no-take reserves in Bonavista Bay, Newfoundland. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*(7). https://doi.org/10.1139/f01-083

Sánchez Lizaso, J. L., Goñi, R., Reñones O., García Charton, J. A., Galzin, R., Bayle, J. T., Sánches Jerez, P., Pérez Ruzafa, A., & Ramos, A. A. (2002). Density dependence in marine protected populations: a review. *Environmental Conservation 27*(2). https://doi.org/10.1017/S0376892900000187

Sciberras, M., Jenkins, S. R., Kaiser, M. J., Hawkins, S. J., & Pullin, A. S. (2013). Evaluating the biological effectiveness of fully and partially protected marine areas *Environmental Evidence 2*(4), Article 4. https://doi.org/10.1186/2047-2382-2-4

Sheehy, M. R. J., & Bannister, R. C. A. (2002). Year-class detection reveals climatic modulation of settlement strength in the European lobster, *Homarus gammarus*. *Canadian Journal of Fisheries and Aquatic Sciences*, *59*(7). https://doi.org/10.1139/f02-083

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). https://doi.org/10.1139/f99-116

Skud, B. E. (1969). *The effect of fishing on size composition and sex ratio of offshore lobster stocks* (Fiskeridirektoratets skrifter, Serie Havundersøkelser). http://hdl.handle.net/11250/114420

Steneck, R. S. (2006). Possible Demographic Consequences of Intraspecific Shelter Competition among American Lobsters. *Journal of Crustacean Biology*, *26*(4). https://doi.org/10.1651/S-2753.1

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). https://doi.org/10.1371/journal.pone.0058160

Sørdalen, T. K., Halvorsen, K. T., Harrison, H. B., Ellis, C. D., Vøllestad, L. A., Knutsen, H., Moland, E., & Olsen, E. M. (2018). Harvesting changes mating behaviour in European lobster. *Evolutionary Applications*, *11*(6). https://doi.org/10.1111/eva.12611

Sørdalen, T. K., Halvorsen, K. T., & Olsen, E. M. (2022). Protection from fishing improves body growth of an exploited species *Proceedings Of The Royal Society B*, *289*(1987). https://doi.org/10.1098/rspb.2022.1718

Tandberg, A. H. S., Walseng, B., Glenner, H., Meland, K., Djursvoll, P., & Falkenhaug, T. (2021). *Krepsdyr: Vurdering av hummer Homarus gammarus for Norge.* Artsdatabanken Retrieved 30. January from https://artsdatabanken.no/lister/rodlisteforarter/2021/14133

Thorbjørnsen, S. H., Moland, E., Huserbråten, M. B. O., Knutsen, J. A., Knutsen, H., & Olsen, E. M. (2018). Replicated marine protected areas (MPAs) support movement of larger, but not more, European lobsters to neighbouring fished areas. *Marine Ecology Progress Series*, *595*. https://doi.org/10.3354/meps12546

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed Effects Models and Extensions in Ecology with R*. Springer.

Appendix A

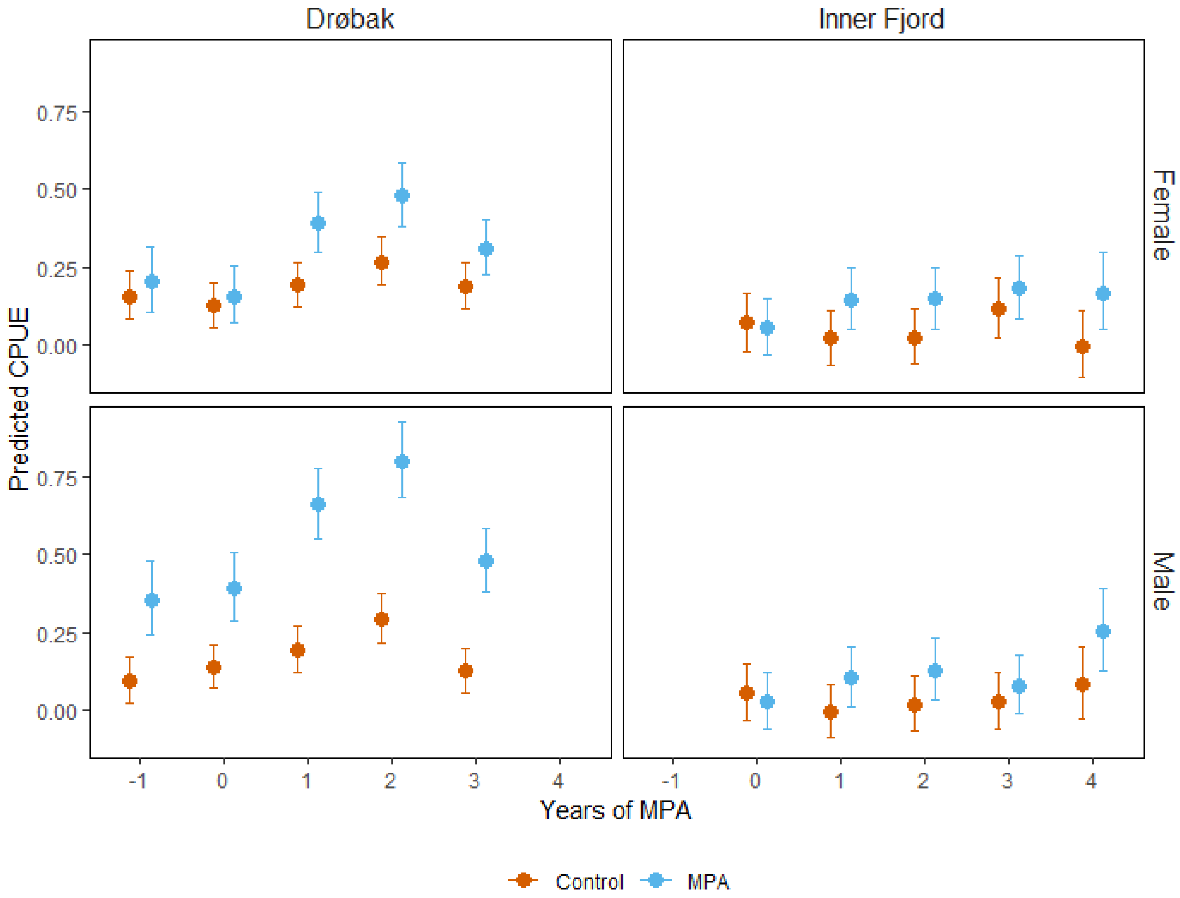

Figure A.1: Point estimates with a 95% confidence interval of CPUE (lobster/trap/24 hour) for males and females over five years in Drøbak and the Inner Fjord.

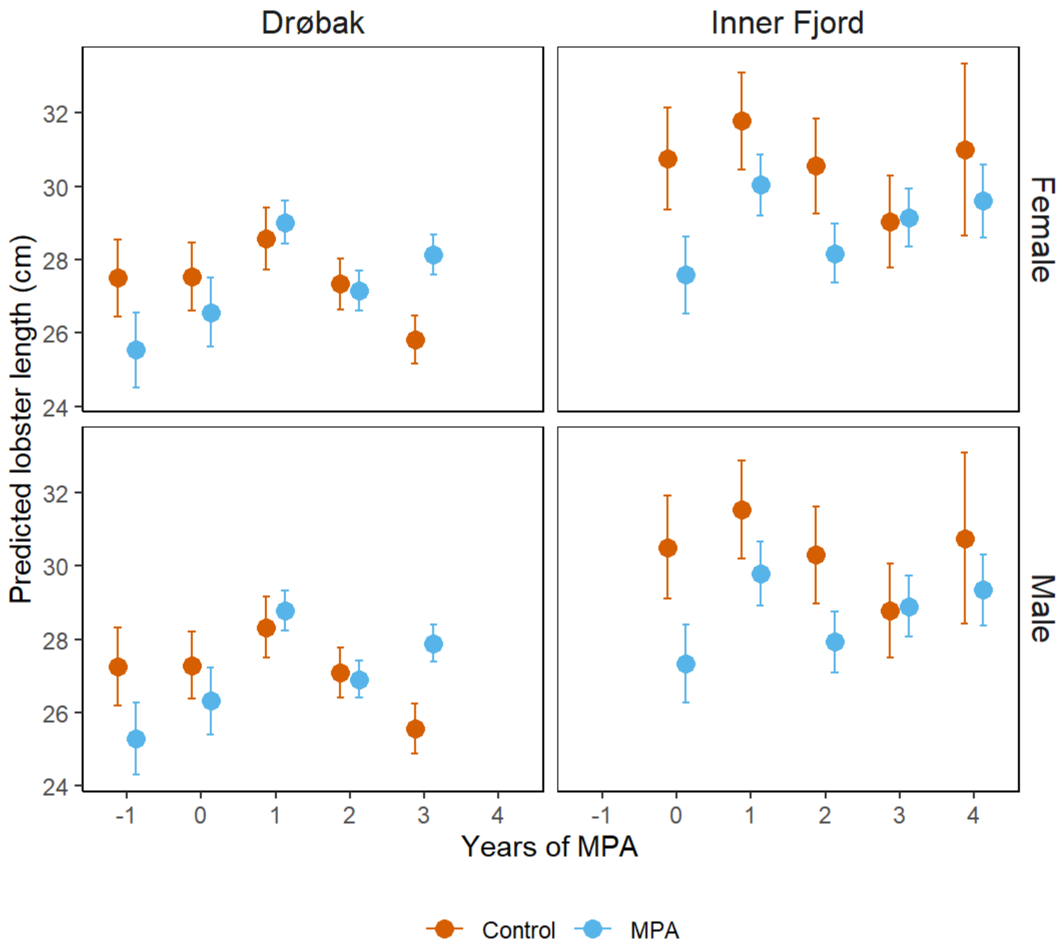

Figure A.2: Point estimates with a 95% confidence interval for total length (cm) for males and females over five years in Drøbak and the Inner Fjord.

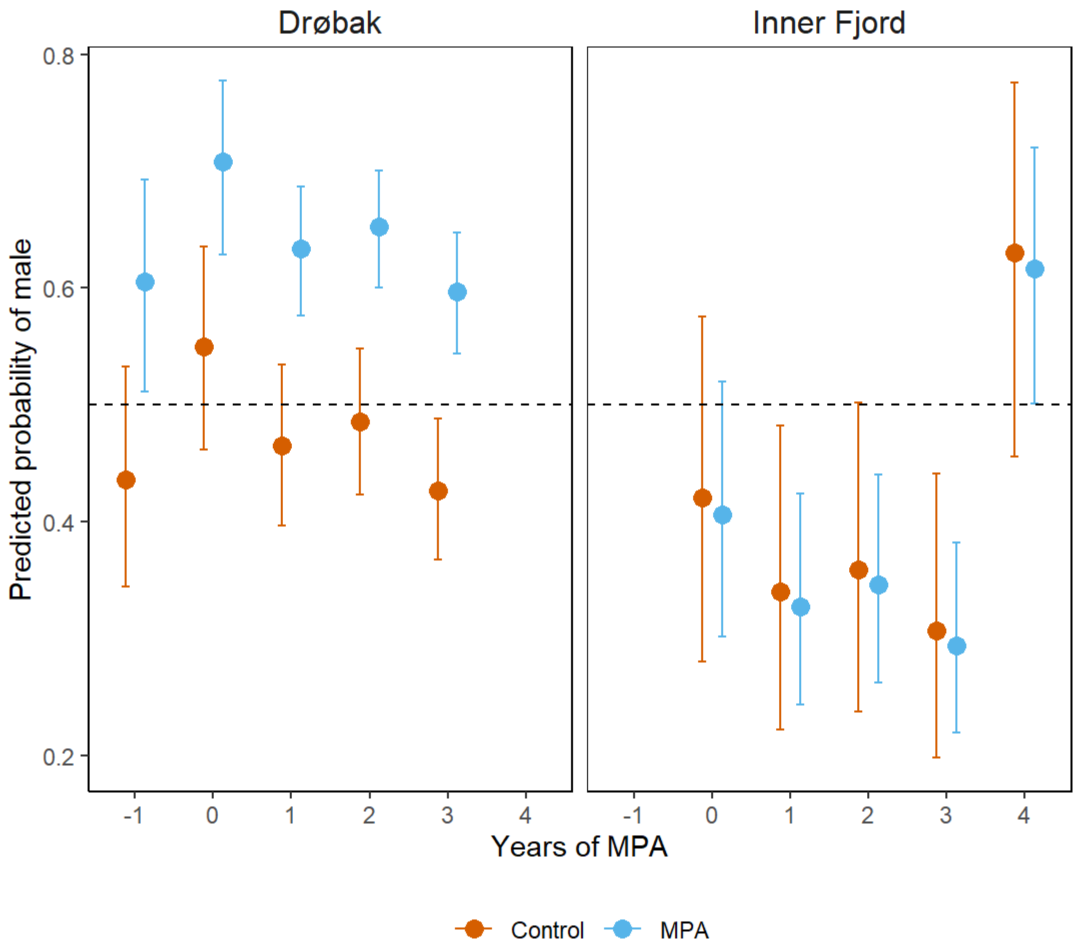

Figure A.3: Point estimates with a 95% confidence interval for proportion of males and females in Drøbak and Inner Fjord. The black, stapled line represents a 50% sex ratio.

Norges miljø- og biovitenskapelige universitet
Noregs miljø- og biovitenskapelege universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway