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THE IMPACT OF MARINE PROTECTION ON THE SIZE DISTRIBUTION AND SURVIVAL OF THE LOBSTER POPULATION IN THE INNER OSLOFJORD.

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Preface

This journey has been life changing, I’m grateful to God for helping me thus far. Special thanks to my supervisors Stein R Moe, Louise Chavarie and Thrond Haugen. Thank you so much for the feedback, suggestions, guidance and corrections. Thank you for your endless patience. I also appreciate Knut and Odd for their help during the sampling sessions. I appreciate the effort of all my lecturers, every course taken has enhanced my ability to critically assess events. I also appreciate everyone on the NMBU lobster monitoring project. Thank you to everyone who supported me on this journey, especially my family.

Abstract

The elimination of fishing pressure through the establishment of marine protected areas (MPAs) have been positioned as one of the ways to conserve the declining lobster population in Norway. MPAs have been credited with improved survival, abundance, growth rate, rebuilding of size structure and the strengthening of sexual selection observed in protected lobster populations. There is however insufficient documentation on the efficacy of small-sized MPAs in restoring the depleted lobster stock. I performed a short-term replicated Before-After Control-Impact (BACI) study using capture-mark-recapture data obtained from the MPA in Drøbaksundet and two adjacent harvested sites two years before and two years after the MPA was established. Investigations were done to test the potential long-term effect of protection and the short-term effect of harvesting on population parameters such as catch-per-unit-effort (CPUE), sex ratio, body length, proportion of berried females and the probability of lobsters to be legal sized in both the MPA and fished sites. Lobster sampling sessions were conducted in September and December, i.e., before and after the lobster harvest season. Two years after the MPA was established, there was a rise in lobster CPUE in the MPA with more than a two-fold increase over the pre-MPA values, males responded more positively than females. A moderate rise in CPUE was also observed in the harvested sites. Mean length of lobsters in the MPA rose, with the increase in males doubling that of females. There was also an increase in the proportion of females in the MPA with the potential of a more balanced sex ratio after protection. Additionally, the proportion of legal sized lobsters in the MPA increased, accompanied by a non-linear relationship between lobster length and the probability to be berried, females attained a peak probability to be berried at 30 - 32.5 cm and a subsequent decline thereafter. The impact of harvest (October-November) was marked by a general decline in lobster CPUE from the pre- and post-harvesting sampling periods. There were also site-specific responses in mean length and an increased probability for lobsters to be female after harvest. The impact of harvest resulted in females being more likely to be berried at 27.5-30 cm with lobsters in areas open to harvest having a reduced probability to be legal sized compared to those in the MPA after harvest. I conclude that even a small sized MPA, like the one in Drøbaksundet, despite being in its early phase can be effective in restoring the depleted lobster population in the inner Oslofjord.

Contents

1 Introduction

Landings of the European lobster (*Homarus gammarus*), hereafter referred to as lobsters, have reached historically low levels in Norway, with a 92% decline in abundance over the last 90 years because of chronic overfishing (Kleiven et al., 2022). Lobsters are currently classified as "Vulnerable" VU on the Norwegian Red List (Tandberg et al., 2021). Despite the decline, fishing pressure remains high in certain areas, with recreational fishers who are the dominant participants, contributing approximately 65% of the effort and catches (Kleiven et al., 2011). During the lobster harvest season, trap density can be as high as 50 traps/km^2 at the beginning of the fishing season (Kleiven et al., 2011). Fishers commonly relocate and replenish traps every one to three days at the onset of harvest, but with less frequent hauling toward the end of the season (Moland et al., 2019). Although, fishers move traps around, areas identified as prime lobster habitats still experience significant fishing pressure (Wiig et al., 2013). Consequently, as part of efforts to lessen fishing pressure in some designated areas, the establishment of marine protected areas (MPAs) are increasingly being advocated as an effective strategy for lobster conservation in Norway. A growing number of studies have credited the recovery of previously depleted lobster stock in Norway to protective measures implemented in MPAs (Moland et al., 2021).

As of 2023, there are approximately 58 lobster MPAs in Norway with a total area cover of 9,200 ha. One such MPAs, which is the focus of this study, was established in Drøbaksundet in 2021. The MPA in Drøbaksundet is a small 85 ha MPA. Although it is essential that MPAs are adequately sized to achieve the intended conservation benefits (Claudet et al., 2008), small-sized MPAs have been suggested to be beneficial to lobsters because of their limited mobility and high site fidelity (Moland et al., 2021; Moland et al., 2021). Moland et al. (2011) reported that 95% of tagged lobsters were detected within or near the boundaries of a 100-ha MPA, with most lobsters maintaining a home range of between 0.57-4.16 ha (<1 year), while Wiig et al., (2013) reported an average home range of 12.3-17.1 ha for tagged lobsters for a shorter time frame (i.e., 2 months).

Lobsters in two small-sized MPAs; Kvernskjær (50 ha), and Flødevigen (100 ha) and a relatively larger Bolærne (278 ha) MPA, have shown positive responses to protection, albeit with discernible variations across locations, sex and age categories (Fernández-Chacón et al., 2020; Moland et al., 2013). For example, studies on the impact of protection on the lobster population in these MPAs reported an increase in lobster abundance (Fernández-Chacón et al., 2021; Moland et al., 2013; Sørdalen et al., 2022a) (except Bolærne) and mean body size (Fernández-Chacón et al., 2021; Fernández-Chacón et al., 2020; Moland et al., 2013; Sørdalen et al., 2022a) with a higher growth rate for females and development of larger claws for males (except in Flødevigen) (Sørdalen et al., 2022a). There are also reports of the rebuilding of the truncated size and age structures in all three MPAs accompanied by a demographic shift in favour of large-sized individuals of the population (Fernández-Chacón et al., 2021; Fernández-Chacón et al., 2020). These results indicate that lobsters in a protected area have greater survival rates and size diversity compared to those in unprotected areas where they are typically smaller due to the pressures of harvesting (Fernández-Chacón et al., 2021).

In areas open to harvesting, female lobsters generally have higher survival than males due to the existence of the “sex-biased” harvest regulations (Fernández-Chacón et al., 2021), that mandates that captured ovigerous lobsters, which make up approximately 50% of the female population, be returned to the sea (Sørdalen, 2019). Male lobsters are more vulnerable to capture in harvested areas, particularly those with large claws relative to body size because they are more dominant when competing for resources (Sørdalen et al., 2020). Lobster traps are also built to facilitate the escape of small-sized lobsters and management regulations mandates that lobsters below the minimum legal size (MLS) be returned if captured (Wiig et al., 2013). Such size-selective harvesting could therefore counteract natural selection that favours large-bodied individuals (Sheehy et al., 1999). This may cause a harvest-induced shift in the demography in favour of small-sized lobsters, potentially impacting mating behaviour by limiting the choice of mates, especially for large females (Fernández-Chacón et al., 2020). Large females prefer to mate with the bigger members of the opposite sex, while for males, a favourable outcome in their search for partners is directly correlated with their claw to body size ratio, a result of sexual selection. (Sørdalen et al., 2020). Sørdalen et al. (2020) reported that females were generally larger than males in fished areas with a smaller mean size difference compared to protected lobsters. The disparity in size that favour females weakens sexual selection, causing a weaker pattern of size-assortative mating in harvested areas (Sørdalen et al., 2018) and may lead to a decline in lobster stocks, since larger female lobsters contribute disproportionately to offspring production within the population (Moland et al., 2010). However, despite intense exploitation exerting pressure on large claws in males, MPAs could potentially alleviate these conflicting selective pressures, protecting males with large claws and restoring a more natural mating pattern (Sørdalen et al., 2020).

The benefits of lobster MPA can potentially be eroded by fishers redirecting their fishing efforts towards the borders of the MPA to take advantage of the increased abundance of lobsters, a phenomenon known as "fishing the line" (Kellner et al., 2007). This possibility might be exacerbated by the small size of the Drøbaksundet MPA, particularly considering that the effectiveness of similar sized (<100 ha) MPAs in rebuilding depleted lobster stocks in Norway remains inadequately documented. This insufficient documentation may be attributed to the fact that most MPAs in Norway are typically larger in size, ranging from 22-2,316 ha with an average size of 354 ha. Therefore, this study aims to assess to what extent a small-sized MPA may contribute to restoring a depleted local lobster population in the inner Oslofjord. I explored trends in lobster catch-per-unit-effort, sex ratio, body length of lobsters, proportion of egg-bearing females and the probability of lobsters to be legal-sized. Investigating the effect of protection of the Drøbaksundet MPA, I made the following predictions on population parameters:

Catch- per- unit- effort (CPUE): I expected the cessation of harvest-induced mortality in the MPA to result in an increased density of lobsters in the protected area compared to the harvested areas (Moland et al., 2013) with a more positive response in males compared to females.

Body length: I expected the mean length of lobsters in the MPA to be greater than that of lobsters in adjacent harvested areas (Fernández-Chacón et al., 2020).

Sex ratio: I expected that the absence of size and sex-specific selection from fishing mortality in the MPA will result in more balanced sex ratio in the MPA compared to the harvested area.

Berried lobsters: I expected that with the ban on capture of berried lobsters in both the MPA and fished areas, the proportion of berried to non-berried females in the population will be lower in the MPA compared to the harvested area.

Probability to be legal-sized: I expected that more lobsters in the protected area will fall in the legal-sized category due to the elimination of harvest induced mortality compared to the harvested sites.

2 Materials and methods

2.1 Study area

The Oslo oslofjord is approximately a 110-kilometer-long fjord system situated along the southeastern coast of Norway. It links the city of Oslo in the north with the Skagerrak, which is a strait that stretches from the North Sea, running between Norway, Sweden, and Denmark, to the south (Martell et al., 2022). It is part of a geographical rift (Larsen et al., 2008), separated into the outer and inner parts by a 12 km long Drøbak sound (Staalstrøm et al., 2012) which is a relatively shallow sill. The Drøbak sound positioned near the town of Drøbak acts as an effective barrier that separates the inner portion of the Oslofjord from the middle and outer regions. This barrier restricts the exchange of deep water into the inner basins and contributes to the distinctive characteristics of the Oslofjord (Baalsrud & Magnusson, 2002). The MPA in Drøbaksundet established in 2021 is situated within the Oslofjord (Fig.1). Drøbaksundet serves as a strait connecting Drøbak and Hurum. Sampling was conducted within three zones in Drøbaksundet (Fig. 2). One of these zones, the (Middle zone) located in the Jetéen area is designated as the MPA. Jetéen which is part of the Oscarsborg Fortress, is an entirely man-made lobster habitat made of large boulders and was originally intended to prevent larger vessels from moving freely in the western fjord. Presently, the jet has two small openings allowing small boats to pass through. The remaining two zones are designated as control areas. The first control area (the Southern zone) also known as Biologen, covers 18.2 ha, extending from Badeparken to the southern part of Lehmannsbrygga (Fig. 2). The second, larger control area (the Northeastern zone) covering 115 ha encompasses Askholmene and extends from Håøya to the mainland (Fig.2).

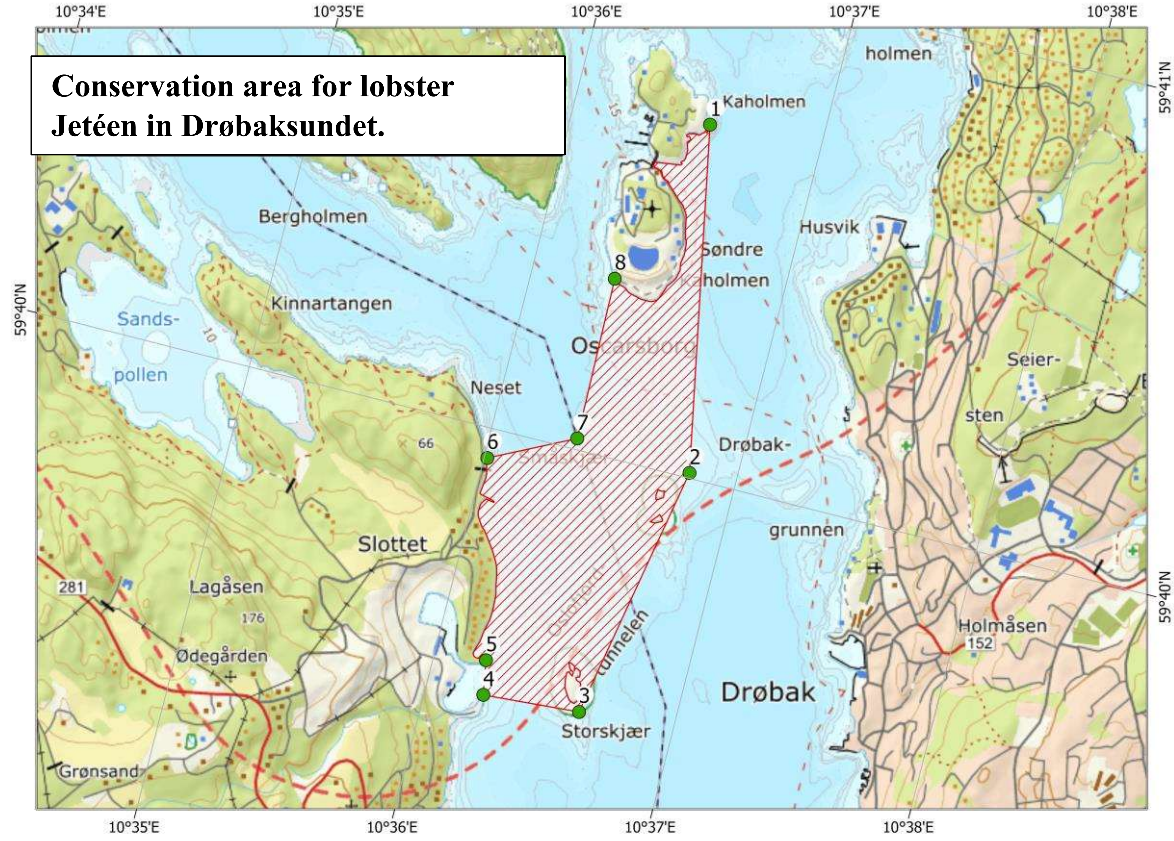

Figure 1. Study site showing the MPA (Source: Norwegian directorate of fisheries).

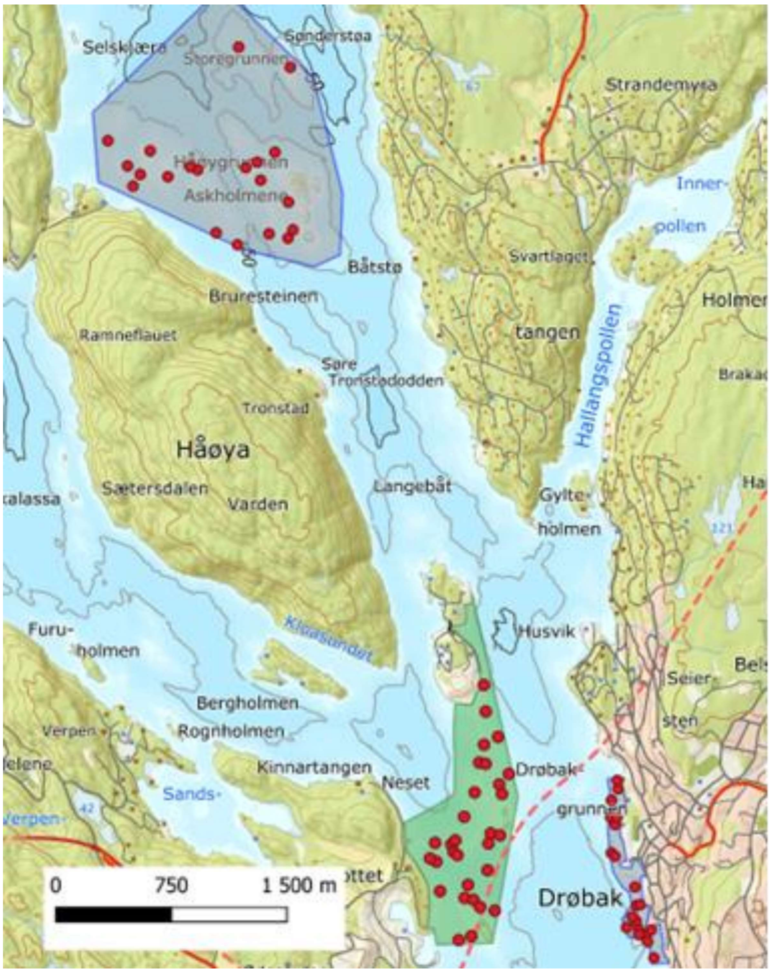

Fig. 2. Map of the MPA and the harvested sites with the red dots indicating trap locations of the sampling rounds from 2020-2023: Source-Haugen et al., 2023.

2.2 Study species and management

Lobsters are large, sexually dimorphic species, with great economic and ecological value. (Fernández-Chacón et al., 2021). Its distribution covers a wide geographical range, extending from Trondheimsfjord southwards along the coast of Norway and all the way south to the Mediterranean coast. There is also an isolated population genetically different from other lobster populations found as far north as Tysfjord and Nordfolda (Agnalt et al., 2009). Male lobsters exhibit a faster growth rate, smaller size at maturity and larger claws compared to females (Sørdalen et al., 2018). Female lobsters attain sexual maturity at about 5-6 years at an estimated carapace length of between 80-85mm (Beard & McGregor, 1991). Older lobsters are more fertile than their younger counterparts (Tully et al., 2001). Lobsters are mainly stationary, dispersal is usually done by larval flow rather than movement of adults (Huserbråten et al., 2013). Their site fidelity and restricted mobility makes them ideal organism for studying how protective measures impact demographic parameters (Moland et al., 2011). Lobsters can possibly attain a total body length (TL) of up to 50 cm (Tully et al., 2001). Although, there is enforced regulations on catches including length-based limits with a legal-size range of 25-32 cm (the 32 cm size limit is specific to southern Norway), resulting in the removal of a substantial portion of legal-sized males each season (Moland et al., 2019). However, since lobsters above 32 cm are exempted from being harvested, there is still the possibility for certain lobsters to attain large size and age even in unprotected areas.

Other management regulations to mitigate the decline in lobster stock include, approving only lobster traps equipped with biodegradable panels with two 60 mm diameter escape openings that allows the release of undersized lobster (Thorbjørnsen et al., 2018). There is also a limit on the number of traps to a maximum of 10 per boat and regulating fishing season duration (i.e., October-November in Southern and Eastern Norway but extending to December in western Norway) and banning the harvest and sale of berried females (Kleiven et al., 2022; Pettersen et al., 2009; Zimmermann et al., 2023). Unfortunately, the time lag required for regulatory effects to manifest (Watt & Arthur, 1996), coupled with the estimated high (80%) mortality of legal-sized male lobsters harvested during each fishing season (Wiig et al., 2013) have led to uncertainties about the efficacy of these regulations. Therefore the Drøbaksundet MPA established as a no-take MPA with only hook and line fishing allowed while prohibiting the use of fixed fishing gear is aimed at providing comprehensive protection to the local lobster population.

2.3 Lobster sampling design.

A total of seven trapping sessions have been conducted between 2020-2023 (Fig. 3). The sessions in September of 2020 and 2021 before the establishment of the MPA enabled us to establish a baseline and facilitate scientific monitoring of the absence of fishing mortality impact over time, using the Before-After-Control-Impact (BACI) method. After the establishment of the MPA, a sampling session was done in December 2021. From 2022 onwards, two sampling sessions have been conducted annually. Sampling was done in September (just before the harvest season) and December (immediately after the harvest season), to capture the impact of harvesting and the total protection the MPA provides. Sampling was done through a standardized capture–mark–recapture method using Scottish lobster traps “skotteteine”. The escape vents were closed to broaden the size range of captured lobsters. Traps were attached to a labelled buoy and baited with frozen mackerel. Each sampling session consisted of five days (24h) with a sampling effort of 20 traps. Sampling was done simultaneously in both the MPA and control areas to account for shared temporal effects. After the 2021 sampling sessions, it was determined that the MPA exceeded the initially proposed size. Consequently, the allocated number of daily traps for the MPA was increased to 30 for both the 2022 and 2023 sessions. This made it a total of 350 traps for each of the individual sessions for both years (Fig. 3).

Lobster CPUE was calculated as the number of lobsters captured for every trap haul per day. Randomization and stratification routines were implemented for trap placement, ensuring a representative distribution between depths of three to thirty meters. Lobster traps were randomly distributed within two depth layers (strata), specifically 3-15 m and 15-30 m, utilizing the randomization routine in QGIS's vector tools within their respective zones. Records of length (measured from the rostrum to the posterior end of the telson), sex (determined by examining the first pair of pleopods), the presence/absence of external eggs, and recaptures, were documented for every captured lobster, along with the date, time, and sampling zone. Captured lobsters were tagged with uniquely numbered 60 mm white T-bar tags (FD-94, T-bar, Floy-tag Inc). These tags were inserted between the cephalothorax and abdomen using a standard tag applicator. All captured lobsters were subsequently released at capture location.

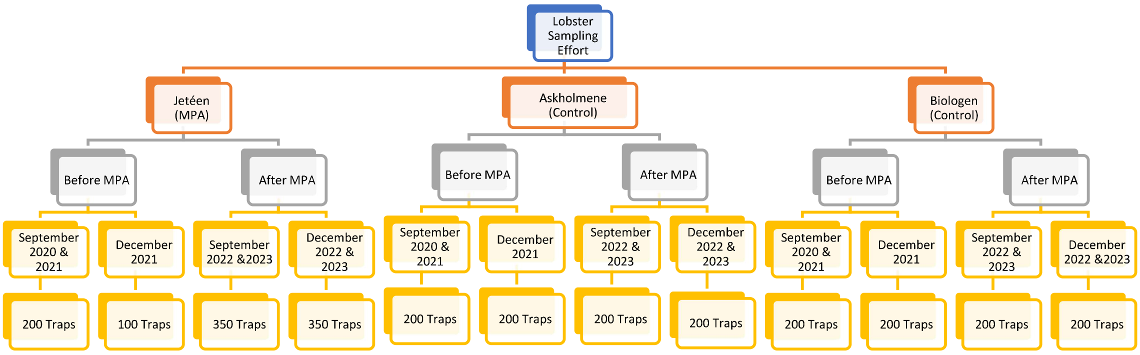

Figure 3. Conceptual figure representing the lobster BACI (Before-After Control-Impact) sampling design in the protected and control sites.

Figure 4. A lobster trap "skotteteine" being baited with frozen mackerel for use in the lobster sampling session in September 2023.

3 Statistical analyses

All statistical analysis was performed in R v.4.3.3 (R Core Team, 2024). The impact of protection and fishing effort (harvesting) were used as the basis to investigate the hypotheses in this study. To test the impact of harvesting, data from December 2020 was excluded due to the absence of before and after fishing data for that year. Similarly, to evaluate the effect of protection, only September data was used, with the aim to maintain consistency in the sampling period.

3.1 Catch per unit effort (CPUE).

Candidate models was constructed using, a negative binomial generalized linear mixed-effects model (GLMM) to account for overdispersion of the dataset (Lüdecke et al., 2021). Predictors were specified as before MPA vs after, before harvesting vs after, control vs MPA, the capture location, the sex of lobsters and the year of sampling. Models were fitted using the glmer.nb. Trap identification and sampling rounds were added as random effects to correct for repeated measurements. Backward elimination was performed to reduce the model, the selected candidate model was then subjected to an ANOVA, to test for significance.

3.2 Body length.

Candidate models were constructed using linear mixed-effects models (LMM) with before MPA vs after, before harvesting vs after, the capture location, control vs MPA, and the sex of lobsters defined as predictors while trap identification nested within sampling rounds were included as random effects. Models were fitted using the lmer function in R. To test for the effect of fishing effort, (Burnham & Anderson, 2004) for AIC. Akaike Information Criteria (AIC) was used to select the most parsimonious model, identified by the lowest AIC value within the set of candidate models. Models with AIC differences of less than two points ($\Delta AIC < 2$) were deemed to be statistically equivalent, after which Analysis of Variance (ANOVA) test type III, was performed to test for the significance of individual predictors. To test the effect of protection, the model with the highest AIC support was an interaction between before MPA vs after, capture sites and sex. To achieve a more parsimonious model retaining only the significant predictors, backward selection was used to refine the selected model, eliminating the non-significant interaction terms. The reduced model was updated using the “update function” with REML (Restricted Maximum Likelihood) estimation enabled (Lüdecke et al., 2021). Next, Analysis of Variance (ANOVA) test, Type III, was conducted on the reduced model using the car Anova function, with a test statistic of “F”.

3.3 Sex ratio

Analysis to assess the impact of harvesting and protection on lobster sex ratios was performed using a generalized linear mixed-effects model (GLMM) with a binomial distribution. The predictor variables in the candidate models included length of lobsters, the capture sites with three levels: " Jetéen, (the MPA), "Askholmene, (the northeast zone), and " Biologen (the southern zone), before MPA vs after, and control vs MPA. The polynomial transformation of lobster length up to the second degree was included to investigate the potential non-linear effects of size, because only mid-sized lobsters are at risk of being harvested. To account for the varying risk exposure of different age categories, the predictor "Size group" was included, with three levels: “small” for lobsters below the legal size (25 cm), “at risk” for legal-sized lobsters and “big” for lobsters above the legal size (32 cm). Finally, to control for repeated measurement of recaptures, Trap ID and rounds were added as random effects. Model selection was done with AICc and tested with ANOVA as previously described.

3.4 Berried lobsters

Only female lobsters were included in this analysis. GLMM models were constructed with binomial distribution and the link function set to “logit”. The response variable was assigned the binary outcome of 1 for the presence of eggs and 0 for its absence. Predictor variables included the period before vs after protection, before vs after harvesting, the capture sites, the length of lobsters, the control v impacted sites, a polynomial transformation of lobster length up to the second degree, and size group of lobsters. Trap identification was nested within sampling round to account for the non-independence of observations within traps and rounds. Model selection was done with AICc and tested with ANOVA as previously described.

3.5 Probability of meeting the legal-size requirement for harvest

Generalized linear mixed-effects regression (GLMER) analysis was used to investigate the correlation between the response variable “at risk of harvest” (representing the likelihood of meeting the legal-size requirement for harvest) and predictors including, the control and impacted sites, the capture zones, and the sex of lobsters. Random effects were nested within trap identification and sampling rounds. Lobsters outside the legal-sized range were categorized as “No risk” while legal-sized lobsters were classified as “At risk”. Model was fitted using the "binomial" family and a logit link function. Although berried females are exempted from harvesting in both the MPA and the harvested sites, I did not account for this in investigating the probability of lobsters to be berried to focus solely on assessing the effects of fishing effort and protective measures.

4 Results

4.1 Population density

A total of 1,792 lobsters (including recaptures) were encountered in all the sampling sessions. Number of captured lobsters increased from 118 in 2020 to 860 in 2023 (Fig.5) with more males encountered than females. The protected area consistently had the highest number of captured lobsters, even before the establishment of the MPA, comprising 52.5% of the total captures in 2020 and increasing to 60.7% in 2023. Only one lobster has been encountered in all the seven sampling sessions (Table 1).

Table 1. Total number of captured lobsters (including recaptures) in the MPA and control in all sampling sessions from 2020-2023.

Encounter (s)	**Number of individual(s)**
1	834
2	191
3	51
4	11
5	3
6	2
7	1

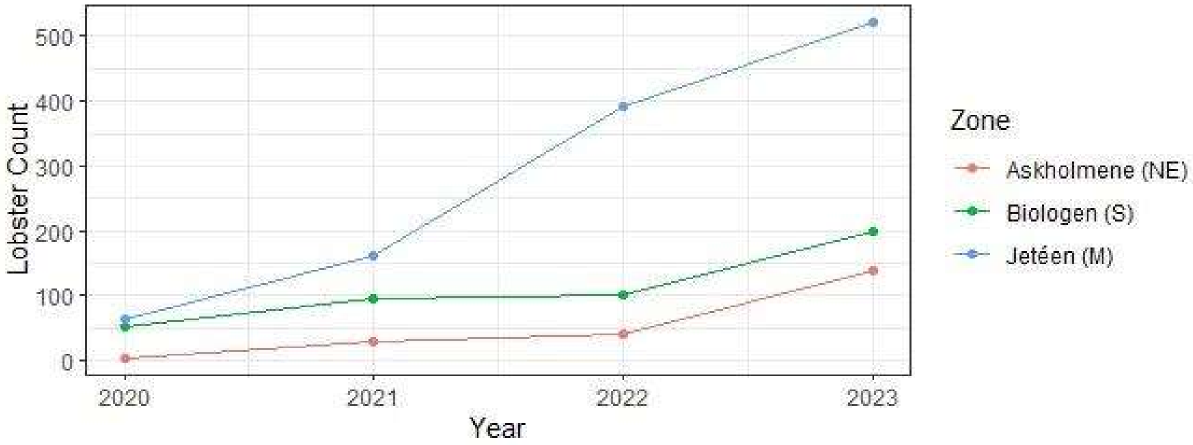

Figure 5. Lobsters that were encountered and recaptured in the three capture locations, Jetéen (MPA) and the control (Askholmene and Biologen) across the sampling years 2020-2023. Coloured lines represent the different zones and points represent the total encountered lobsters in each zone for each year.

To assess the impact of protection on lobster CPUE, the model selection amongst candidate models fitted to catch per unit effort data (only September) favoured two models as best candidates (AICc <2). The first model was an interaction model that included before MPA vs after, control vs MPA and sex, and the second model (year * control vs MPA * sex (Table 2). After backward elimination of the model with the lowest AICc, a reduced model was obtained. The one-way interaction effect was highly significant with before MPA vs after (χ^2=24.53, p<0.0001), and control vs MPA * sex (χ^2=20.77, p<0.0001) being significantly associated with CPUE (Table 3). Protection resulted in a substantial increase in the CPUE of male and female lobsters in the MPA (Fig. 6). CPUE also increase in the control areas in the same period (Fig. 6). Both males and females responded positively to protection, but females less than males (Fig.6). In the control, CPUE of male and female lobsters increased at similar rates in the same period (Fig.6).

Table 2. Models predicting the impact of protection on the predicted CPUE of lobsters from sex, before vs after protection, control vs impact, the capture site and the year of capture were ranked by AICc. K = number of parameters, AICc= corrected AIC statistic, ΔAICc = AICc difference, AICcWt = relative likelihood of being the "best" model, ModelLik= likelihood of the model given the data and LL=goodness of fit describes the statistical framework for model evaluation.

Model	K	AICc	ΔAICc	ModelLik	AICcWt	LL
Before MPA vs after *control (vs MPA) *female (vs male)	11	3432.73	0.00	1.00	0.60	-1705.32
Year*control (vs MPA) *female (vs male)	19	3433.55	0.82	0.66	0.40	-1697.64
Before MPA (vs after) * control (vs MPA) * female (vs male)	8	3449.12	16.39	0.00	0.00	-1716.53
Capture sites * female (vs male)	9	3476.32	43.59	0.00	0.00	-1729.13
Before MPA (vs after) *control (vs MPA)	7	3479.63	46.90	0.00	0.00	-1732.80
Before MPA (vs after) + control (vs MPA)	6	3480.94	48.21	0.00	0.00	-1734.46
Before MPA (vs after)	5	3488.40	55.67	0.00	0.00	-1739.19
Control (vs MPA)	5	3533.61	100.88	0.00	0.00	-1761.79

Table 3. Analysis of Deviance Table (Type III Wald chisquare tests), showing significance of variables from the model with the lowest AICc that predicted the effect of protection on CPUE of lobsters.

Model was subjected to backward elimination before being tested for significance.

Predictor (s)	**Chisq**	**Df**	**Pr (>Chisq)**
Intercept	170.84	1	<0.0001
Before harvest (vs after)	24.53	1	<0.0001
Control (vs MPA)	0.68	1	0.41
Before harvest (vs after): control (vs MPA)	3.61	1	0.058
Control (vs MPA): female (vs male)	20.7693	1	<0.0001

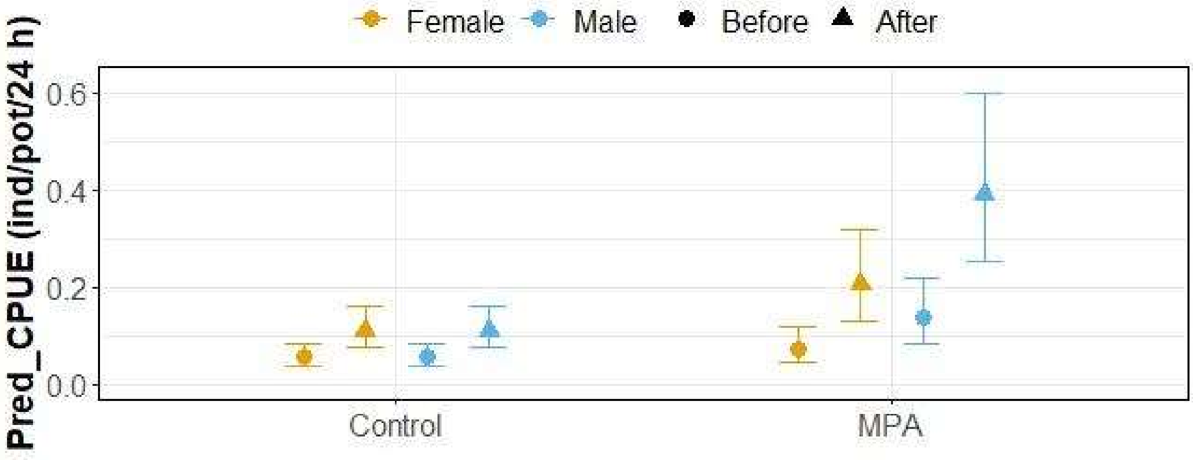

Figure 6. The effect of protection (before and after) on predicted mean (± 95% CI) CPUE of female and male lobsters in the MPA and control generated from the model with the lowest AICc in table 2 after it was reduced.

To assess the impact of harvest on lobster CPUE, the model selection amongst candidate models fitted to catch per unit effort data (excluding 2020) favoured an interaction model that included before harvest vs after, capture site and sex (Table 4). After the backward elimination, a reduced model was obtained. This one -way interaction effect was highly significant with before MPA vs after (χ^2=6.03, p=0.01), the capture sites (χ^2=23.91, p<0.0001), before MPA vs after * capture site (χ^2=11.52, p<0.01), and capture sites * sex (χ^2=20.82, p<0.0001) being significantly associated with CPUE (Table 5). Harvesting reduced lobster CPUE in the sites open for fishing, with a decreased CPUE for both female and male CPUE while male and female CPUE increased in the MPA in the same period (Fig. 7).

Table 4. Models predicting the impact of harvest on the predicted CPUE of lobsters from sex, before vs after protection, control vs impact and the capture site were ranked by AICc. K = number of parameters, AICc= corrected AIC statistic, ΔAICc = AICc difference, AICcWt = relative likelihood of being the "best" model, ModelLik= likelihood of the model given the data and LL=goodness of fit describes the statistical framework for model evaluation.

Model	K	AICc	*ΔAICc*	ModelLik	AICcWt	LL
Before harvest (vs after) *capture site* female (vs male)	15	5577.47	0.00	1.00	0.98	-2773.68
Capture sites * female (vs male)	9	5585.93	8.46	0.02	0.01	-2783.94
Year* before harvest (vs after) +capture site	39	5590.13	12.67	0.00	0.00	-2755.69
Before harvest (vs after) * control (vs MPA) * female (vs male)	11	5592.42	14.95	0.00	0.00	-2785.18
Year * before harvest (vs after) * control (vs MPA)	27	5594.24	16.77	0.00	0.00	-2769.94
Year*control (vs MPA) * female (vs male)	15	5608.74	31.27	0.00	0.00	-2789.31
Before harvest (vs after) * control (vs MPA) + female (vs male)	8	5613.58	36.11	0.00	0.00	-2798.77
Year * before harvest (vs after) *capture site	21	5633.00	55.53	0.00	0.00	-2795.39
Year * before harvest (vs after) +capture site	11	5636.75	59.29	0.00	0.00	-2807.35
Year* before harvest (vs after) * control (vs MPA)	15	5644.60	67.13	0.00	0.00	-2807.24
Before harvest (vs after) *control (vs MPA)	7	5650.08	72.62	0.00	0.00	-2818.03
Before harvest (vs after) +control (vs MPA)	6	5658.64	81.17	0.00	0.00	-2823.31
Control (vs MPA)	5	5658.86	81.40	0.00	0.00	-2824.43
Before harvest (vs after)	5	5722.20	144.74	0.00	0.00	-2856.09

Table 5. Analysis of Deviance Table (Type III Wald chisquare tests), showing significance of variables from the model with the lowest AICc that predicted the effect of harvest on CPUE of lobsters. Model was subjected to backward elimination before being tested for significance.

Predictors	**Chisq**	**Df**	**Pr (>Chisq)**
Intercept	138.51	1	<0.0001
Before harvest (vs after)	6.03	1	0.01
Capture site	23.90	2	<0.0001
Female (vs male)	0.21	1	0.64
Before harvest (vs after): capture site	11.52	2	<0.01
Capture site: female (vs male)	20.82	2	<0.0001

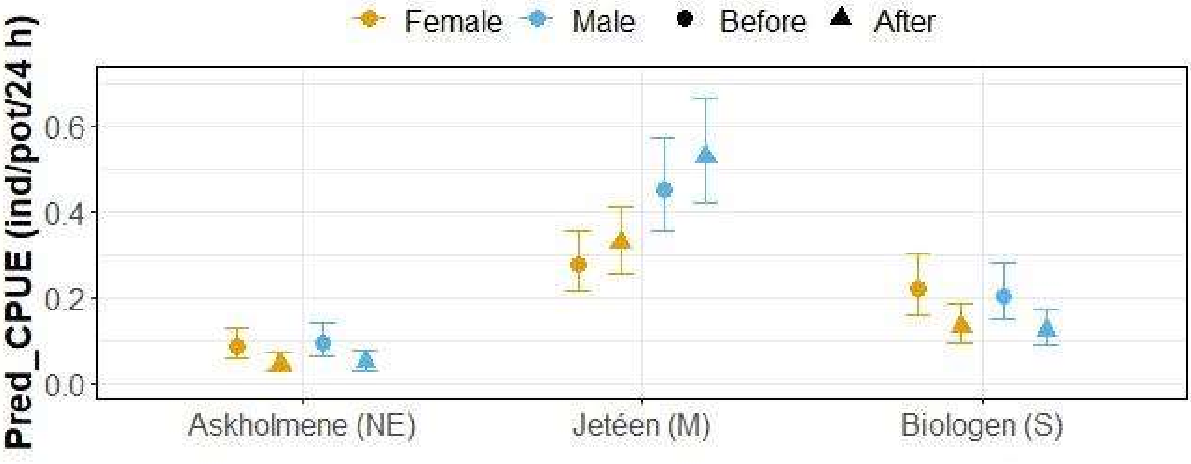

Figure 7. The effect of harvest (before (September) and after (December)) on predicted mean (± 95% CI) CPUE of female and male lobsters in the MPA (Jetéen) and harvested sites (Askholmene and Biologen) generated based on the model with the lowest AICc in table 4 after it was reduced.

4.2 Body length

Body length of captured lobsters ranged from 14.5- 41.0 cm (Fig. 8). Results are presented as mean ± SE unless otherwise stated. Lobsters in Askholmene had the highest length (30.16 ± 0.30 cm), followed by the MPA (27.27 ± 0.10 cm), and Biologen (26.55 cm ± 0.2 cm) (Fig. 8). Mean length of females was larger than of the mean length of males at Biologen, where the mean length of females was 4.40% larger than that of males.

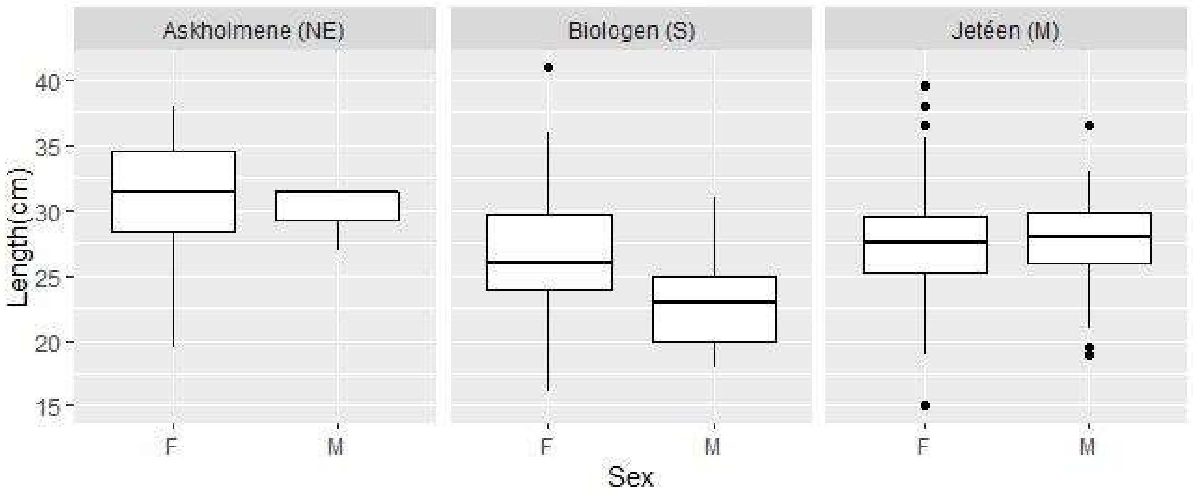

Figure 8. Length of female (F) and male (M) lobsters is depicted in the different sampling sites, Jetéen (MPA) and the control Askholmen and Biologen. Black horizontal lines represent the median values, boxes represent the interquartile range of values from the 25th to the 75th percentile, vertical lines extend to 1.5 times the interquartile range, and points represent outliers.

To assess the impact of protection on the mean length of lobsters, the model selection amongst candidate models fitted to only September data favoured two models as best candidates (AICc < 2). The first model was an interaction model that included before MPA vs after, capture site and sex (Table 6). While the second model included capture site, before MPA vs after and sex (Table 6). After the backward selection of the model with the lowest AICc, a reduced model was obtained. The one-way interaction effect was highly significant with capture site (F=4.99, p<0.01), before MPA vs after *capture site (F=3.33, p=0.04), and before MPA vs after * sex (F=11.28, p<0.001) being significantly associated with mean length (Table 7). Protection had a positive impact on mean length of male lobsters in the MPA, increasing at almost twice the rate of females (Fig. 9).

Table 6. Models predicting the impact of protection on the predicted length of lobsters from sex, before vs after protection, control vs impact and the capture site were ranked by AICc. K = number of parameters, AICc= corrected AIC statistic, ΔAICc = AICc difference, AICcWt = relative likelihood of being the "best" model, ModelLik= likelihood of the model given the data and LL=goodness of fit describes the statistical framework for model evaluation.

Model	**K**	**AICc**	**ΔAICc**	**ModelLik**	**AICcWt**	**LL**
Before MPA (vs after) *capture site* female (vs male)	15	4846.69	0.00	1.00	0.49	-2408.07
Capture site+ before MPA (vs after) * female (vs male)	9	4846.84	0.15	0.93	0.45	-2414.31
Before MPA (vs after) *capture site	9	4851.40	4.71	0.10	0.05	-2416.60
Control (vs MPA) * before MPA (vs after) *capture site	11	4855.68	8.99	0.01	0.00	-2416.69
Before MPA (vs after) + capture site	7	4857.49	10.80	0.01	0.00	-2421.68
Control (vs MPA) + before MPA (vs after) *capture site	8	4857.82	11.13	0.00	0.00	-2420.83
Before MPA (vs after) + capture site*female (vs male)	10	4859.09	12.40	0.00	0.00	-2419.42
Capture site +before MPA (vs after) + female (vs male)	8	4859.43	12.74	0.00	0.00	-2421.64
Control (vs MPA) * before MPA (vs after)	8	4859.43	12.74	0.00	0.00	-2421.64
Control (vs MPA) * before MPA (vs after)	7	4861.22	14.54	0.00	0.00	-2423.55
Before MPA (vs after)	5	4865.61	18.93	0.00	0.00	-2427.77
Capture site	6	4866.37	19.68	0.00	0.00	-2427.14
Control (vs MPA) + before MPA (vs after)	6	4867.61	20.93	0.00	0.00	-2427.76
Control (vs MPA) + before MPA (vs after)	6	4867.61	20.93	0.00	0.00	-2427.76
Control (vs MPA) *female (vs male) + before MPA (vs after)	8	4867.84	21.16	0.00	0.00	-2425.84
Control (vs MPA) +before MPA (vs after) + female (vs male)	7	4869.58	22.89	0.00	0.00	-2427.73

Table 7. Analysis of Deviance Table (Type III Wald chisquare tests), showing significance of variables from the model with the lowest AICc that predicted the effect of protection on mean length of lobsters. Model was subjected to backward elimination before being tested for significance.

Predictors	F	Df	Df. Res	Pr (>F)
(Intercept)	5535.95	1	106.82	< 0.0001
Before MPA vs after	1.95	1	257.12	0.16
Capture site	4.99	2	97.76	<0.01
Female (vs male)	2.33	1	839.27	0.13
Before MPA (vs after): capture site	3.33	2	190.06	<0.1
Before MPA (vs after): female (vs male)	11.29	1	865.70	<0.001

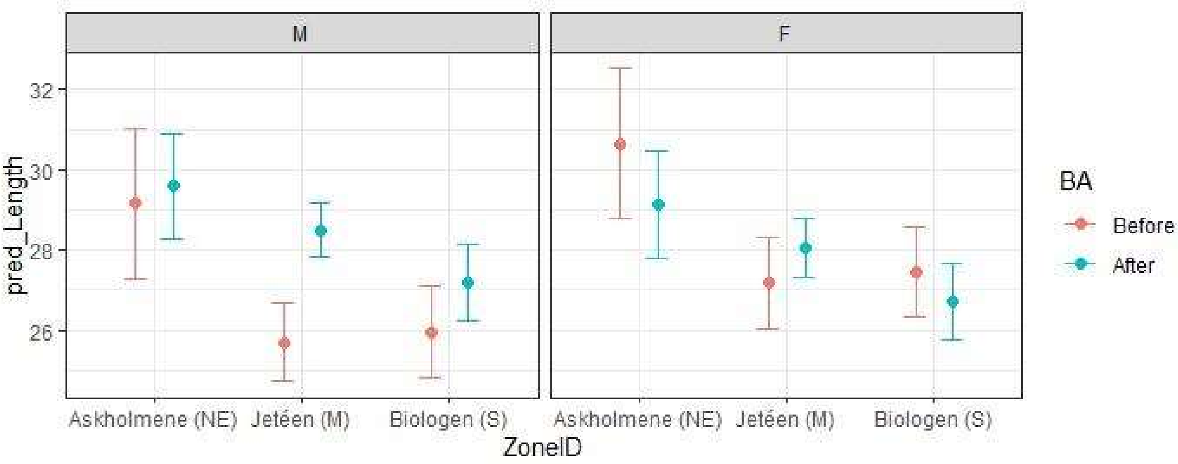

Figure 9. The effect of protection (before and after) on predicted mean (± 95% CI) length (cm) of female (F) and male (M) lobsters in the MPA (Jetéen) and harvested sites (Askholmene and Biologen) generated based on the model with the lowest AICc in table 6 after it was reduced.

To assess the impact of harvest on the mean length of lobsters, the model selection amongst candidate models fitted to data excluding that of 2020, favoured an interaction model that included before harvest vs after and capture sites (Table 8). Specifically, before harvest vs after (χ^2=14.51, p<0.001), capture site (χ^2=51.86, p<0.0001) and before harvest vs after * capture sites (χ^2=16.40, p<0.001) were significantly associated with mean length (Table 9). Harvesting had a positive impact on mean length of lobsters in Askholmene, while length reduced in Biologen. (Fig. 10).

Table 8. Models predicting the impact of harvest on the predicted length of lobsters from sex, before vs after protection, control vs impact and the capture site were ranked by AICc. K = number of parameters, AICc= corrected AIC statistic, ΔAICc = AICc difference, AICcWt = relative likelihood of being the "best" model, ModelLik= likelihood of the model given the data and LL=goodness of fit describes the statistical framework for model evaluation.

Model	**K**	**AICc**	**ΔAICc**	**ModelLik**	**AICcWt**	**LL**
Before harvest (vs after) * capture sites	9	7768.02	0.00	1.00	0.98	-3874.95
Before harvest (vs after) * capture sites * female (vs male)	15	7776.43	8.42	0.02	0.02	-3873.05
Before harvest (vs after) + capture sites	7	7779.74	11.72	0.00	0.00	-3882.83
Before harvest (vs after) + capture sites + female (vs male)	8	7781.75	13.73	0.00	0.00	-3882.82
Capture sites + before harvest (vs after) * female (vs male)	9	7782.55	14.53	0.00	0.00	-3882.21
Before harvest (vs after) + capture sites * female (vs male)	10	7783.70	15.68	0.00	0.00	-3881.77
Capture sites	6	7788.69	20.67	0.00	0.00	-3888.32
Before harvest (vs after)	5	7810.10	42.08	0.00	0.00	-3900.03
Control (vs MPA) + before harvest (vs after)	6	7812.11	44.09	0.00	0.00	-3900.03
Control (vs MPA) * before harvest (vs after)	7	7812.14	44.12	0.00	0.00	-3899.03
Control (vs MPA) +before harvest (vs after) +female (vs male)	7	7814.13	46.11	0.00	0.00	-3900.03
Control (vs MPA) +before harvest (vs after) * female (vs male)	8	7814.85	46.83	0.00	0.00	-3899.37
Control (vs MPA) * female (vs male) + before harvest (vs after)	8	7814.86	46.84	0.00	0.00	-3899.38
Control (vs MPA) * before harvest (vs after) * female (vs male)	11	7817.61	49.59	0.00	0.00	-3897.71

Table 9. Analysis of Deviance Table (Type III Wald chisquare tests), showing significance of variables from the model with the lowest ΔAICc that predicted the effect of harvest on mean length of lobsters.

Variable	**Chisq**	**Df**	**Pr (>Chisq)**
Intercept	9132.32	1	< 0.0001
Before harvest (vs after)	14.51	1	<0.001
Capture sites	51.86	2	<0.0001
Before harvest (vs after): capture sites	16.40	2	<0.001

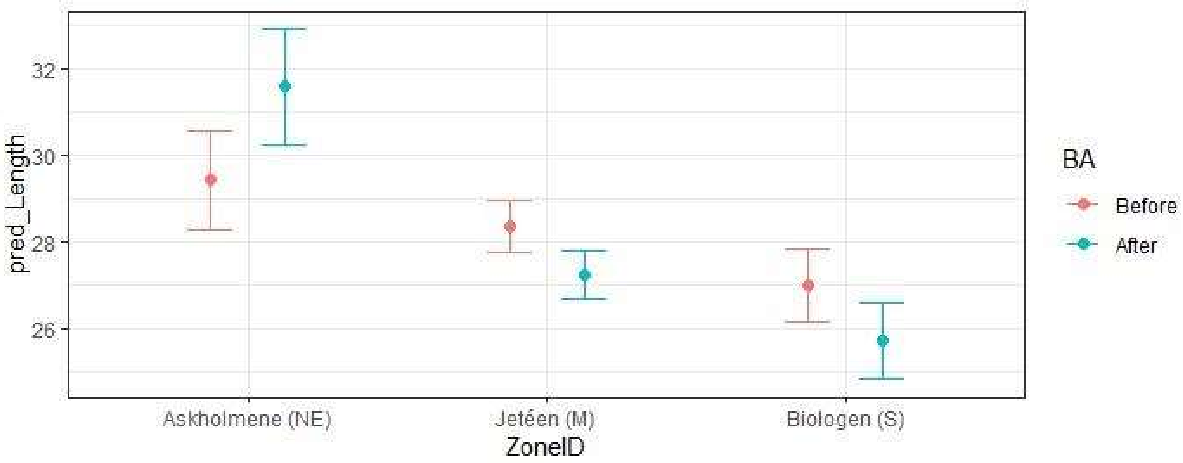

Figure 10. The effect of harvest (before and after) on predicted mean (± 95% CI) length (cm) of lobsters in the MPA (Jetéen) and harvested sites (Askholmene and Biologen) generated based on the model with the lowest AICc in table 8.

4.3 Sex ratio

More male lobsters were observed compared to females (42.8%), with males consistently outnumbering females across all the sampling years (Table 10). A total of 685 females and 914 males were encountered (including recaptures) in both the MPA and harvested areas from 2020-2023 (Table 10). The MPA had the lowest mean percentage of females (26.8%), while Biologen had the highest mean percentage of females (52.9%), the sex ratio in Askholmene was relatively similar (Table 10).

Table 10. Sex composition of lobsters that were captured at the sampling sites; Jetéen (MPA) and the control sites, Askholmene and Biologen for the sampling years 2020-2023.

Sampling site	Year	Female	Male
Jetéen	2020	21	41
	2021	60	97
	2022	149	240
	2023	188	300
Askholmene			
	2020	4	0
	2021	16	14
	2022	15	24
	2023	24	20
Biologen			
	2020	31	21
	2021	52	39
	2022	51	49
	2023	60	64

To assess the impact of protection on sex ratio, the model selection amongst candidate models fitted to only September data, favoured three models as best candidates (AICc < 2). The first included control vs MPA, before MPA vs after and the polynomial transformation of length. While the two other models were (capture site + before MPA vs after * length) and (capture site + before MPA vs after * length^2). Specifically, control vs MPA (χ^2 =11.63, p<0.001) and before MPA vs after * polynomial transformation of length (χ^2=14.93, p<0.001) were significantly associated with sex of lobsters. There was a sizeable increase in the proportion of female lobsters after the MPA was established, however this was also accompanied by a decrease in the probability to be female with increase in lobster length. The same trend was also observed in the control (Fig.11). Before the MPA was established, the model revealed a decline in the probability to be female with increase in the length of lobsters up on till the 22.5 cm length mark (Fig.11). Lobsters between 22.5-27.5cm range, had the highest likelihood to be male (Fig. 11). As lobsters become larger than 27.5cm, they had a higher likelihood to be female with the trend becoming more pronounced with increase in length. In the control the model predicted that lobsters between the 15-17.5cm range were more likely to be female with the probability decreasing with increase in length. The trend of decrease in the probability to be female continued beyond the 17.5 cm mark and being most pronounced as lobsters fall into the 22.5cm-25cm range (Fig. 11). As lobsters attain the MLS and beyond, the probability to be female increased with increase in length. After the MPA was established, there was a general trend of decrease in the probability to be female with the trend becoming less pronounced with increasing in length and resulting in an almost equal sex ratio between 25-27cm length, after 27cm, the curve levelled off after 27cm (Fig. 11).

*Table 11. Models predicting the impact of protection on the predicted sex ratio of lobsters from the polynomial transformation of length, before vs after protection, length, control vs impact and the capture site were ranked by AICc. K = number of parameters, AICc= corrected AIC statistic, ΔAICc = AICc difference, AICcWt = relative likelihood of being the "best" model, ModelLik= likelihood of the model given the data and LL=goodness of fit describes the statistical framework for model evaluation. *Length^2 = polynomial transformation of length.*

Model	**K**	**AICc**	**ΔAICc**	**ModelLik**	**AICcWt**	**LL**
Control (v MPA) +before MPA v(after) * length^2	9	1175.53	0.00	1.00	0.39	-578.66
Capture site +before MPA (v after) * length	8	1177.16	1.63	0.44	0.18	-580.50
Capture site +before MPA (v after) * length^2	10	1177.21	1.68	0.43	0.17	-578.48
Control (v MPA) *before MPA *v after) * length^2	14	1177.76	2.22	0.33	0.13	-574.64
Control (v MPA) +before MPA (v after) * Sizegroup	9	1178.42	2.89	0.24	0.09	-580.11
Before MPA (v after) * capture sites+ length	14	1182.72	7.19	0.03	0.01	-577.12
Capture sites* before MPA v (after) * length^2	20	1183.20	7.67	0.02	0.01	-571.12
Control (v MPA) *before MPA (v after) * Size group	14	1184.04	8.51	0.01	0.01	-577.78
Control (v MPA) * size group+ before MPA (v after)	9	1184.98	9.44	0.01	0.00	-583.39
Control (v MPA) + before MPA (v after) +size group	7	1185.63	10.10	0.01	0.00	-585.75
Control (v MPA) + before MPA (v after) + length^2	7	1186.14	10.60	0.01	0.00	-586.00
Before MPA (v after) +capture sites+length	7	1186.72	11.19	0.00	0.00	-586.30
Before MPA (v after) + capture sites +length	9	1187.59	12.05	0.00	0.00	-584.69
Capture sites+before MPA (v after) +length^2	8	1187.82	12.29	0.00	0.00	-585.83
Control (v MPA) * length^2	9	1188.03	12.50	0.00	0.00	-584.91
Capture sites	5	1188.29	12.76	0.00	0.00	-589.11
Before MPA (v after) + capture sites	6	1190.26	14.73	0.00	0.00	-589.08
Before MPA (v after) *capture sites	8	1192.55	17.02	0.00	0.00	-588.19
Before MPA (v after)	4	1199.17	23.64	0.00	0.00	-595.56

Table 12. Analysis of Deviance Table (Type III Wald chisquare tests), showing significance of variables from the model with the lowest AICc that predicted the effect of protection on sex ratio of lobsters.

Variable	Chisq	Df	Pr (>Chisq
Intercept	0.84	1	0.36
Control v impact	11.63	1	<0.001
Before v after	1.79	1	0.18
Polynomial transformation of lobster length	1.91	2	0.39
Before v after * polynomial transformation of length	14.93	2	<0.001

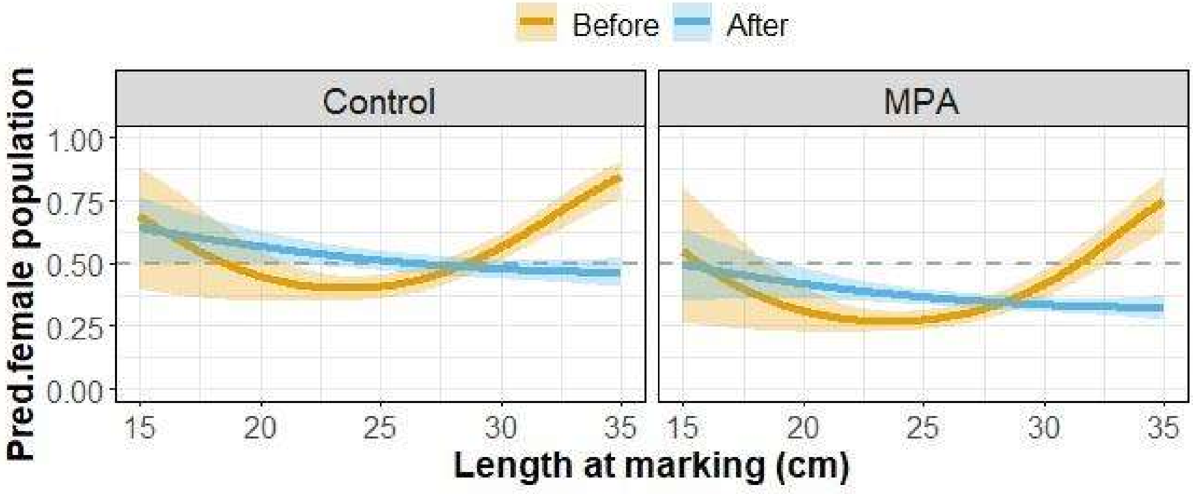

Figure 11. The effect of protection (before and after) on sex ratio in the MPA and control with the dashed line indicating an equal sex ratio and the shaded areas represent the 95% confidence interval. The prediction plot is based on the model with the lowest AICc in table 11.

To assess the impact of harvest on sex ratio, the model selection amongst candidate models fitted to data excluding 2020, favoured three models as best candidates (AICc < 2). The first model was an additive model that included control vs MPA, before harvest vs after and the polynomial transformation of length (Table 13). While the two other models were (before harvest vs after + capture site + length), (capture site + before harvest vs after + length^2 Table 13). Control vs MPA (χ^2=15.11, p<0.001), before harvest vs after (χ^2=6.21, p=0.01) were significantly associated with body length (Table 14). After harvest, there was an increased probability for lobsters in areas open to fishing to be female (Fig.12). While before harvest, there was an almost equal sex ratio in the control. A similar trend was observed in the MPA despite being closed to fishing (Fig.12).

*Table 13. Models predicting the impact of harvest on the predicted sex ratio of lobsters from the polynomial transformation of length, before vs after protection, length, control vs impact and the capture site were ranked by AICc. K = number of parameters, AICc= corrected AIC statistic, ΔAICc = AICc difference, AICcWt = relative likelihood of being the "best" model, ModelLik= likelihood of the model given the data and LL=goodness of fit describes the statistical framework for model evaluation. *Length^2 = polynomial transformation of length.*

Model	K	AICc	ΔAICc	ModelLik	AICcWt	LL
Control (v MPA) +before harvest (v after) + length^2	7	1955.58	0.00	1.00	0.32	-970.75
Before harvest (v after) +capture sites +length	7	1957.12	1.54	0.46	0.15	-971.52
Capture sites + before harvest (v after) + length^2	8	1957.17	1.59	0.45	0.15	-970.53
Capture sites + before harvest (v after) *length	8	1958.49	2.91	0.23	0.08	-971.20
Control (v MPA) +before harvest (v after) * length^2	9	1958.60	3.02	0.22	0.07	-970.24
Control (v MPA) * sizegroup+ before harvest (v after)	9	1958.69	3.11	0.21	0.07	-970.28
Control (v MPA) * length^2	9	1958.98	3.40	0.18	0.06	-970.43
Control (V MPA) + before harvest (v after) * sizegroup	9	1959.69	4.11	0.13	0.04	-970.78
Before harvest (v after) + capture site * length	9	1959.83	4.24	0.12	0.04	-970.85
Capture site + before harvest (v after) * length^2	10	1960.11	4.53	0.10	0.03	-969.98
Control (v MPA) * before harvest (v after) * sizegroup	14	1967.01	11.43	0.00	0.00	-969.36
Control (v MPA) * before harvest (v after) * length^2	14	1967.86	12.28	0.00	0.00	-969.78
Before harvest (v after) * capture sites * length	14	1968.87	13.29	0.00	0.00	-970.29
Before harvest (v after) + capture sites	6	1970.42	14.84	0.00	0.00	-979.18
Before harvest (v after) * capture sites	8	1974.38	18.80	0.00	0.00	-979.14
Capture sites	5	1975.03	19.45	0.00	0.00	-982.49
Capture sites * before harvest (v after) * length^2	20	1977.71	22.13	0.00	0.00	-968.56
Before harvest (v after)	4	1981.22	25.64	0.00	0.00	-986.60

Table 14. Analysis of Deviance Table (Type III Wald chisquare tests), showing significance of variables from the model with the lowest AICc that predicted the effect of harvest on sex ratio of lobsters.

Variable	**Chisq**	**Df**	**Pr (>Chisq)**
Intercept	2.81	1	0.09
Control (vs MPA)	15.12	1	<0.001
Before harvest (vs after)	6.21	1	0.01
Polynomial transformation of length (length^2)	2.70	2	0.26

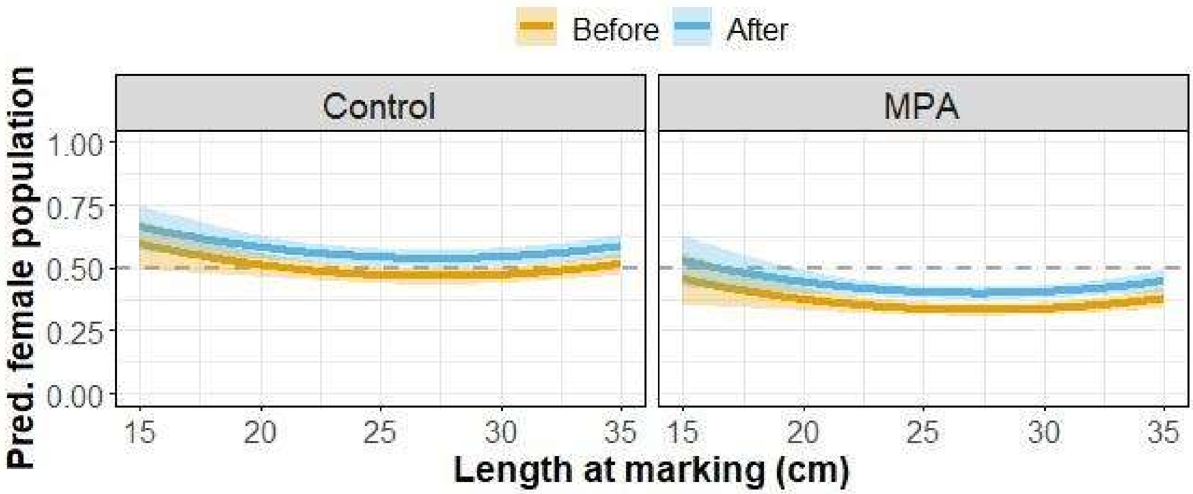

Figure 12. The effect of harvest (before and after) on sex ratio in the MPA and control with the dashed line indicating an equal sex ratio and the shaded areas representing the 95% confidence interval. The prediction plot is based on the model with the lowest AICc in table 13.

4.4 Berried lobsters

Generally, the percentage of berried lobsters in the female population was 40.6% (Table 15). The MPA had the highest number of berried females (167), but the lowest percentage (40%) of berried females compared to non-berried females in each of the zones (Table 15). The northeast zone had the smallest number of berried females with 26, but the highest percentage (44%), while the 79 berried females in the southern zone made up 41% of the female population (Table 15).

Table 15. Berried females that were encountered in the lobster population at Jetéen (MPA) and the control Askholmene and Biologen for the sampling years (2020-2024). The presence of eggs is depicted as "Yes" and absence of eggs as "No".

Sampling Site	**Year of sampling**	**Presence of eggs**	**Presence of eggs**
		Yes	No
Jetéen (MPA)			
	2020	5	16
	2021	16	44
	2022	62	87
	2023	84	104
Askholmene			
	2020	1	3
	2021	5	11
	2022	7	8
	2023	13	11
Biologen			
	2020	21	10
	2021	17	34
	2022	17	34
	2023	24	36

To assess the impact of protection on the probability of lobsters to be berried, the model selection amongst candidate models fitted to only September data, favoured four models as best candidates (AICc < 2). The model with the lowest AICc was an additive model that included before MPA vs after and the polynomial transformation of length (Table 16). While the other models were (length^2), (control vs MPA + length^2), (control vs MPA + before MPA vs after + length^2). Only the polynomial transformation of length (χ^2=19.99, p<0.0001) was significantly associated with the probability of lobsters to be berried (Table 17). Protection resulted in an increased probability of lobsters to be berried with increasing length (Fig.13). Starting from almost zero probability for the smallest lobsters and peaking at the 30-32.5 cm range (Fig.13). Beyond that range, there was a decline in the probability to be berried with increase in length (Fig.13).

*Table 16. Models predicting the impact of protection on the probability of lobsters to be berried from the polynomial transformation of length, before vs after protection, length, control vs impact and the capture site were ranked by AICc. K = number of parameters, AICc= corrected AIC statistic, ΔAICc = AICc difference, AICcWt = relative likelihood of being the "best" model, ModelLik= likelihood of the model given the data and LL=goodness of fit describes the statistical framework for model evaluation. *Length^2= polynomial transformation of length.*

Model	K	AICc	ΔAICc	ModelLik	AICcWt	LL
Before MPA (v after) + length^2	6	442.94	0.00	1.00	0.35	-215.35
Length^2	5	443.22	0.27	0.87	0.31	-216.52
Control (v MPA) + length^2	6	444.89	1.95	0.38	0.13	-216.33
Control (v MPA) +before MPA (v after) + length^2	7	444.92	1.97	0.37	0.13	-215.30
Capture sites +before MPA (v after) + length^2	8	446.68	3.74	0.15	0.05	-215.14
Control (v MPA) * length^2	9	448.68	5.74	0.06	0.02	-215.09
Control (v MPA) +before MPA (v after) +size group	7	453.56	10.62	0.01	0.00	-219.62
Control (v MPA) * sizegroup +before MPA (v after)	9	455.82	12.88	0.00	0.00	-218.65
Before MPA (v after) + capture sites +length	7	455.88	12.94	0.00	0.00	-220.78
Control (v MPA) * before MPA (v after) * size group	14	456.75	13.80	0.00	0.00	-213.77
Capture sites +before MPA (v after) * length	8	457.03	14.09	0.00	0.00	-220.31
Control (v MPA) +before MPA (v after) * size group	9	457.36	14.42	0.00	0.00	-219.43
Before MPA (v after) + capture sites + length	9	459.73	16.79	0.00	0.00	-220.61
Before MPA (v after) * capture sites * length	14	463.31	20.36	0.00	0.00	-217.04
Before MPA (v after)	4	467.60	24.66	0.00	0.00	-229.75
Control (v MPA) * before MPA (v after)	6	469.96	27.02	0.00	0.00	-228.86
Before MPA (v after) + capture sites	6	470.99	28.05	0.00	0.00	-229.38
Capture sites	5	471.13	28.19	0.00	0.00	-230.48
Before MPA (v after) * capture sites	8	472.07	29.13	0.00	0.00	-227.83

Table 17. Analysis of Deviance Table (Type III Wald chisquare tests), showing significance of variables from the model with the lowest AICc that predicted the effect of protection on the probability of lobsters to be berried.

Variable	**Chisq**	**Df**	**Pr (>Chisq)**
Intercept	15.12	1	<0.001
Before MPA (vs after)	2.25	1	0.13
Polynomial transformation of length (length^2)	19.99	2	<0.0001

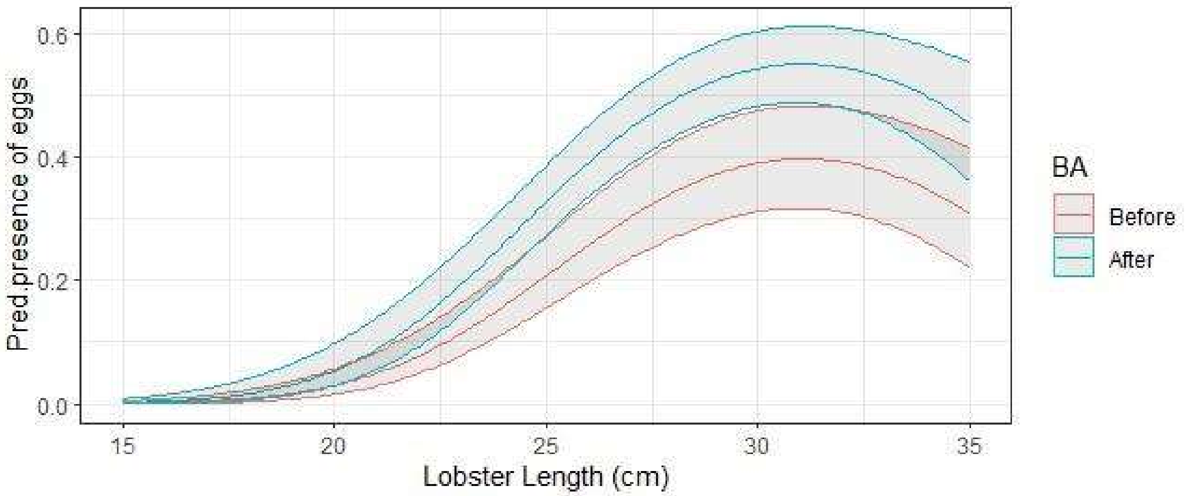

Figure 13. The effect of protection (before and after) on the probability of lobsters to be berried, with the shaded areas representing the 95% confidence interval. The prediction plot is based on the model with the lowest AICc in table 16.

To assess the impact of harvest on the probability of lobsters to be berried, the model selection amongst candidate models fitted to data excluding 2020, favoured two models as best candidates (AICc < 2). The first model was an additive model that included control vs MPA, before harvest vs after and the polynomial transformation of length, while the other model was (capture site + before harvest vs after + length^2 Table 18). Only the polynomial transformation of length (χ^2=154.15, p<0.0001) was significantly associated with the probability of lobsters to be berried (Table 19). Harvesting resulted in an increased probability to be berried with increase in length (Fig.14). This probability peaked when lobsters where between the 27.5-30 cm range, declining with increasing length thereafter (Fig.14).

*Table 18. Models predicting the impact of harvest on the probability of lobsters to be berried from the polynomial transformation of length, before vs after protection, length, control vs impact and the capture site were ranked by AICc. K = number of parameters, AICc= corrected AIC statistic, ΔAICc = AICc difference, AICcWt = relative likelihood of being the "best" model, ModelLik= likelihood of the model given the data and LL=goodness of fit describes the statistical framework for model evaluation. *Length^2 = polynomial transformation of length.*

Model	**K**	**AICc**	**ΔAICc**	**ModelLik**	**AICcWt**	**LL**
Control v (MPA) +before harvest (v after) +length^2	7.00	784.03	0.00	1.00	0.55	-384.92
Capture site +before harvest (v after) + length^2	8.00	785.05	1.02	0.60	0.33	-384.41
Control (v MPA) * length^2	9.00	787.88	3.85	0.15	0.08	-384.79
Control (v MPA) * before harvest (v after) * size group	14.00	789.12	5.09	0.08	0.04	-380.20
Control (v MPA) +before harvest (v after) * size group	9.00	796.17	12.14	0.00	0.00	-388.93
Control (v MPA) + before v after + size group	7.00	797.75	13.72	0.00	0.00	-391.78
Capture sites +before harvest (v after) * length	8.00	801.26	17.24	0.00	0.00	-392.51
Before harvest (v after) * capture site * length	14.00	801.31	17.28	0.00	0.00	-386.30
Control (v MPA) * size group + before harvest (v after)	9.00	801.43	17.40	0.00	0.00	-391.56
Before harvest (v after) + capture sites +length	7.00	805.54	21.52	0.00	0.00	-395.68
Before harvest (v after) + capture sites *length	9.00	809.53	25.50	0.00	0.00	-395.61
Before harvest (v after) * capture site	8.00	810.46	26.43	0.00	0.00	-397.11
Before harvest (v after)	4.00	814.15	30.12	0.00	0.00	-403.04
Capture sites	5.00	815.20	31.17	0.00	0.00	-402.55
Before harvest (v after) + capture site	6.00	817.12	33.09	0.00	0.00	-402.49

Table 19. Analysis of Deviance Table (Type III Wald chisquare tests), showing significance of variables from the model with the lowest AICc that predicted the impact of harvest on the probability of lobsters to be berried.

Predictor	**Chisq**	**Df**	**Pr (>Chisq)**
Intercept	135.89	1	<0.0001
Control (vs MPA)	0.37	1	0.54
Before harvest (vs after)	0.17	1	0.68
Polynomial transformation of length (length^2)	154.15	2	<0.0001

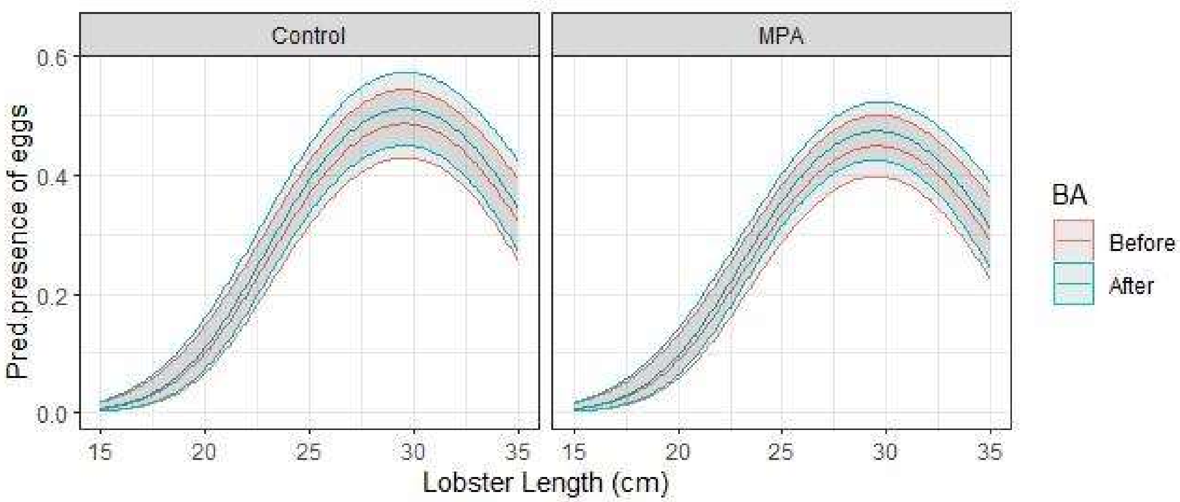

Figure 14. The effect of harvest (before and after) on the probability of lobsters to be berried in the MPA and control with the shaded areas represent the 95% confidence interval. The prediction plot is based on the model with the lowest AICc in table 18.

4.5 The probability of lobsters to be legal-sized

On average, 62.8% of encountered lobsters were legal sized with more legal sized males (59.8%) encountered than females (Table 20). For instance, on average, there were more legal-sized males in the MPA (63.6%) and Askholmene (53.2%), while in the Biologen legal sized females (53.6%) outnumbered males (Table 20). Generally, in all the 3 sampling sites, legal sized lobsters made up at least half of the total population, with the protected area having the highest proportion of 72% (Table 20).

Table 20. Size-group distribution of female and male lobsters that were captured at the sampling sites; Jetéen (the MPA), Askholmene and biologen. The size ranges are described as Small= lobsters <25 cm, Legal-sized = lobsters between 25-32 cm, Large= lobsters > 32 cm.

Sampling site	Size-group	Females	Males
MPA			
	Small	92	123
	Legal-sized	285	499
	Large	35	54
Askholmene			
	Small	5	5
	Legal-sized	29	33
	Large	24	19
Biologen			
	Small	61	67
	Legal-sized	104	90
	Large	29	16

To assess the impact of protection on the probability of lobsters to be legal-sized, the model selection amongst candidate models fitted to only September data, favoured four models as best candidates (AICc < 2). The model with the lowest AICc was an additive model that included control vs MPA, before MPA vs after and sex (Table 21). The other models were (control vs MPA + before MPA vs after + sex), (before MPA vs after + capture site), (control vs MPA + sex + before MPA vs after). Control vs MPA (χ^2=11.55, p<0.001), before MPA vs after (χ^2= 6.43, p=0.01) were significantly associated with the probability of lobsters to be berried (Table 22). Protection resulted in a general increase in the probability of lobsters in both the MPA and control to fall into the legal-size category after the MPA was established, however the increase was more in the MPA (Fig.15).

Table 21. Models predicting the impact of protection on the probability of lobsters to be legal sized from before vs after protection, sex, control vs impact and the capture site were ranked by AICc. K = number of parameters, AICc= corrected AIC statistic, ΔAICc = AICc difference, AICcWt = relative likelihood of being the "best" model, ModelLik= likelihood of the model given the data and LL=goodness of fit describes the statistical framework for model evaluation.

Model names	K	AICc	ΔAICc	ModelLik	AICcWt	LL
Control +v (MPA) + before MPA (v after) + female (v male)	6	1134.56	0.00	1.00	0.26	-561.23
Control (v MPA) + before MPA (v after) * female (v male)	7	1135.63	1.07	0.59	0.15	-560.75
Before MPA (v after) +capture sites	6	1136.09	1.53	0.47	0.12	-562.00
Control (v MPA) * female (v male) +before MPA (v after)	7	1136.15	1.59	0.45	0.12	-561.01
Before MPA (v after) +capture sites + female (v male)	7	1136.59	2.03	0.36	0.09	-561.23
Capture sites +before MPA (v after) + female (v male)	7	1136.59	2.03	0.36	0.09	-561.23
Capture sites +before MPA (v after) * female (v male)	8	1137.66	3.10	0.21	0.06	-560.75
Before MPA (v after) * capture sites	8	1137.81	3.25	0.20	0.05	-560.82
Before MPA (v after) + capture site * female (v male)	9	1139.75	5.19	0.08	0.02	-560.77
Control (v MPA) * before MPA (v after) * female (v male)	10	1140.03	5.47	0.07	0.02	-559.89
Capture sites	5	1140.23	5.67	0.06	0.02	-565.08
Before MPA (v after)	4	1142.78	8.22	0.02	0.00	-567.37
Before MPA (v after) * capture sites * female (v male)	14	1145.60	11.04	0.00	0.00	-558.56

Table 22. Analysis of Deviance Table (Type III Wald chisquare tests), showing significance of variables from the model with the lowest AICc that predicted the impact of protection on the probability of lobsters to be legal-sized.

Predictor	Chisq	Df	Pr (>Chisq)
Intercept	2.95	1	0.086
Control (vs MPA)	11.55	1	<0.001
Before MPA (vs after)	6.44	1	0.01
Female (vs male)	1.55	1	0.21

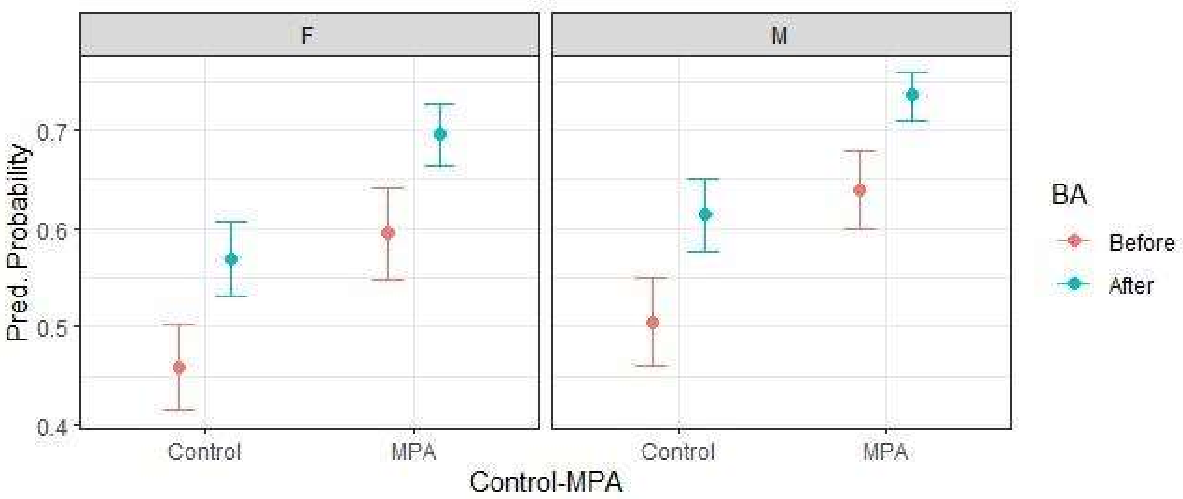

Figure 15. The effect of protection (before and after) on predicted (± 95% CI) probability of female and male lobsters in the MPA and control meeting the legal-size requirement for harvest. The prediction plot is based on the model with the lowest AICc in table 21.

To assess the impact of harvest on the probability of lobsters to be legal sized, the model selection amongst candidate models fitted to data excluding 2020, favoured two models as best candidates (AICc < 2). The first model was an additive model that included control vs MPA, before harvest vs after and sex (Table 23), while the second model only contained capture site. Only control vs MPA (χ^2=34.96, p<0.0001) was significantly associated with the probability of lobsters to be legal-sized (Table 24). Harvesting resulted in lobsters in the MPA having a higher probability to be legal-sized than lobsters in the control (Fig.16)

Table 23. Models predicting the impact of harvest on the probability of lobsters to be legal sized from before vs after protection, sex, control vs impact and the capture site were ranked by AICc. K = number of parameters, AICc= corrected AIC statistic, ΔAICc = AICc difference, AICcWt = relative likelihood of being the "best" model, ModelLik= likelihood of the model given the data and LL=goodness of fit describes the statistical framework for model evaluation.

Model	K	AICc	ΔAICc	ModelLik	AICcWt	LL
Control (v MPA) +before harvest (v after) + female (v male)	7	1798.15	0.00	1.00	0.30	-892.03
Capture sites	5	1799.88	1.74	0.42	0.12	-894.92
Before harvest (v after) +capture sites +female (v male)	8	1800.16	2.02	0.36	0.11	-892.03
Capture sites +before MPA (v after) + female (v male)	8	1800.16	2.02	0.36	0.11	-892.03
Control (v MPA) + before harvest (v after) * female (v male)	9	1800.71	2.56	0.28	0.08	-891.29
Control (v MPA) * female (v male) +before harvest (v after)	9	1800.84	2.70	0.26	0.08	-891.36
Before harvest (v after) + capture sites	6	1801.89	3.74	0.15	0.05	-894.92
Before harvest (v after) *capture sites	8	1802.53	4.39	0.11	0.03	-893.22
Capture sites +before harvest (v after) * female (v male)	10	1802.73	4.59	0.10	0.03	-891.29
Before harvest (v after) + capture sites * female (v male)	12	1803.29	5.14	0.08	0.02	-889.54
Control (v MPA) * before harvest (v after) * female (v male)	13	1803.40	5.26	0.07	0.02	-888.58
Capture sites * before harvest (v after) * female (v male)	17	1810.31	12.16	0.00	0.00	-887.94
Before harvest (v after) * capture sites * female (v male)	17	1810.31	12.16	0.00	0.00	-887.94
Before harvest (v after)	4	1827.89	29.74	0.00	0.00	-909.93

Table 24. Analysis of Deviance Table (Type III Wald chisquare tests), showing significance of variables from the model with the lowest AICc that predicted the impact of harvest on the probability of lobsters to be legal-sized.

Predictor	Chisq	Df	Pr (>Chisq)
Intercept	2.88	1	0.09
Control (vs MPA)	34.96	1	<0.0001
Before harvest (vs after)	0.0003	1	0.99
Female (vs male)	4.59	2	0.10

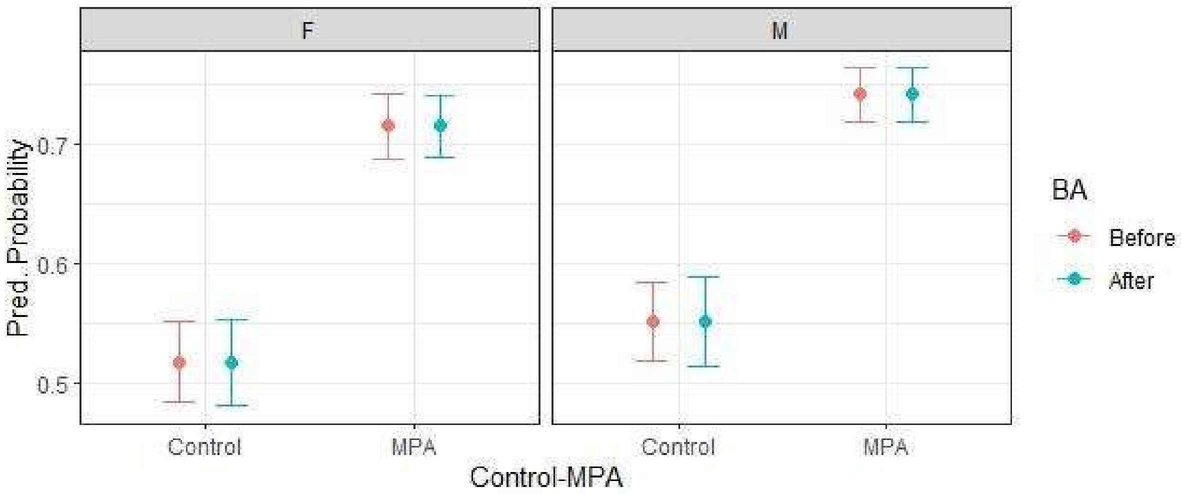

Figure 16. The effect of harvest (before and after) on predicted (± 95% CI) probability of lobsters in the MPA and control meeting the legal-size requirement for harvest. The prediction plot is based on the model with the lowest AICc in table 23.

5 Discussion

Using a BACI design, the examination of the impact of protection and harvesting on the lobster population in this study enabled the quantification of the short-term impact of fishing effort and the potentially long-term impact of protection on lobster population parameters such as CPUE, sex ratio, body length, the proportion of legal sized lobsters and berried lobsters. The two-year absence of fishing pressure in the MPA has led to an increase in lobster CPUE, mean length, and an increased proportion of females in the MPA. Importantly, there was notable differences in the rate of response of the protected male and female population parameters such as lobster CPUE and mean length with males responding more positively compared to females.

5.1 CPUE

As hypothesized, the cessation of fishing mortality in the MPA resulted in an increase in lobster density in the MPA compared to the control. An increase in lobster CPUE after the establishment of MPA has also been reported in previous studies in MPAs of different size (Kvernskjær (50 ha), Flødevigen (100 ha) and Bolærne (278)) and after four (Moland et al., 2013) to 14 years (Sørdalen et al., 2022a) since establishment. The increase in CPUE is likely due to the elimination of harvest induced mortality in the MPA due to the implementation of full protection measures. The difference in CPUE between the MPA and control after the establishment of the MPA may further support the concept of lobster residency within the MPAs. This means that a small sized MPA might be effective in lobster conservation. Regarding the sex differences in lobster protection within the MPA, males exhibited a more positive response compared to females. The reasons behind this disparity remain uncertain, especially considering that male CPUE was higher than female CPUE even before MPA establishment, despite existing sex-biased regulations aimed at providing more protection to females. Although I did not explore survival probabilities, however, if increased survival chances correlates with greater CPUE, then this findings are contrary to a previous survival analysis of lobsters where protected females were reported to have had higher survival rates than protected males (Fernández-Chacón et al., 2021). Another explanation for the observed lower CPUE in females may be associated with lower detectability (Fernández-Chacón et al., 2021), since female are less active during brooding periods (and thus catchability decrease) and are also more risk adverse compared to males (Moland et al., 2019).

Harvesting clearly affected lobster CPUE, with a marked decrease from pre- to post-harvest in the harvested areas while there was an increase in CPUE in the MPA. Here also, the sex-biased regulations did not seem to confer special advantage to females, especially in Biologen where the rate of the post-harvest decline was slightly more distinct in females.

5.2 Body length

As expected, there was an increase in mean length following the establishment of MPA, as also reported in previous studies (Fernández-Chacón et al., 2020; Moland et al., 2013; Thorbjørnsen et al., 2018) although those studies were conducted 4-9 years after the establishment of the MPA. There was a noticeable difference in mean length response between male and female lobsters in the MPA, with male mean length increasing at twice the rate of females. The exact cause of this difference is uncertain, however, protected legal-sized males were found to have a faster growth rate than similarly sized females in the MPA (Sørdalen et al., 2022b). It is plausible that higher feeding activity in males, driven by their riskier behaviour (Moland et al., 2019) led to higher growth rates. It's worth noting that without protection, such behaviour could have increased male vulnerability to trap capture (Moland et al., 2019). Therefore, the prohibition of fishing traps in the MPA ensured that male lobsters can engaged in high feeding activity without facing detrimental consequences. Also, the size disparity post MPA establishment favouring males may potentially strengthen sexual selection in the MPA since larger males are preferred by larger females but were also targeted for harvesting (Sørdalen et al., 2018).

There was a post-harvest increase in mean length of lobsters in Askholmene despite fishing pressure. A plausible explanation for this increase could be that lobsters in Askholmene were majorly above the legal-size limit which exempted them from being harvested. While in Biologen, the post-harvest decrease in mean length could be linked to a sizeable portion of the population meeting the legal-size requirement for harvest, meaning that more lobster will be lost to harvest mortality with the subsequent decrease in mean length. I can only speculate that the larger size of Askholmene compared to Biologen might have led to lower catchability. Moland et al. (2019) suggested that less dominant lobsters with larger home ranges could be less susceptible to baiting. Alternatively, I speculate that the opposite happened in Biologen, where the smaller area size may have increased the risk of lobsters being baited in traps. Further, despite being closed to fishing, mean length in the MPA decreased after the harvest seasons. Although data concerning movement between MPA and control is lacking, I speculate, that this could be attributed to movement of larger individuals to nearby fished areas. Thorbjørnsen et al. (2018) reported that lobsters leaving the MPA to the fished areas were larger than those moving from the control area, potentially leading to a decrease in mean length without necessarily reducing abundance. However, since the potential for spillover nor movement of pattern of lobsters was investigated in this study, this interpretation should be taken with caution. Additionally, the timeframe of this study might be too limited to detect density-dependent migration patterns.

5.3 Sex ratio

My expectation of an even sex ratio in the MPA due to protection was not fully supported, although there was a sizeable increase in the proportion of female lobsters after the MPA was established, this was also accompanied by a decrease in the probability to be female with increase in lobster length. Notably, sex ratio of lobsters above 27 cm changed to favour males post-MPA establishment. The reversal in trend might be the result of full protection leading to a better survival of legal-sized males. While the same trend was observed in the control despite sex-biased regulations that observed that favours females, I speculate that it might be the result of movement of large sized females away from the control. Thorbjørnsen et al. (2018) reported that 60% of lobsters migrating from control areas to the MPA were female and were larger than those in the controL. However, since a similar trend was observed in the MPA and because migration patterns were not investigated, this explanation should be treated with caution.

As for how sex ratio was changed due to the impact of harvest, the increase in the probability to be female observed after harvest in the control was expected. Females are more protected and there is also report of a very high mortality (80%) of male lobsters after the harvest season (Wiig et al., 2013).

5.4 Berried lobsters

The increase in reproductive capabilities (number of berried lobsters) with increasing size found in this study is supported by previous studies (Agnalt, 2007; E. Moland et al., 2010; Tully et al., 2001). Notable, however is the decline in the probability to be berried after attaining the maximum legal size, i.e., as the size confers protection on lobsters irrespective of location or ovigerous status. It is uncertain if this decline is representative of a diminished reproductive capability as lobsters grow older since Sheehy et al. (1999) reported that the oldest females in a sample of wild caught lobsters were unberried. However, this should be treated with caution since lobster length is not necessarily a good predictor of age. Sheehy et al. (1999) suggested that age and length of lobsters do not always follow a linear pattern, with reports of large, but comparatively young lobsters and older but comparatively small sized lobsters. However, they also noted that the variations in such age-length relationship was more noticeable in younger than older lobsters.

Harvesting resulted in lobsters reaching peak likelihood of being berried at 27.5-30 cm, however this comes with the likelihood of having less eggs as larger and older lobsters are able to release eggs in successive seasons without undergoing a moulting process between each spawning event (Agnalt, 2007; Waddy & Aiken, 1986), but see (Comeau & Savoie, 2002). It is uncertain if this earlier peak in the probability to be berried is a strategy for lobsters to reproduce earlier in order to remain within the realms of protection that their two year reproductive cycle confers on them (Agnalt, 2007). This may suggest the potential for a trade-off in life-history strategies between growth and reproduction, where females are more inclined to reproduce than grow (Sørdalen et al., 2022b). However, this trade-off might impact negatively on lobster stock in the future. Moland et al. (2010) suggested a positive correlation between offspring size and maternal size, where large mothers produce better "quality" eggs, ultimately impacting on larval quality and recruitment.

5.5 Probability to be legal-sized

The general increase in the probability for lobsters to be legal sized after full protection measures was implemented in the MPA was as expected. This might be related to the elimination of harvest induced mortality, resulting in the better survival of legal-sized lobsters. There is also previous studies reporting an increase in the proportion of legal size lobsters after the establishment of the MPA (Fernández-Chacón et al., 2020). However, the substantial increase recorded in the control despite being open to fishing was surprising, since the presence of fishing mortality should have resulted in a decrease in the probability to be legal-sized. Wiig et al. (2013) reported mortality as high as 80% for legal males during a fishing season. However, I speculate that this might not be unconnected with the moderate rise in CPUE reported earlier. Permissible traps for lobster harvest are built to prevent the entrapment of small-sized lobsters or to facilitate their escape if trapped (Wiig et al., 2013). It is likely that this regulation boosted the survival of small sized lobsters allowing their transition into the legal-sized range.

Harvesting resulting in lobsters in areas open to fishing having a lower probability to be legal sized compared to those in the MPA was as expected. The absence of fishing pressure will most likely mean protected lobsters have a higher chance of attaining the legal-size requirement for harvest, compared to those in the areas open to harvesting.

6 Conclusion

This study indicated a rise in lobster CPUE, body length, and the possibility of a balanced sex ratio in the MPA, despite the short duration since full protective measures were put in place. Thus, there are some evidence for the effectiveness of a small-scale MPA in restoring a depleted lobster population. The MPA in Drøbaksundet is still in its early years, therefore continuous monitoring of both the MPA and control areas is crucial to facilitate a more comprehensive scientific assessment of its efficacy on the long term. This knowledge will inform future management decisions regarding the establishment of similar-sized MPAs (<100 ha) in other regions, and it will also aid in making any necessary adjustments to meet management objectives as required.

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