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Effect of marine protected areas on female size and estimated fecundity after two decades in European lobster (*Homarus gammarus*).

Master's thesis in Natural Science with Teacher Education
Supervisor: Trond Amundsen
Co-supervisor: Even Moland and Tonje Knutsen Sørдалen
June 2024



Norwegian University of
Science and Technology



INSTITUTE OF MARINE RESEARCH

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Preface

This thesis was carried out and funded as part of the long-term monitoring programme on lobster populations in Skagerrak by the Institute of Marine Research (IMR). It is part of the 5-year MLREAL program at the Norwegian University of Science and Technology in Trondheim. Throughout this process I have gained knowledge in academic writing, fieldwork, and data analysis. These are all important parts of the teacher profession and in the field of natural science. Specifically, gaining information on the effects of conservation for marine biodiversity is directly linked to the UNs 2030 Agenda for Sustainable Development, Goal number 14 "Conserve and sustainably use the oceans, seas and marine resources for sustainable development" (United Nations, 2015). Protection versus use of resources is a frequent dilemma regarding sustainable use of nature. As values and attitudes starts forming at young ages, different perspectives and evidence should be presented and discussed in school.

I would like to send my deepest gratitude to my supervisors Trond Amundsen (NTNU), Even Moland (IMR) and Tonje Knutsen Sjørdalen (UiA & IMR) for giving me feedback, support, and helping me with ideas and questions to my thesis. I have learnt a lot from our interesting discussions and conversations and would not have managed this without your help. I would also like to thank Even Moland and the staff at the Institute of Marine Research in Flødevigen specifically for letting me take part in the lobster survey and field work. It has been a pleasure to get an insight into your impressive and admirable work of creating knowledge and take care of the ocean that we all rely on. A big thank you also goes to Christophe Pélabon, Ivain Martinossi-Allibert, Agnes Holstad and Maria Aasdalen for great discussions and help with challenges regarding data analysis. Lastly, a special gratitude to my boyfriend, family, and friends for supporting me through this work, listening patiently to all my ideas and discussing dilemmas. This process would not have been the same without your encouragement.

Abstract

Marine resources are in many cases not sustainably managed, and many species are overexploited. Marine protected areas (MPAs) are management tools well documented to have good effects on rebuilding populations, manage fisheries and reversing harvest selection effects. Fecundity is found to increase in protected populations, but information comparing MPAs and fished areas is restricted. Here, I present almost two decades of mean individual egg carrying capacity of sexually mature female European lobsters (*Homarus gammarus*), comparing three MPAs and fished control areas in Southern Norway. Additionally, a highly selective fishing pressure is suggested to select for females allocating energy to reproduction instead of growth. Therefore, I wanted to investigate if abdominal broadening, to increase the area available for egg attachment, happens at a relatively larger lobster length when the highly selective fishing pressure is removed. Fecundity models based on abdominal width and carapace length developed by Agnalt (2008) were employed to calculate egg carrying capacity, while linear models were used for the size analysis. From 2007 to 2023 mean individual egg carrying capacity increased with 75% in MPAs, with a steady increase from year to year. Despite restrictions in harvest regulations, adjacent fished control areas experienced only a small increase of 14%. In all areas, increased egg carrying capacity was a response to increased mean female sizes. However, in 2023 females inside MPAs had approximately 20% broader abdomen and 15% larger body length than in adjacent fished control areas. This is due to being allowed to grow larger and older, and thereby create a wider size distribution. This was translated into a 44-78% higher mean individual egg carrying capacity than adjacent fished areas. There was found a weak tendency of females in MPAs having a relatively smaller abdominal width to body length. This was mostly driven by the largest females in the MPAs, as no differences were found when restricting the comparison to overlapping size ranges. Increased egg carrying capacity and female size together with a wider size distribution give more evidence into MPAs being useful management tools to rebuild and protect a heavily exploited long-lived species.

Sammendrag

Marine ressurser forvaltes i mange tilfeller ikke bærekraftig, og mange arter er overutnyttet. Marine verneområder (MPA) er forvaltningsverktøy godt dokumentert å ha gode effekter på gjenoppbygging av bestander, forvaltning av fiskerier og reversering av effekter knyttet til høstingsdrevet seleksjon. Fekunditet er funnet å øke i beskyttede populasjoner, men informasjon som sammenligner verneområder og fiskede områder er begrenset. Her presenterer jeg nesten to tiår med gjennomsnittlig individuell eggkapasitet hos kjønnsmodne europeiske hummerhunner (*Homarus gammarus*) som sammenligner tre verneområder og fiskede kontrollområder i Sør-Norge. I tillegg foreslås det at et høyt selektivt fisketrykk selekterer for hunner som tildeler energi til reproduksjon i stedet for vekst. Derfor undersøkte jeg om utvidelse av buken for å øke arealet tilgjengelig for å feste egg, skjer ved en relativt større hummerlengde når det høye selektive fisketrykket fjernes. Fekunditetsmodeller basert på bukbredde og ryggskjoldlengde utviklet av Agnalt (2008) ble benyttet for å beregne eggkapasitet, mens lineære modeller ble brukt til størrelsesanalysen. Fra 2007 til 2023 økte gjennomsnittlig individuell eggkapasitet med 75% i verneområder, med en jevn økning fra år til år. Til tross for restriksjoner i høstingsforskriftene opplevde tilstøtende kontrollområder kun en liten økning på 14%. Økt eggkapasitet var et resultat av økt gjennomsnittsstørrelse på hunnene i alle områder. I 2023 hadde imidlertid hunner i verneområder omtrent 20% bredere buk og 15% større kroppslengde enn i tilstøtende fiskede kontrollområder. Dette er ettersom de har mulighet til å vokse seg større og eldre, og dermed danne en bredere størrelsesfordeling. Dette ble overført til 44-78% større gjennomsnittlig individuell eggkapasitet enn i tilgrensende fiskede områder. Det ble funnet en svak tendens av at bukutvidelse skjedde ved en relativt større hummerlengde i verneområder. Dette ble for det meste drevet av de største hunnene i verneområdene, da det ikke ble funnet forskjeller ved begrensning av sammenlikningen til overlappende størrelser. Økt eggkapasitet og hunnstørrelse sammen med en bredere størrelsesfordeling gir mer belegg for at verneområder kan være nyttige styringsverktøy for å gjenoppbygge og beskytte en tungt utnyttet langlivet art.

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1 Introduction

Marine ecosystems are under pressure with an increasing number of stressors such as overfishing, pollution, climate change, ocean acidification, habitat destruction, and aquaculture (FAO, 2022; IPBES, 2019; Pörtner et al., 2021). In 2020, the Food and Agriculture Organization of the United Nations (FAO, 2022) reported that fisheries and aquaculture production supplied the human population with 214 million tonnes of aquatic food in total, and the consumption of aquatic food has more than doubled per capita since the 1960s. Industrial fishing takes place in at least 55% of the oceans' areas (IPBES, 2019). As a result of the high pressure, ecosystems are changing, and marine fish stocks are declining, with about 33% classified as overexploited (IPBES, 2019). Fishing is often selective of large individuals, which might lead to a population with slower growing individuals, and may influence evolution if the traits are heritable (Boukal et al., 2008; Heino et al., 2015; Law, 2007; Moland et al., 2019; Sørvalen et al., 2022).

1.1 Marine protected areas as management tools

Fisheries management is crucial but often lacking or insufficient to conserve populations due to for instance big gaps between intent and practice, economic interests, or lack of including other stakeholders (Cullis-Suzuki & Pauly, 2010; Dankel et al., 2008).

Management may also be implemented too late for stocks to be able to rebuild (Olsen et al., 2004). Marine protected areas (MPAs) are management tools for biodiversity conservation and are defined by IUCN as "Any area of intertidal or subtidal terrain, together with its overlying water and associated flora, fauna, historical and cultural features, which has been reserved by law or other effective means to protect part or all of the enclosed environment" (Kelleher, 1999). What kind of MPA, size and protection level are incorporated, depends among other factors on other interests in the area and the protection target.

Protection allows the study of population and ecological responses when an area is undisturbed, especially when compared to control sites where the disturbance is not removed. Implementation of MPAs has been shown to have positive effects on rebuilding populations by increasing density, average size, species richness, and biomass of the targeted species within the MPA in fish, algae, and invertebrates (Babcock et al., 2007; Díaz et al., 2016; Howarth et al., 2017; Kraufvelin et al., 2023; Lester et al., 2009; Moland et al., 2013; Sciberras et al., 2013). Increased body size of species protected in MPAs has several important effects. Size and age is known to confer benefits on fecundity and the viability of the offspring, and a wide size and age distribution increase variation, and thereby resilience against stressors (Bobko & Berkeley, 2004; Planque et al., 2010). This is found for instance in black rockfish *Sebastes melanops* (Berkeley et al., 2004; Bobko & Berkeley, 2004) and Atlantic cod *Gadus morhua* (Marteinsdottir & Begg, 2002; Marteinsdottir & Steinarsson, 1998; Roney et al., 2018). Large and old individuals were found to be more fecund and produce larvae with better quality. This was translated into higher survival potential than larvae from smaller fish (Berkeley et al., 2004; Bobko & Berkeley, 2004). Large body size in Atlantic cod can also play an important role in connecting spawning habitats as they move further with increasing size (Olsen et al., 2023).

There is often conflict between fisheries and other stakeholders' interests and the biological and conservation approach. Therefore, interests are increasing for evidence that protection can lead to increased supply to the fisheries. This happens due to spill-over effects (migration) from the MPAs to adjacent fished areas (Kerwath et al., 2013; Roberts et al., 2005). Studies have demonstrated that over time, MPAs benefit the fishery of depleted species such as roman *Chrysoblephus laticeps* (Kerwath et al., 2013) and white shrimp *Litopenaeus occidentalis* (Cuervo-Sánchez et al., 2018) due to increased abundance and spill-over. In 2020, New Zealand's most productive lobster fishery was due to the protection of large areas spanning 46 000 hectares (New Zealand Fisheries, 2020; Starr, 2019). This protection led to notable enhancement in commercial catch per unit effort (CPUE) and total allowable commercial catch of the red rock lobster *Jasus edwardsii* (New Zealand Fisheries, 2020; Starr, 2019).

1.2 Lobster fisheries and protection effects

Fisheries of crustaceans are increasing faster than other fisheries globally (Anderson et al., 2011; Boenish et al., 2022). It is suggested that 18, 21 and 13% of invertebrate fisheries are fully exploited, over-exploited/restrictively managed and collapsed/closed, respectively (Anderson et al., 2011). An example of a species of high commercial interest is the European lobster (*Homarus gammarus*) (hereafter, lobster), which is distributed from northern Norway to Morocco (Triantafyllidis et al., 2005). Fisheries for lobster in southern Norway go back to the 1660s (Knutsen et al., 2009). The fishing pressure has been high over time which resulted in historically low populations in the start of the 21st century (Moland et al., 2021; Varpe et al., 2005). According to the International Union for Conservation of Nature (IUCN) criteria, the species is now categorised as vulnerable (VU) on the Norwegian red list (Tandberg et al., 2021). This has been a negative development since 2010 when it was listed as near threatened (NT) (Tandberg et al., 2021).

The first lobster reserves in Norway were implemented in 2006 (Pettersen et al., 2009). Despite the small size of the reserves, they showed rapid benefits, which have led to 64 reserves along the Norwegian coast today (Forskrift om fredningsområder for hummer, 2006; Knutsen et al., 2022; Moland et al., 2013). Using a control versus no take study design (before-after-control-impact; BACI), several effects of protection have been found in the lobster including increased sizes and abundance (Fernández-Chacón et al., 2020; Knutsen et al., 2022; Moland et al., 2013). Fisheries have been shown to selectively remove big male lobsters with big claws which are important traits for sexual selection and competition (Moland et al., 2019; Sørvalen et al., 2020). A study found that males with large claw size (relative to body size) are preferred by females as mating partners and large claw size is under sexual selection (Sørvalen et al., 2018). It has also been found that lobsters in MPAs grow faster and moult more frequently than in fished areas (Sørvalen et al., 2022).

1.3 Lobster fecundity

Fecundity is a measure of the total number of offspring produced by an individual or a population's reproductive potential (Bradshaw & McMahon, 2008). There is ample evidence in the literature that MPAs increase the fecundity in several targeted species due to increased size and abundance. Examples are the population productivity of the tropical reef fish *Lutjanus carponotatus* (Evans et al., 2008), and the spiny lobsters *Panulirus cygnus* (Babcock et al., 2007) and *Jasus edwardsii* (Jack & Wing, 2010).

Increases have also been found in individual fecundity of the spiny lobster *Palinurus elephas* (Díaz et al., 2011; Goñi et al., 2003) and tropical coral trout grouper *Plectropomus leopardus* (Carter et al., 2014).

Methods for quantifying the egg carrying capacity of European lobsters are well established (Agnalt, 2008; Agnalt et al., 2007; Coleman et al., 2019; Ellis et al., 2015; Howarth et al., 2017; Tully et al., 2001). However, studies comparing the egg carrying capacity in MPAs and fished areas is still limited. In MPAs in Scotland, Denmark, and Norway, individual egg carrying capacity of females was higher compared to fished areas (Calef, 2016; Freitas et al., 2023; Howarth et al., 2017). Calef (2016) estimated mean individual egg carrying capacity in three MPAs and control areas in Skagerrak from 2006 to 2015. It increased with 160% and 12% in MPAs and control areas, respectively. However, estimates included females of all sizes, also under the size of maturation. Hence, individual egg carrying capacity for mature females in these areas have not been estimated.

When female lobsters mature, they go through a period of allometric growth through several moults (Pugh et al., 2023). This results in a gradual broadening of the abdomen relative to body length. Hereby the area and volume available for eggs increase, as they are carried and develop under the tail before hatching (brooding). Protecting ovigerous (egg-bearing) females decrease the chance of being captured for small females with frequent reproduction compared to females investing energy on growth. This may select for females using energy on producing eggs instead of moulting (Sørdalen et al., 2022). In that case it may be seen as a relatively larger AW to body length than one would expect in an undisturbed population. Harvesting is also known to have the potential to select for slow growth if growth rate is positively correlated with bold behaviour, increasing the vulnerability of capture (Biro & Post, 2008; Biro & Sampson, 2015). Animals will maximize their reproduction depending on the environment (Ford & Seigel, 1989; Peluc et al., 2008; Reger et al., 2018). Thus, as size and age is known to confer benefits on fecundity (Bobko & Berkeley, 2004; Planque et al., 2010), I wanted to explore if removing the highly selective fishing pressure would lead to a change in females protected in MPAs, switching back to abdominal broadening at a relatively larger size.

1.4 Aim of the study

The overall aim of the study is to test the hypothesis that the individual fecundity of sexually mature female lobsters is higher in protected areas than in fished control areas, due to the rebuilding of the population structure inside the reserves. If this hypothesis is supported, I expect to see higher individual egg carrying capacity in three MPAs than in their respective adjacent control areas. Female body length and abdominal width will be regarded to explain changes in lobster size as these measures are used to calculate egg carrying capacity. Additionally, I expect the egg carrying capacity to increase more with increasing time of protection inside the MPAs. Secondly, I will test whether protection has led to changes in abdominal broadening at a relatively larger body size compared to fished control areas when the highly selective fishing pressure is removed. This study demonstrates almost two decades of changes in lobster fecundity comparing mature females in MPAs and fished control areas.

2 Materials and methods

2.1 Study species

The European lobster (*Homarus gammarus*) is a large decapod crustacean that can live for several decades (Tandberg et al., 2021). The average ages of large (150–170 mm CL) males and females has been found to be 31 and 54 years, respectively (Sheehy et al., 1999). The generation time is 18 years (Tandberg et al., 2021). Lobsters show high site-fidelity. During a three-year period in southwestern Norway, 40% of recaptured lobsters were found inside their release zone of 100-200 meters, 84% were found within 500 m and only a few were found more than 1000m away (Agnalt et al., 2007). By ultrasonic tracking in the Flødevigen MPA, 95% of tagged lobsters were found to remain inside or near (< ~200m) the reserve boundaries of ~1 km² during one year (Moland et al., 2011). Lobsters are sexually dimorphic, with males growing faster and growing relatively larger claws than females (Lizarraga-Cubedo et al., 2003; Sjørdalen et al., 2020; Templeman, 1935). Females go through a gradual broadening of the abdomen when maturing (Pugh et al., 2023), providing more space for eggs under the tail. Females and males grow at the same rate when small (less than 200 mm long). However, as they get larger, female growth slows down (Sjørdalen et al., 2022).

Size of maturation (SoM) is commonly denoted as the body size at which 50% of the females in the population are sexually mature (Tully et al., 2001). The age of ovigerous females has been estimated to between 6.9 to 49.5 years (Sheehy et al., 1999), which indicate a potential reproductive life span of about four decades. The SoM varies geographically and temporally. In Northern Norway all females were mature at 66 mm carapace length (CL) (Agnalt et al., 2009). Lobster sizes increases when moving south, and in England, Scotland and Ireland SoM is between 78 and 98 mm CL (Free, 1994; Lizarraga-Cubedo et al., 2003; Tully et al., 2001). Mating takes place mainly in late summer after moulting, and males deliver sperm packages that females store for up to a year before fertilising the eggs (Kristiansen et al., 2004). After fertilization, the eggs are carried under the abdomen between the pleopods for about 11 months before hatching in late spring to early autumn. The larvae go through three pelagic stages before metamorphosis to small, clawed lobsters settling at the sea bottom in a fourth stage (Kristiansen et al., 2004).

The Norwegian lobster fishery is regulated by a closed fishing season and a minimum legal size (MLS) of 250 mm total length (TL). This was increased from 240 mm in 2008 (Kleiven et al., 2017). Additionally, a maximum legal size of 320 mm TL in Skagerrak was implemented in 2017, and a ban on harvesting ovigerous females in 2008 (Sundelöf et al., 2015; Sjørdalen et al., 2018; Thorvik et al., 2007). As sexually mature female lobsters spawn on average every second year, the preservation of ovigerous females could reduce the fishing mortality of sexually mature lobsters by half (Agnalt et al., 2007; Sundelöf et al., 2015).

2.2 Study system

In 2006, four lobster reserves were implemented in the Skagerrak coast in Norway by the Ministry of Fisheries and Coastal Affairs to test how the lobster populations would

respond to small MPAs where lobster fisheries were prohibited (Pettersen et al., 2009). The MPAs are protected under the Saltwater Fishery Law which prohibit the use of standing gear and only allow for hook and line fishing, which fully protects lobsters from fishing (Pettersen et al., 2009). A monitoring program started in 2004 to detect effects of protection, which included three of the four MPAs. The three MPA sites in Skagerrak are located in Bolærne in the Oslo fjord (N 59° 13', E 10° 31'), Kvern skjær island in the Hvaler archipelago (N 59° 02', E 10° 58') and Flødevigen in Arendal (N 58° 25', E 8° 45') (Figure 1) (Fernández-Chacón et al., 2021). Control areas are located 1700, 2250 and 850 m from its associated MPA centre to control area centre. The size of the MPAs and control areas are approximately equal of about 1.0, 0.7 and 0.5 km² in Flødevigen, Bolærne and Kvern skjær, respectively (Fernández-Chacón et al., 2021).

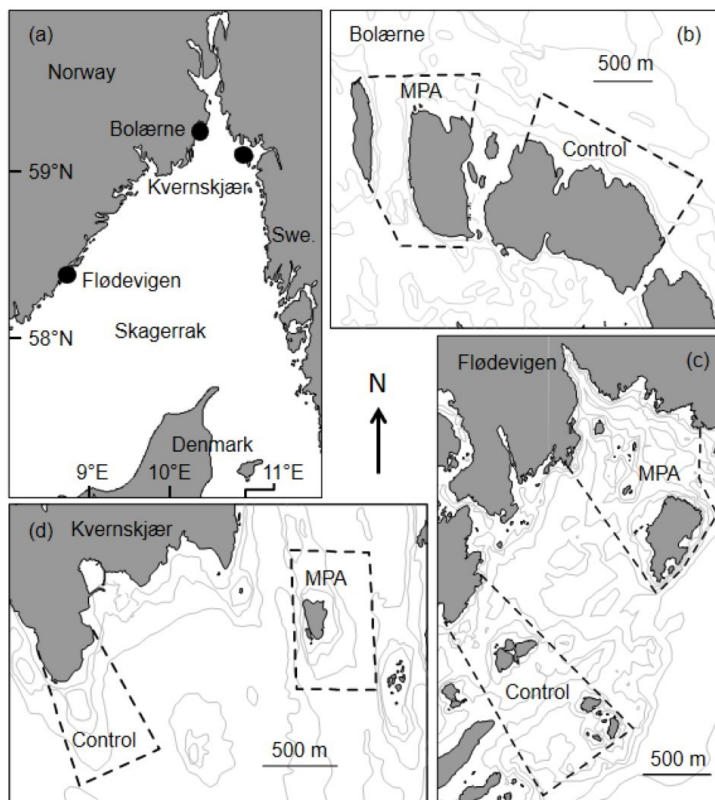


Figure 1: (a) Location of the three lobster reserves (MPAs) in the Norwegian Skagerrak, (b) the Bolærne MPA and control area in outer Oslo fjord, (c) the Flødevigen MPA and control area in Arendal and (d) the Kvern skjær MPA and control area in Hvaler. All areas are marked with dashed lines (figure reproduced with permission from Fernández-Chacón et al., 2021).

2.3 Sampling design

In the present study, I used data from an ongoing BACI (before-after-control-impact) study of lobsters run by the Norwegian Institute of Marine Research (IMR) (Knutsen et al., 2022; Moland et al., 2021). This long-term monitoring project covers the three MPAs and control areas from 2006 (the last sampling season prior to establishment of the MPAs) until 2023. Additionally, two years of before-data from inside the proposed MPAs prior to establishment in 2006 are included. I participated in the sampling in Flødevigen in 2023. Since 2006, the annual fishing effort is 100 trap days per site per year, 25 in each of the MPAs and control areas four days in a row (Knutsen et al., 2022). The traps

were dropped randomly at different positions in the MPAs and control areas on depths between 5 and 30 metres and hauled after approximately 24 h. The position of the traps was changed every day to ensure covering as much of the area as possible. Every year the sampling has been conducted between 20th of August and 10th of September, each area the same week every year (Moland et al., 2013). Lobsters were sampled using two types of two-chambered 'parlour' traps (Kleiven et al., 2022). Entrance diameter was 120 and 180 mm (20 and 5 traps in each site, respectively) and traps were baited with frozen mackerel (*Scomber scombrus*). Introduction of five traps with entrance diameter of 180 mm in 2016 was to better track size increase of the populations (Helms, 2023).

The lobsters were measured and sexed on board on the boat immediately after capture and released at the sampling site. The abdominal width (AW), carapace length (CL) and total length (TL) of all lobsters were measured to the nearest millimetre (mm) to track changes in size, estimate egg carrying capacity and analyse the morphological relation of length and width. Using vernier callipers, AW was measured as the maximum width of the second abdominal segment (Templeman, 1935). Measures of AW is available for Flødevigen in 2010-2014 and was measured in all areas in 2023 for the purpose of this thesis. A yardstick was used to measure TL from the tip of the rostrum to the margin of the telson (Moland et al., 2013) and CL from behind the eye socket to the rear of the carapace (Free, 1994). If the rostrum was broken this was noted and TL was not measured. Data on TL exists from all areas since 2004, while measurement of CL was initiated in 2007 after MPA implementation. The sex was determined by examining the first pair of pleopods. Males have a modified first pair designed for delivery of sperm packages during mating. Some field data, including approximately 13 individuals (of both sexes in total) in Flødevigen control area, were accidentally lost during field work in 2023.

2.4 Data analyses

Data was analysed using the R software (Rstudio Team, 2023) with version 4.3.0 (R Core Team, 2023). Prior to conducting the analysis, potential outliers were inspected using boxplots and summary overviews of the minimum, maximum, median, and mean values of the data. Some observations were found to be typing errors, with CL being a copy of TL, thus were removed when filtering on $CL < TL$. Errors were checked against raw data and field papers for 2023 and were removed if not finding the correct value. A simple linear model was made for AW with TL as response variable to look at model diagnostics to detect further outliers. Six additional extreme outliers were removed as they were assumed errors that may have a large effect on the results as the dataset is small for parts of the analysis. Data was not corrected for recaptures within or between years.

2.4.1 Female size

To test the effect of protection on lobster size (AW, CL, and TL) and obtain estimates of mean sizes, linear models were fitted to the data for years with available AW data. Estimates were restricted to these years as models built to calculate egg carrying capacity were based on AW and CL, thus I wanted information on size these current years. Separate models were fitted with each of the size measures as response variable. Three predictor variables and their interactions were included for CL and TL models: status with two levels (MPA, control), area with three levels (Flødevigen, Kvernshjær and Bolærne) and year periods (year) with two factors (2010-2014 and 2023). For AW, 2023 data was used to compare size in different areas with the predictor variables status and area. A second model to test temporal variation in AW had the predictor variables year

and status for Flødevigen alone. The R package ggplot2 (v4.3.0; Wickham, 2016) was used to visualise the mean sizes and frequency size distributions for 2023.

To test whether protection has changed the relationship between AW and TL when removing the highly selective fishing pressure, two linear regression models were fitted. The reason to use two models testing the same relationship was to investigate temporal variation in the relationship between AW and TL in Flødevigen, as well as examine if other areas showed the same trend in 2023. Both models had AW as response variable with TL and status as predictor variables. The Flødevigen model included the variable year period (year). The interaction term year: status was included to account for potential differences in AW with protection status across the two periods. If AW was relatively smaller to TL in MPAs, this would be seen as steeper slopes in control areas. In the 2023 model the variable year was replaced with area. Geographical variation in AW was accounted for by including the interaction status: area.

Before fitting the models, data exploring was done starting with a linear model on arithmetic scale. A slightly non-linear trend in the residuals plot was corrected for by including a power term. This was significant and improved the fit of the model, indicating non-linear data. Difficulties of interpreting the results of power models together with log transforming being an often-preferred representation for morphology (Pélabon et al., 2014; Pélabon et al., 2018), log-log transformed linear models were decided for the models. The starting models (prior to model selection) were tested with the following structures:

$$\log AW \sim \beta_0 + \beta_1 \log TL + \beta_2 status + \beta_3 year + \beta_4 status: year + \beta_5 status: \log TL \quad (\text{Eq. 1})$$

$$\log AW \sim \beta_0 + \beta_1 \log TL + \beta_2 status + \beta_3 area + \beta_4 status: area + \beta_5 status: \log TL \quad (\text{Eq. 2})$$

Model selection was conducted using p-values of the main effects and interactions from three-way ANOVA, and R^2 . A higher R^2 indicates more variation in the data is described by the included variables. P-values > 0.05 indicated non-significant variables. This hypothesis testing model selection was chosen to be able to investigate the p-values for all variables. Model validation with investigation of normality and homoscedasticity of variance was done with the chosen models using plots of residuals vs fitted values, Q-Q residuals, scale-location, and Cooks distance. The same models (Eq. 1 and 2) were fitted replacing TL with CL to compare the results as CL often is referred to in literature about allometric growth.

In the above analysis the whole size range of lobsters were included to show differences in AW relative to body size with protection level. However, size distributions in MPAs and control areas differ and not all sizes overlap with the big size classes only present in MPAs. The relationship between AW and TL may vary across different size classes. Hence, differences observed between the two areas may be partly driven by the presence of large females in MPAs, rather than solely attributed to differences in fishing pressure. To get a more conservative test on harvest selection effects and avoid this potential confounding factor, data was cut to only allow sizes that were present in both MPAs and control areas ($TL_{\min} = 190$ mm, $TL_{\max} = 372$ mm). New analyses were run on models (Eq. 1 and 2) with this size range.

2.4.2 Estimation of individual egg carrying capacity

To assess the effect of protection on individual egg carrying capacity in the three MPAs, models developed by Agnalt (2008) were used. Agnalt measured the number of eggs

relative to AW and CL of female lobsters at Kvitsøy, southwestern Norway. This was to test whether hatchery-produced females performed as well as wild females in terms of egg carrying capacity. Resulting models represent the expected number of eggs carried by an ovigerous female of given size, corrected for egg loss (Agnalt, 2008). No significant differences in size-specific fecundity were found. Among the models considered, a power fit model was chosen ($R^2 = 0.85$ and 0.84 for CL and AW, respectively) due to the superior fit to data, hence the volumetric characteristics of the egg storage (Agnalt, 2008). Several recent studies have favoured a power fit model (Babcock et al., 2007; Coleman et al., 2019; Jack & Wing, 2010; Tully et al., 2001), while others preferred a linear fit (Bennett & Howard, 1987; Goñi et al., 2003; Hepper & Gough, 1978). In my analysis, egg carrying capacity estimates were restricted to a size of maturation (SoM) of 80 mm CL based on documented SoM in geographical proximity of 86 mm in Denmark (Freitas et al., 2023) and 80 mm in Western Norway (Kristiansen et al., 2004). Additionally, I did not want to exclude too many samples, especially in control areas where the sample size is smaller, and lobsters are of smaller size. To examine the hypothesis that females in MPAs have higher individual egg carrying capacity due to larger sizes, estimates were generated for all ovigerous females for the years with AW measures available. Two power fit models based on CL and AW (Agnalt, 2008) were used to compare the results:

$$F_{CL} = 0.0045 * CL^{3.2214}$$

$$F_{AW} = 0.2548 * AW^{2.5993}$$

Both models were used to investigate how these estimates would be expressed when comparing a fished population with a protected population where all ages and sizes are present. To further investigate changes through the years, estimation with F_{CL} was extended to all three areas from 2007 (first year after protection) to 2023. To allow for easier comparison of the two different egg carrying capacity models, the percentage number of eggs per female in MPAs relative to control areas was calculated using the formula:

$$Percentage\ difference = \frac{|MPA - Control|}{Control} * 100$$

3 Results

3.1 Female size

After removal of outliers (N = 43), 426 female lobsters were included in the analyses from 2023, with 90, 171 and 165 from Flødevigen, Kvernskjær, and Bolærne, respectively (Table A1). Lobsters sampled inside all MPAs had significantly higher mean abdominal width (AW), carapace length (CL) and total length (TL) compared to adjacent control areas (ANOVA: $p < 0.001$). The three-way interaction and interaction of status with area were non-significant for all three size measures, thus were removed. In 2010-2014 females in Flødevigen MPA had 17% larger mean AW, and mean length (CL and TL) was 10% larger in all MPAs compared to respective control areas. From 2010-2014 to 2023 mean length (CL and TL) increased 9-15% in MPAs and 4-10% in control areas. Simultaneously, mean AW increased by 14% and 12% in Flødevigen MPA and control area, respectively (Figure 2).

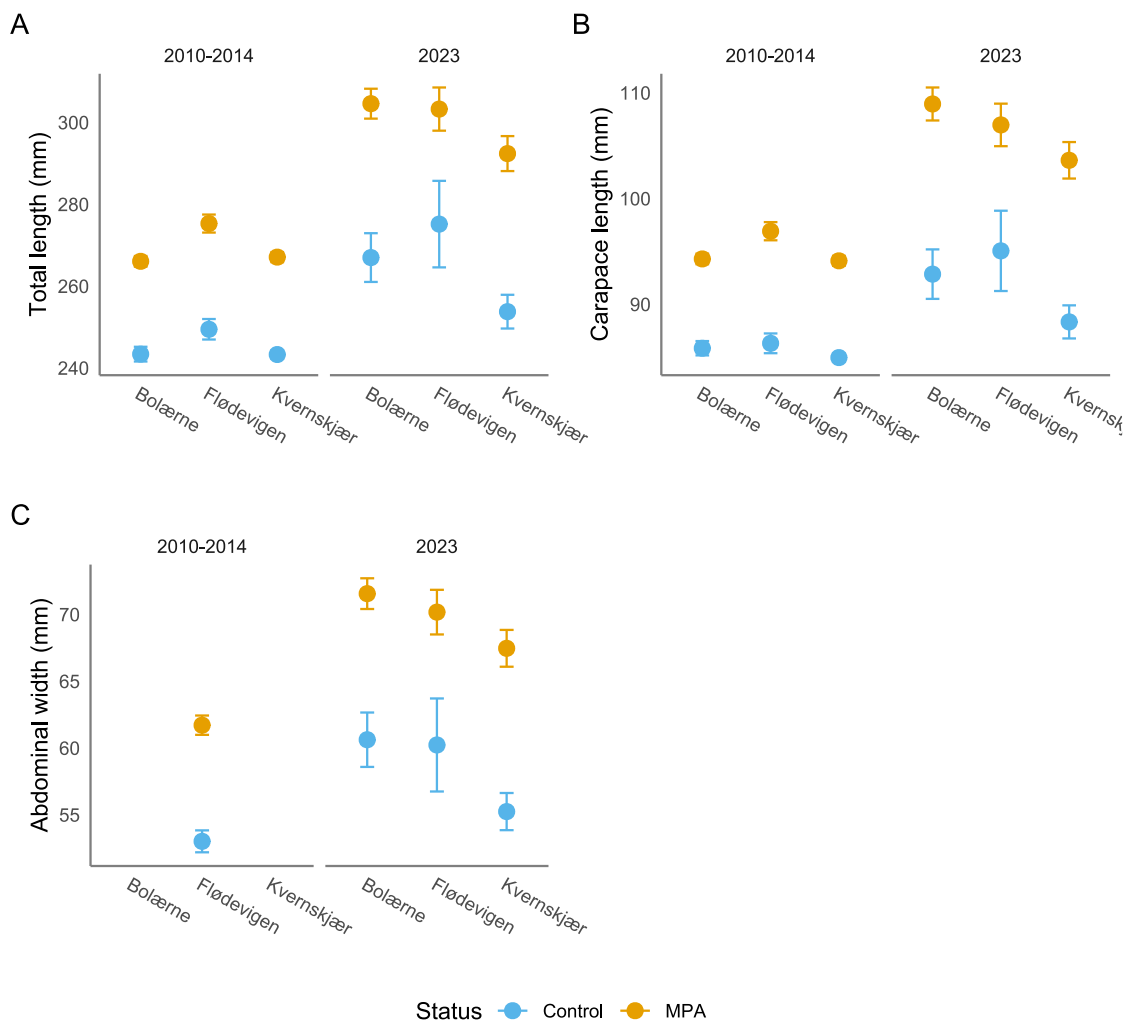


Figure 2: Overview of mean total length (A), carapace length (B), and abdominal width (C) in mm of female lobsters (*H. gammarus*) in Flødevigen, Kvernskjær and Bolærne. MPAs (yellow) and control areas (blue) in the two periods 2010-2014 and 2023. In 2010-2014 AW measures were only available in Flødevigen. Points = population mean, whiskers = ± 1 SE.

In 2023 the AW, CL, and TL in MPAs had increased to be approximately 20%, 17%, and 14% larger compared to adjacent control areas, respectively (Table A2). Frequency distributions in MPAs and control areas in 2023 (Figure 3, A1) show a noticeable higher proportion of bigger sized lobsters in MPAs. The number of captured lobsters inside MPAs was also higher (N = 318) compared to control areas (N = 108) (Table A1). The range of CL in control areas was 59-133 mm with the bulk of the catch around 80-85 mm. In MPAs it ranged between 66-160 mm with the bulk around 100 mm (Figure 3). The range of AW was 31-92 mm in control areas (bulk at 50 mm) and 31-105 mm in MPAs (bulk at 60-65 mm). The proportion of females smaller than MLS of 250 mm TL in 2023 were 12.3% in MPAs compared to 42.6% in control areas (Figure A1).

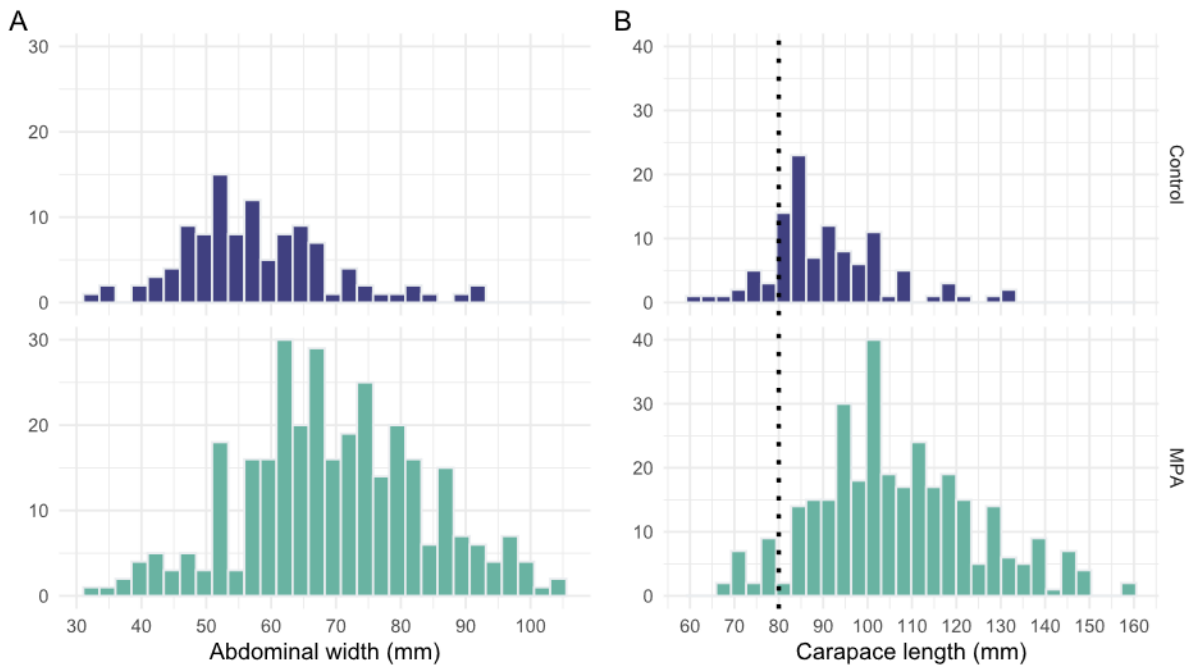


Figure 3: Frequency distributions of (A) abdominal width and (B) carapace length of female lobsters (*H. gammarus*) in MPAs (green) and control areas (blue) in 2023 for Flødevigen, Kvernskjær, and Bolærne together. The vertical dotted line denotes size at maturity for female lobsters (80 mm CL).

3.2 Abdominal width relative to female length

The years 2010-2014 were combined to one period instead of separate years (Eq. 1) as a preliminary test revealed no significant between year variation in AW-TL (close to $p = 1$). In Flødevigen there was no significant difference in status effect between the two periods (ANOVA: $F_{1,508} = 1.37$, $p = 0.24$) and the interaction was therefore removed. Intercepts were lower in 2023 compared to 2010-2014 ($p = 0.01$), and in control areas compared to MPAs ($p = 0.04$ and < 0.001 in Eq. 1 and 2, respectively; Table 1). Positive allometric increase in AW was found in all control areas and MPAs with $1.51 \pm 0.03\%$ and $1.38 \pm 0.04\%$ increase per 1% increase in TL, respectively (Table 1, Figure 4, Eq. 2). The same was found in both periods in Flødevigen control area and MPA with $1.5 \pm 0.03\%$ and $1.44 \pm 0.03\%$ increase per 1% increase in TL, respectively. Differences in slopes indicates AW to be smaller relative to TL in MPAs, as predicted. Both models explained 96% of the variation in the data (adjusted $R^2 = 0.96$; Table 1).

Examining the residual plots indicated a reasonable model fit, however with a slightly curved variance plot (Figure A4, A5). The figure with regression lines (Figure 4) shows all

areas together in 2023 as MPA effect was of main interest. Counties and periods had different intercepts but similar slopes (Table 1). P-values from ANOVA for the models with overlapping size ranges (Figure A2, Table A3) indicated that differences in the relationship of AW and TL were non-significant when the largest females were removed (Eq. 1: $F_{1,499} = 2.83$, $p = 0.09$; Eq. 2: $F_{1,398} = 3.5597$, $p = 0.06$). Relative size of AW to CL showed similar increases in slopes as in the models for TL with all sizes (Figure A3, Table A4). This is due to a 98.76% correlation between TL and CL (Pearson correlation test: $t(424) = 129.38$, $p < 0.001$).

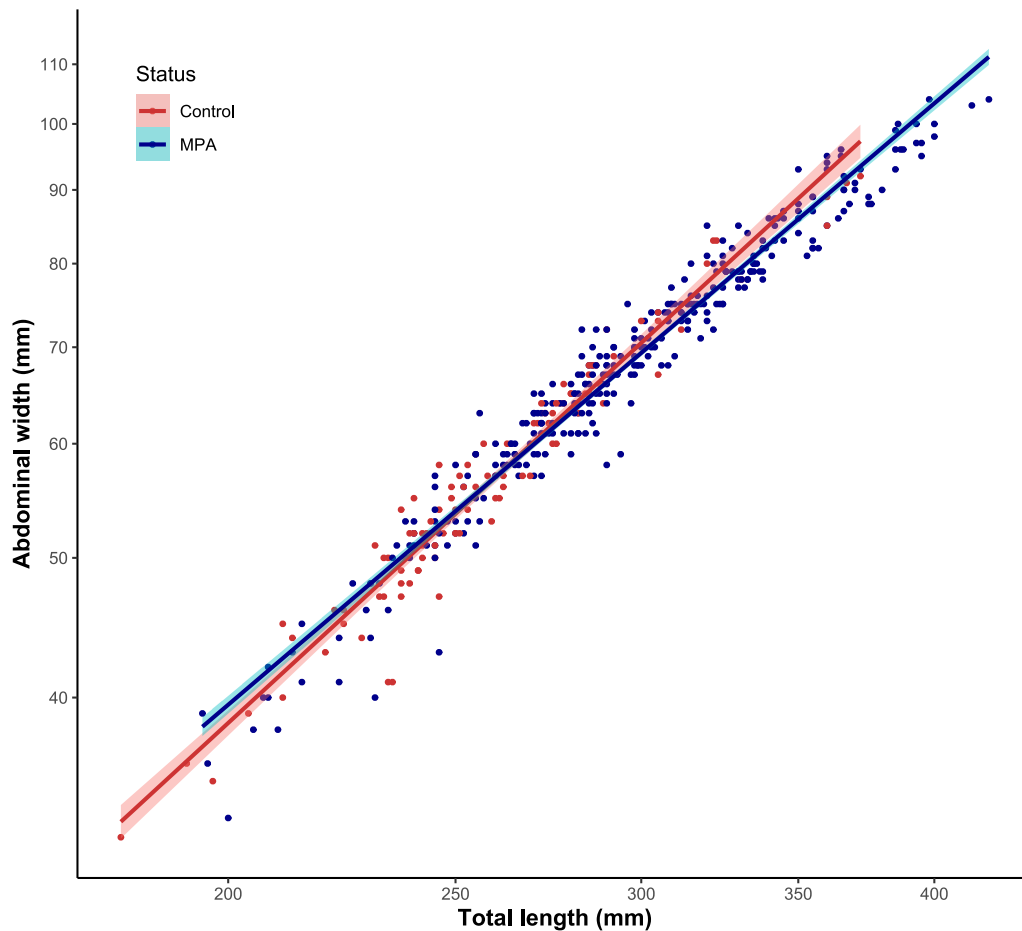


Figure 4: Relationship on a log-log scale (base e) between abdominal width and total length in mm in female lobsters (*H. gammarus*). Axis shows arithmetic values of size measures scaled to fit the linear log regression (Pélabon et al., 2018). Data from the lobster survey in Flødevigen, Kvernskjær, and Bolærne in 2023, all areas combined ($n = 426$ females). MPAs (blue) and control areas (red). With 95% CI.

Table 1: Summary of estimates, standard errors, t- and p-values for the two selected models. The first model (Eq. 1) compares the periods 2010-2014 and 2023 in Flødevigen. The second model (Eq. 2) includes the three areas Flødevigen, Kvernskjær, and Bolærne in 2023. Log with base e.

	Explanatory variable	Estimate	Std.Error	t-value	p
Adjusted R ² = 0.9634	(Intercept)	-4.33	0.16	-27.87	< 0.001
	log TL	1.5	0.03	53.40	< 0.001
	MPA	0.36	0.18	2.02	0.0442
	Year period 2023	-0.01	0.01	-2.52	0.0120
	log TL: MPA	-0.06	0.03	-1.97	0.0496
Adjusted R ² = 9601	(Intercept)	-4.39	0.19	-22.95	< 0.001
	log TL	1.51	0.03	44.31	< 0.001
	MPA	0.72	0.21	3.34	< 0.001
	Kvernskjær	0.04	0.01	3.10	0.0020
	Bolærne	0.05	0.01	4.11	< 0.001
	log TL: MPA	-0.12	0.04	-3.26	0.0012
	Kvernskjær: MPA	-0.03	0.01	-2.07	0.0396
Bolærne: MPA	-0.04	0.01	-2.60	0.0095	

3.3 Estimation of individual egg carrying capacity

In 2023, 298 and 95 sampled sexually mature females (CL ≥ 80 mm) were included in MPAs and control areas, respectively. All areas and periods (2010-2014 and 2023) had between 40 and 78% higher mean individual egg carrying capacity in MPAs compared to adjacent control areas with both models (F_{CL} and F_{AW}) (Table 2).

Table 2: Overview of mean estimated egg carrying capacity of sexually mature female lobsters (*H. gammarus*) (≥ 80 mm CL) in each MPA and control area in Flødevigen, Kvernskjær and Bolærne. Estimates based on two power fit fecundity models (F_{CL} and F_{AW}). Mean egg carrying capacity calculated for the years with available abdominal width (AW) data. Percent diff represents the difference in mean individual egg carrying capacity in each MPA relative to respective control area by the formula $\frac{|MPA - Control|}{Control} * 100$. N = number of individuals measured in each area.

Area	Year	Egg carrying capacity (F_{AW})				
		Control	N _{Control}	MPA	N _{MPA}	% diff
Flødevigen	2010-14	9 604	97	13 484	260	40.4
		(5 348 – 24 031)		(4 765 – 45 696)		
Flødevigen	2023	12 587	16	17 983	70	42.9
		(3 966 – 32 410)		(6 643 – 40 253)		
Kvernskjær	2023	10 025	48	17 477	101	74.3
		(3 966 – 31 502)		(3 719 – 44 573)		
Bolærne	2023	12 828	31	18 352	127	43.1
		(5 656 – 29 734)		(4 488 – 40 253)		
Area	Year	Egg carrying capacity (F_{CL})				
		Control	N _{Control}	MPA	N _{MPA}	% diff
Flødevigen	2010-14	9 398	97	13 202	260	40.5
		(6 079 – 24 301)		(6 079 – 46 055)		
Flødevigen	2023	12 129	16	17 464	70	44
		(6 327 – 42 214)		(6 844 – 42 214)		
Kvernskjær	2023	9 610	48	17 119	101	78.1
		(6 079 – 29 771)		(6 327 – 56 698)		
Bolærne	2023	11 415	31	18 359	127	60.8
		(6 327 – 29 045)		(6 844 – 46 055)		

Percentage difference in mean individual egg carrying capacity in MPAs compared to respective control areas is similar with the two models F_{AW} and F_{CL} with Bolærne as an exception. Frequency distributions show that most of the lobsters had a low number of eggs in control areas (Figure 5). MPAs showed a wider frequency distribution with more lobsters having more eggs, even though the bulk was found at 10 000-16 000 eggs per individual (Table 2, Figure 5).

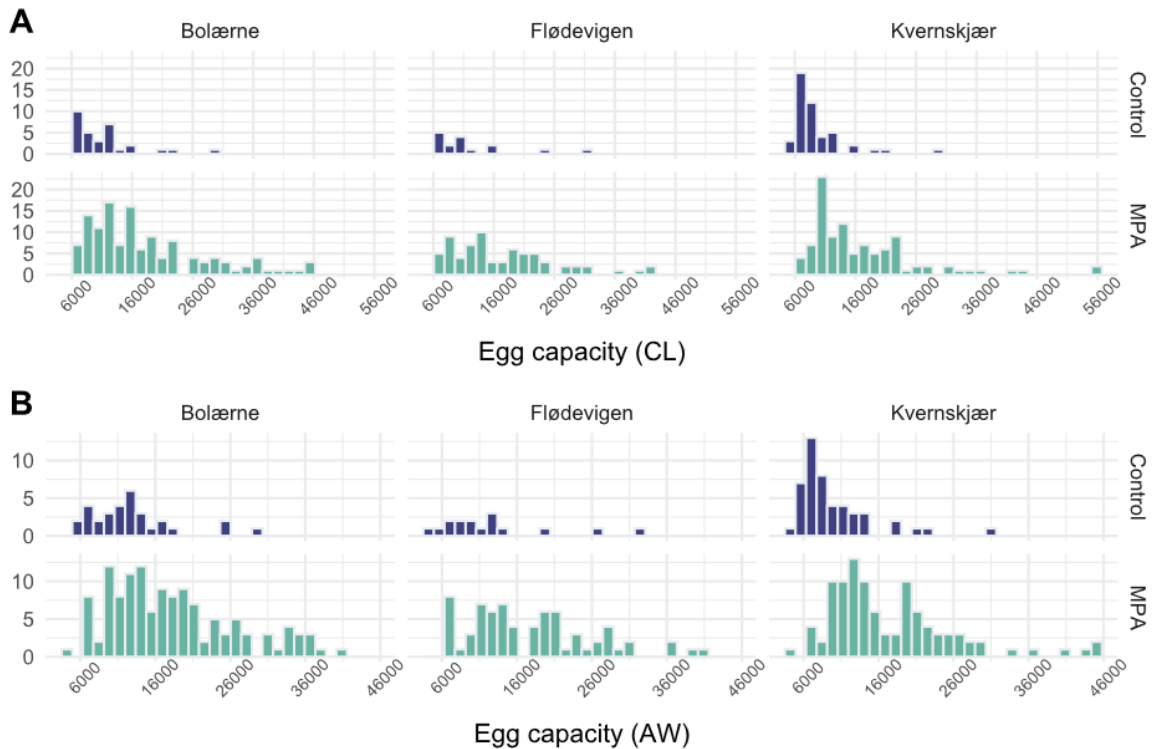


Figure 5: Frequency distributions of individual egg carrying capacity of ovigerous (≥ 80 mm CL) female lobsters (*H. gammarus*). Estimated with F_{CL} (A) and F_{AW} (B) in Flødevigen ($N = 86$), Kvern skjær ($N = 149$) and Bolærne ($N = 158$) in 2023. Blue = control areas, green = MPAs.

When using CL to estimate individual egg carrying capacity through all years in Flødevigen, Kvern skjær and Bolærne, the sample size was 7485 lobsters in total ($N_{MPA} = 4824$, $N_{control} = 2661$). All MPAs showed a steady increase from 2007 until 2023 (Figure 6). The mean fluctuates from year to year (Table A6), but evens out when seeing all areas together (Table A5). Adding MPAs together, mean F_{CL} increased with 74.6% from 2007 to being 17 728 ($N = 298$, range 6 327 – 56 698) in 2023. Contrastingly, this increase was of 14.4% in control areas to 10 623 ($N = 95$, range 6 327 – 31 260) in 2023 (Table A5). This was 67% lower than in MPAs. If the reference year was set to 2008 instead of 2007, MPAs and control areas would have experienced a 79% and 38.7% increase in mean individual egg carrying capacity from 2008 to 2023, respectively.

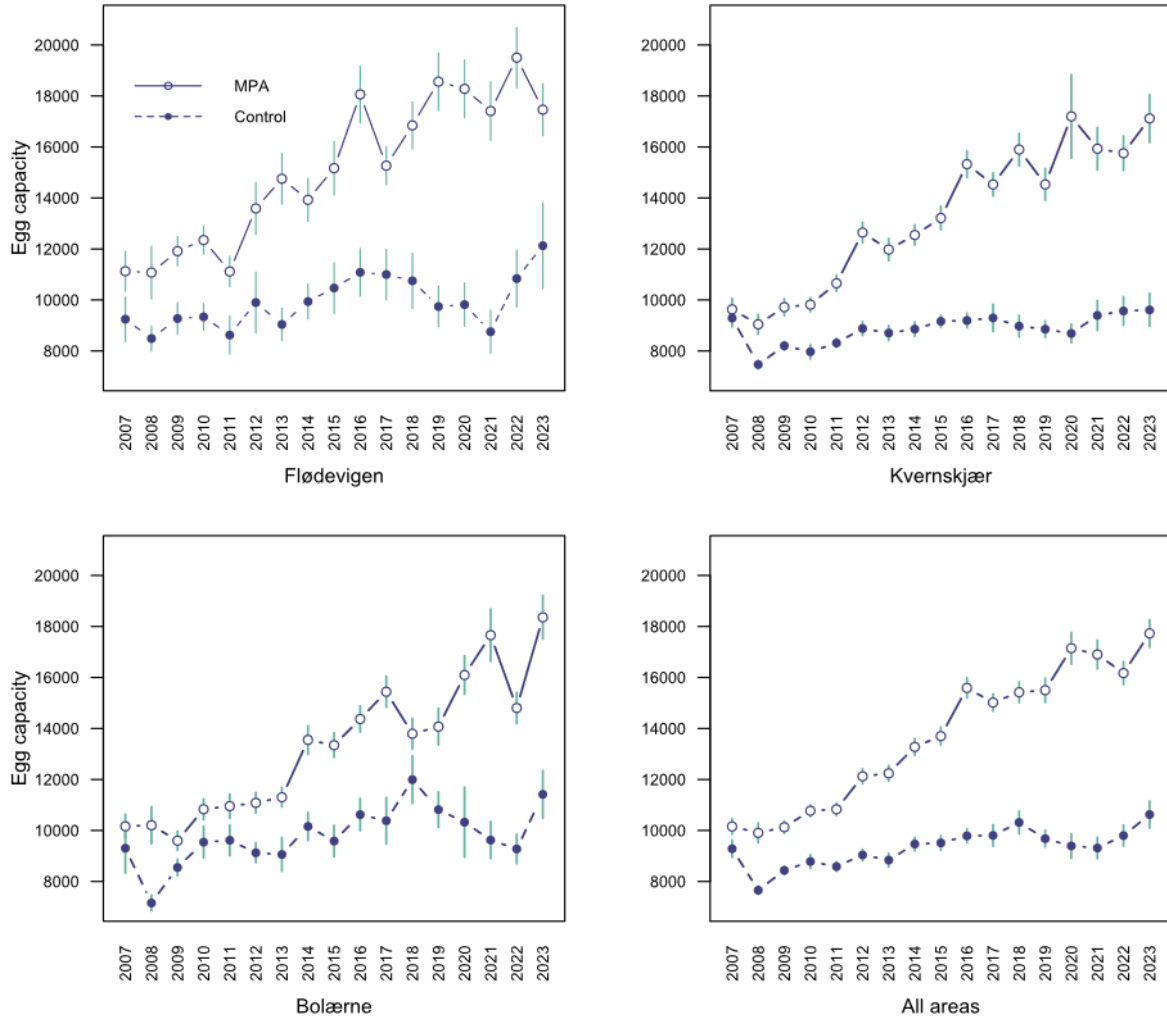


Figure 6: Mean estimated individual egg carrying capacity (F_{CL}) of ovigerous (≥ 80 mm CL) female lobsters (*H. gammarus*) through all years after protection (2007-2023) in the three areas Flødevigen ($N = 1490$), Kvernskjær ($N = 3409$), Bolærne ($N = 2586$) and all areas combined ($N = 7485$). White dots = MPA, filled dots = fished control area. Mean F_{CL} with whiskers = ± 1 SE.

4 Discussion

This thesis demonstrated that MPAs harbour significantly larger female lobsters with a wider size distribution than adjacent fished areas. Even though female size increased substantially in control areas from 2014 to 2023, MPA females were still significantly larger. This was translated into a much higher mean individual egg carrying capacity in MPAs due to the hyperallometric relationship between length and fecundity (Barneche et al., 2018; Marshall et al., 2019). During 17 years of protection mean individual egg carrying capacity increased steadily in the three MPAs whereas adjacent fished control areas experienced small increases. Additionally, there was suggested that females have a relatively smaller abdominal width to body length when being allowed to grow undisturbed in MPAs. However, this is a weak signal that is discussed further below.

4.1 Female size

Overall, I found mean abdominal width (AW) and female length to be larger and increase more in MPAs as in control areas from 2014 to 2023 (Figure 2, Table A2). In 2023, carapace length (CL) and total length (TL) were 17% and 14% larger in MPAs compared to control areas, respectively. This difference is higher than the 9% difference in size of legal sized lobsters in Lundy Island in England, four years after protection (Hoskin et al., 2011). Mean size in control areas decreased (Hoskin et al., 2011), however they measured only legal-sized lobsters. In 2011 female lobsters in Lundy Island alone had 5% larger mean body size in the reserve (Davies et al., 2015). The larger differences detected in size in my thesis is likely to be described by increased age of the MPAs. Even though the effect of the MPAs were large in 2014, the difference in size between MPAs and adjacent control areas were even larger in 2023. Larger difference between MPAs and control areas in AW compared to lobster length is reflecting a higher proportion of mature females in MPAs that have undergone abdominal broadening.

In Flødevigen and Bolærne control areas mean length increased more from 2014 to 2023 (7% and 10% respectively) than found by Moland et al. (2013) from 2006 to 2010 in the same areas (2% and 6%, respectively). Fernández-Chacón et al. (2020) found average lobster length to increase by 5.5 mm/year between 2006 and 2015 in Bolærne and Kvernskjær control areas, while no significant trend was found in Flødevigen. This change is larger than found in this thesis between 2014 and 2023. However, mentioned studies measured both sexes together whereas I present females alone. Increases in mean female size in control areas from 2014 to 2023 may partly be a response to implementation of maximum legal size of 320 mm TL in 2017. To be protected by this, lobsters must survive several years by going clear of the high number of traps or be migrants from the adjacent MPAs. The likelihood of legal sized females surviving every year in the control areas are usually below 0.5 (Fernández-Chacón et al., 2021; Fernández-Chacón et al., 2020). Frequency distributions of TL from 2023 show that a large proportion of females are > 320 mm in MPAs while only a few individuals are above this size in control areas. Due to the short distances between MPAs and adjacent control areas, spill-over between the areas could be expected. This is not largely observed (Agnalt et al., 2007; Huserbråten et al., 2013; Moland et al., 2011), however adults moving from MPAs to adjacent control areas are of bigger size than lobsters moving from

the control areas (Thorbjørnsen et al., 2018). Therefore, increases in mean female size in control areas may partly be explained by spill-over from MPAs.

4.2 Abdominal width relative to female length

I have compared the allometric relationship of AW relative to lobster length (CL and TL) in control areas affected by a highly selective fishing pressure and 17-year-old MPAs. By the results of the analysis, it is a weak signal of female lobsters having a relatively smaller AW to body length in MPAs compared to in control areas. However, differences in allometry seem to be mostly driven by the presence of large females in MPAs as the significance dropped to non-significant when excluding these sizes from the analysis. The effect of protection versus high fishing pressure on AW-TL relationship is more directly tested with only overlapping size ranges. This means that females of the same size in MPAs and control areas does not show differences in AW-TL relationship. However, in large females this relationship is different, shown as a significantly lower slope when including the largest females in MPAs. This contradicts the hypothesis that removed fishing pressure possibly could result in switching back to abdominal broadening at a relatively larger size. In the largest American lobster sizes, there have been found a lower AW:CL ratio (Pugh et al., 2023), and that AW relative to body length exhibit isometry (Emond et al., 2010; Templeman, 1935). This could explain why the slope decreases in MPAs when including the largest females. If present in this data, it may possibly be the reason why neither linear, power or log fit gave perfect model diagnostics. Differences in intercept with protection status in the different areas might be due to random variation in size of the smallest sampled individuals, as the sample sizes for each area are restricted. After working with this project, I think it would be more correct to cut data to only look at females >250 mm TL as responses to removed fishing pressure is expected to be seen firstly in legal-sized females.

4.3 Female fecundity

The two fecundity models using AW and CL to calculate egg carrying capacity gave similar results in estimated means and in how many percent more eggs there are in the MPAs compared to control areas. This indicate that the two models are equally good, and it should not be necessary with additionally use of the AW measure. An exception is Bolærne where the MPAs have 43% and 61% more eggs per individual on average when using AW and CL, respectively. As I have not counted the actual number of eggs, I cannot tell which estimate is best describing the actual amount. The SoM used to restrict which females are included, is based on CL, which cuts the minimum estimated egg carrying capacity to almost the same amounts in all areas. The minimum number of eggs estimated is much lower when using AW which reflects that AW can vary a lot within the same CL.

How many eggs a female can carry depend on the area available under the abdomen. Thus, increased size will directly increase the egg carrying capacity. Seeing all MPAs together, mean individual egg carrying capacity increased steadily to being 75% larger in 2023 compared to the reference in 2007 (the first year after MPA implementation). This is due to the large increase in lobster size discussed above. As opposed to MPAs, control areas experienced no increase in mean individual egg carrying capacity the first six years after 2007. This is surprising as mean female size has been found to increase these years (Calef, 2016). Between 2014 and 2023 egg carrying capacity increased, compatible with increased mean lobster size measures. This led to a percentage increase of 14% from

2007 to 2023. Mean individual egg carrying capacity of 8154 eggs in a harvested area in Scotland, was compatible with estimates from control areas between 2008 and 2013 in this thesis (Lizarraga-Cubedo et al., 2003). However, most of the years my estimates were higher even though size of maturity (SoM) was similar. After the MLS was increased in 2008, lobsters were found to shift to larger sizes (Kleiven et al., 2017). This may partly explain the increased egg carrying capacity in control areas, together with protection of ovigerous females and the maximum legal size. Using 2008 as reference instead of 2007 more than doubled the percentage increase in control areas to 2023. However, 2008 had the lowest egg carrying capacity of all years in all control areas, and percentage increase would still only be half the size as in the MPAs. To avoid this effect of variation between years, it would have been possible to use the mean of the first three years as a reference, compared to the mean of the last three years.

Percentage difference in the mean number of eggs in Flødevigen MPA and control area increased slightly from 2010-2014 to 2023. This is due to higher increase in the MPA compared to the control area as mean female sizes increased even further. In 2010-2014, 4-8 years after protection, individual egg carrying capacity was 40% higher in Flødevigen MPA compared to the control area. This is double the size compared to in and outside a Scottish MPA at similar MPA age (Howarth et al., 2017). A possible explanation for is the use of linear instead of power model to estimate egg capacity, which does not account for the disproportionately higher reproduction of large females (Marshall et al., 2019). A hyperallometric relationship in length and fecundity means that egg carrying capacity increases disproportionately when length increases (Barneche et al., 2018; Marshall et al., 2019). As mean female size was significantly larger in MPAs, this was translated into mean number of eggs per female being 44-78% larger than in control areas in 2023, even though all areas experienced size increases.

Earlier estimates of mean individual egg carrying capacity between 2006 and 2015 (Calef, 2016) were lower than estimated in this thesis. Additionally, from 2006 to 2015 increases in MPAs and control areas were 160 % and 12 %, respectively (Calef, 2016). This is much higher compared to my estimated 35 % and 3% increases, respectively, from 2007 to 2015. Calef (2016) included females of all sizes, also below SoM, which is presumably the reason behind the big differences to my results. The assumptions made regarding SoM and spawning cycle when calculating egg carrying capacity in the studied population, would have affected the individual estimates of fecundity. Generally, lobsters can be both biennial, spawning every second year (Agnalt et al., 2007; Tully et al., 2001), or annual, spawning every year (Laurans et al., 2009; Waddy & Aiken, 1986). For instance, in Denmark SoM was 95.6 mm CL assuming annual reproduction, while assuming biannual reproduction reduced SoM to 86.5 mm CL (Freitas et al., 2023). If SoM is higher than 80 mm CL, the proportion of females being mature in the control areas would decrease even more.

A study at Kvitsøy in Norway found females below the minimum legal size (MLS) of 88 mm CL to contribute just 3–8% of the reproductive potential (Agnalt et al., 2007). Lobsters above the mean sizes targeted by the fishery had the maximum egg production. If the MLS was increased to 100 mm CL, 32–54% of the reproductive potential could potentially be saved (Agnalt et al., 2007). As almost half of the females sampled in control areas in 2023 were smaller than the MLS, this supported a low population productivity in the control areas. The low proportion of legal sized lobsters in control areas indicate that MPAs harbour a higher proportion of ovigerous females. This was

found in Scotland where catches of ovigerous lobsters were twice as high within the reserve as outside (Howarth et al., 2017).

What type of gear used may affect the sampled lobster sizes and thereby bias estimates on the actual individual egg carrying capacity in the studied populations. Helms (2023) found that the two-chambered 'parlour' traps used in lobster harvesting may under-sample individuals > 400 mm TL (Helms, 2023). This would especially affect mean female size and estimated mean egg carrying capacity in MPAs where the lobsters are allowed to grow larger. Irrespective of a possible underestimation of the positive effects of protection, large MPA effects are found. Sizes of lobsters caught before introduction of five large traps in 2016 may also be more influenced by gear-selectivity. However, size increases were evident before 2016 (Calef, 2016; Fernández-Chacón et al., 2020), indicating that this is not of big importance. Lobster size is important to describe egg carrying capacity, however lobster abundance also plays an important role in population productivity. Since protection in 2006, the lobster abundance and catch per unit effort (CPUE) in the three MPAs has increased substantially, with a modest increase in control areas (Fernández-Chacón et al., 2021; Knutsen et al., 2022). This further supports MPA effect on population productivity.

4.4 Fisheries and maternal effects

Additional to increase the number of eggs, big size and age before reproduction also increase the quality of the offspring (Agnalt, 2008; Attard & Hudon, 1987; Moland et al., 2010; Tully et al., 2001). Egg diameter and dry mass in lobsters increase with increasing mother size (Agnalt, 2008; Attard & Hudon, 1987; Tully et al., 2001). Large egg size further increases larvae size and survival (Moland et al., 2010). Sibert et al. (2004) suggest that bigger eggs use yolk lipids more efficiently and have faster embryonic growth than smaller eggs under the same conditions, which may explain why larger eggs often result in larger larvae. Harvest selection removes the largest females. Additionally, protection of ovigerous females may select for females allocating energy on reproduction instead of growth (Sørdalen et al., 2022). This reduces the complexity of female and offspring size, survival and maternal care, and thereby population resilience to environmental variability and change (Planque et al., 2010).

Female size also influences the time of hatching with large females hatching earlier than smaller females (Attard & Hudon, 1987; Gendron & Ouellet, 2009; Templeman, 1935). Thus, a wide size distribution can spread hatching of eggs in a population throughout the season. This will buffer against environmental fluctuations. For instance egg production is affected by temperature and food availability, which if disadvantageous can skew hatching outside the optimal season (van der Meeren et al., 1995). Large females can therefore play an even more important role in population replenishment than only producing more eggs. When the fishery truncates the size distribution in the population by removing the large individuals, there will be less spreading of eggs throughout the season. The maximum legal size is an attempt to increase the number of large females to get more resilient populations. However, as discussed above, the chances of surviving to this size is low due to the high fishing pressure.

4.5 Further research

To get even more correct estimates of mean individual egg carrying capacity it would have been helpful to calculate SoM for the specific populations. Additionally, smaller SoM due to removal of large females is expected over time when exposed to a highly selective

fishing pressure (Olsen et al., 2004). MPAs are proven to prevent fisheries induced evolution by increasing mean size, size distribution and natural growth (Fernández-Chacón et al., 2020; Sjørdalen et al., 2022; Sjørdalen et al., 2020). This is further supported by findings in this thesis. Comparing SoM in MPAs and fished areas over time could therefore be an indication if this evolutionary process will happen in the long-lived species if continuing the high fishing pressure. This information could be important in the continued management of the populations.

Estimated individual egg carrying capacity has been shown to be significantly higher in MPAs than in fished control areas. This likely helps rebuilding the protected population. Information on MPA effects on the adjacent fished areas would be of high valuable. High gene flow has been demonstrated within studied populations from approximately 400 km coastline in Skagerrak (Huserbråten et al., 2013). It was suggested that connectivity between lobster populations is primarily driven by larval export as the adult spill-over is restricted. It would therefore be interesting to quantify larval spill-over from MPAs to investigate to what degree increased egg carrying capacity in MPAs also benefits the adjacent populations.

4.6 Conclusion

In this thesis I have demonstrated how mean abdominal width and body length increased over time in female lobsters in three MPAs and control areas in Skagerrak. As predicted, mean individual egg carrying capacity was higher in MPAs, and increased steadily through almost two decades due to increased lobster sizes. Harvest regulation with protection of ovigerous females, increased minimum legal size and a maximum legal size is designed to help the harvested populations rebuild or at least to sustain them at present levels. Mean abdominal width and body length increased in control areas but was only translated into a small increase in egg carrying capacity due to the volumetric characteristics of egg-carrying. Updated fecundity estimates provided in this thesis are of value for the continued management of lobster populations, as the species is still heavily exploited in many areas. It demonstrates how protection can increase individual fecundity in sexually mature females. I have also suggested that protection has not changed the relationship of abdominal width to body length in same sized females, as detected differences were mainly driven by the largest females that were only present in the MPAs. The importance of a wide size distribution in populations, and the benefits of large females are discussed, and strongly points to total protection as the most effective tool to rebuild fecundity and resilience in the population.

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Appendix

Appendix 1 – Data overview

Appendix 2 – Female size

Appendix 3 – Relationship between AW and TL, overlapping size ranges

Appendix 4 – Relationship between AW and CL

Appendix 5 – Model diagnostics

Appendix 6 – Estimates of mean individual egg carrying capacity

Appendix 1 – Data overview

Table A1: Number of sampled female lobster (*H. gammarus*) in Flødevigen, Kvernskjær, and Bolærne each year after protection (2007-2023). Numbers after removing outliers (N = 43). In total 7485 observations.

Year	Flødevigen		Kvernskjær		Bolærne		Total
	Control	MPA	Control	MPA	Control	MPA	
2007	17	34	57	86	42	74	310
2008	26	39	107	99	29	80	380
2009	25	56	129	95	70	133	508
2010	38	62	95	111	59	108	473
2011	19	59	167	152	35	77	509
2012	20	49	125	137	72	139	542
2013	24	67	120	131	69	140	551
2014	30	59	86	90	62	100	427
2015	24	66	79	117	38	113	437
2016	18	57	82	97	25	96	375
2017	18	70	65	137	24	110	424
2018	25	81	62	140	39	107	454
2019	29	93	89	134	66	119	530
2020	15	85	35	35	24	93	287
2021	22	65	75	101	26	82	371
2022	36	72	74	129	40	130	481
2023	17	73	56	115	35	130	426

Appendix 2 – Female size

Table A2: Mean abdominal width (AW), carapace length (CL) and total length (TL) in mm \pm SE of female lobsters (*H. gammarus*). Estimates for all three areas in the two periods 2010-2014 and 2023. Only Flødevigen MPA and control area had data on AW in 2010-2014. Separated by protection status (control area, MPA). Estimates conducted with ANOVA, including all female sizes after removal of outliers.

Area	Year	MPA		
		AW	CL	TL
Flødevigen	2010-14	61.8 \pm 1.18	96.5 \pm 0.74	274.7 \pm 1.90
Kvernskjær	2010-14		94.1 \pm 0.56	267.1 \pm 1.44
Bolærne	2010-14		94.5 \pm 0.52	266.5 \pm 1.32
Flødevigen	2023	70.4 \pm 1.76	107.5 \pm 1.80	304.9 \pm 4.62
Kvernskjær	2023	67.2 \pm 1.48	103.5 \pm 1.48	292.2 \pm 3.82
Bolærne	2023	71.7 \pm 1.51	108.7 \pm 1.50	304.4 \pm 4.04

Area	Year	Control		
		AW	CL	TL
Flødevigen	2010-14	52.9 \pm 1.00	87.3 \pm 0.74	250.9 \pm 1.90
Kvernskjær	2010-14		85.0 \pm 0.56	243.3 \pm 1.44
Bolærne	2010-14		85.4 \pm 0.54	242.7 \pm 1.40
Flødevigen	2023	59.1 \pm 1.76	92.6 \pm 1.80	268.4 \pm 4.62
Kvernskjær	2023	55.8 \pm 1.48	88.5 \pm 1.48	255.2 \pm 3.82
Bolærne	2023	60.3 \pm 1.58	93.7 \pm 1.57	267.9 \pm 4.04

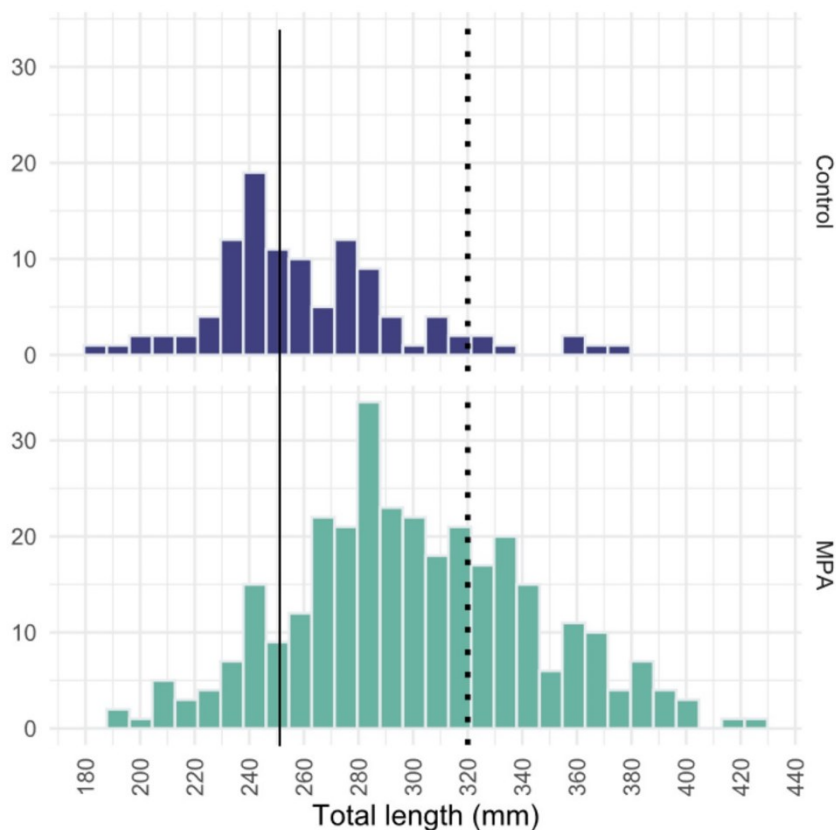


Figure A1: Frequency distributions of total length (TL) in millimetres (mm) of female lobsters (*H. gammarus*) in MPAs (green) and control areas (blue) in 2023. Data from Flødevigen, Kvernskjær, and Bolærne together. Vertical solid line denotes minimum legal size of 250 mm TL, and dotted line denotes maximum legal size of 320 mm TL.

Appendix 3 – Relationship between AW and TL, overlapping size ranges

The interaction term status: year in the temporal model was non-significant (ANOVA: $F_{1,498} = 1.78$, $p = 0.18$) and was removed from the model. This means that AW did not vary significantly with protection status in the two periods. Examining the residual plots indicated a reasonable model fit.

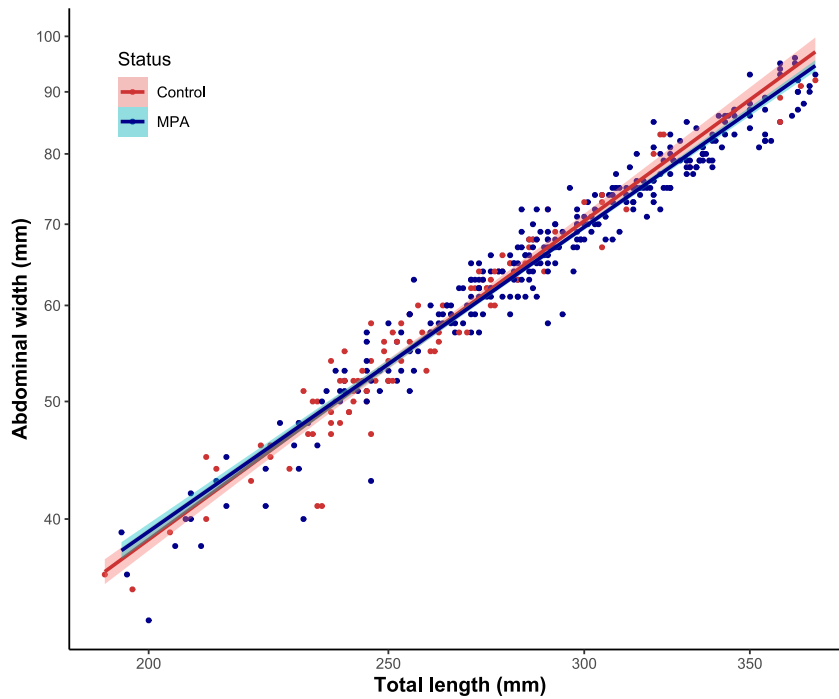


Figure A2: Relationship on a log-log scale (base e) between abdominal width (AW) and total length (TL) in mm in female lobsters (*H. gammarus*). Axis shows arithmetic values of size measures scaled to fit the linear log regression (Pélabon et al., 2018). Data only include overlapping size ranges in 2023. Regression in MPAs (blue) and control areas (red) in Flødevigen, Kvernskjær, and Bolærne areas together. With 95% CI.

Table A3: Summary of estimates, standard errors, t- and p-values for the two selected models. The first model (Eq. 1) compares the periods 2010-2014 and 2023 in Flødevigen. The second model (Eq. 2) includes the three areas Flødevigen, Kvernskjær, and Bolærne in 2023. Based on data after restricting to overlapping size intervals. Non-significant variables (> 0.05) in italics. Log with base e.

	Explanatory variable	Estimate	Std.Error	t-value	p
Adjusted $R^2 = 0.9597$	(Intercept)	-4.35	0.17	-25.95	< 0.001
	log TL	1.51	0.03	49.72	< 0.001
	MPA	0.33	0.19	1.73	<i>0.0848</i>
	Year period 2023	-0.01	0.01	-2.21	0.0277
	log TL: MPA	-0.06	0.03	-1.68	<i>0.0931</i>
Adjusted $R^2 = 0.9553$	(Intercept)	-4.34	0.20	-21.89	< 0.001
	log TL	1.50	0.04	42.50	< 0.001
	MPA	0.45	0.23	1.97	0.0495
	Kvernskjær	0.04	0.01	3.07	0.0023
	Bolærne	0.06	0.01	4.21	< 0.001
	log TL: MPA	-0.08	0.04	-1.89	<i>0.0599</i>
	MPA: Kvernskjær	-0.03	0.01	-1.90	<i>0.0582</i>
MPA: Bolærne	-0.04	0.02	-2.57	0.0106	

Appendix 4 – Relationship between AW and CL

Variation in AW with periods and over time with status was non-significant ($F_{1,508} = 1.01$, $p = 0.31$ and $F_{1,509} = 0.46$, $p = 0.50$, respectively). The selected models (Table A4) describe 96% and 95% of the data (adjusted $R^2 = 0.96$ and 0.95). The AW and AW-TL relationship varies significantly with status ($F_{1,510} = 10.26$, $p = 0.0014$ and $F_{1,510} = 10.14$, $p = 0.0015$, respectively) (Table A4). Model diagnostics indicate a reasonable fit to the data but showed a slightly curved variance plot (Figure A6, A7).

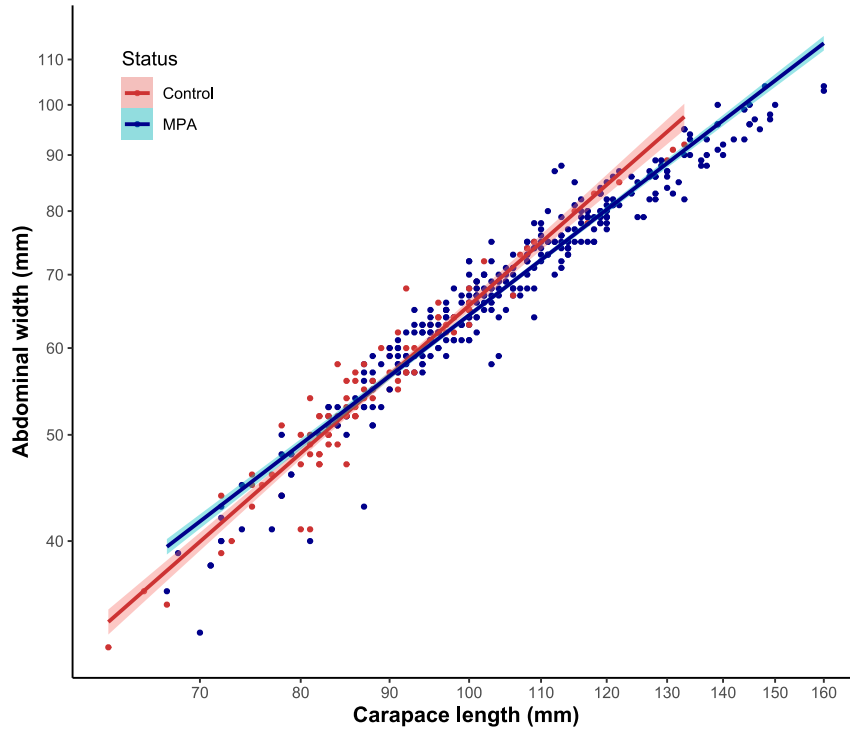


Figure A3: Relationship on a log-log scale (base e) between abdominal width (AW) and carapace length (CL) in mm in female lobsters (*H. gammarus*). Axis shows arithmetic values of size measures scaled to fit the linear log regression (Pélabon et al., 2018). MPAs (blue) and control areas (red) in Flødevigen, Kvernskjær, and Bolærne in 2023. With 95% CI.

Table A4: Estimates, standard errors, t- and p-values for the two selected models. The first model (Eq. 1) compares the periods 2010-2014 and 2023 in Flødevigen. The second model includes the three areas Flødevigen, Kvernskjær, and Bolærne in 2023 (Eq. 2). Based on data after cutting to overlapping size intervals. Non-significant variables (> 0.05) in italics. Log with base e.

	Explanatory variable	Estimate	Std.Error	t-value	p
Adjusted $R^2 = 0.9591$	(Intercept)	-2.34	0.12	-18.79	<0.001
	log CL	1.41	0.02	50.67	<0.001
	MPA	0.45	0.14	3.18	0.0015
	log CL: MPA	-0.10	0.03	-3.20	0.0014
Adjusted $R^2 = 0.949$	(Intercept)	-2.24	0.16	-13.83	< 0.001
	log CL	1.39	0.04	39.07	< 0.001
	MPA	0.81	0.18	4.50	<0.001
	Kvernskjær	0.02	0.01	1.42	<i>0.1579</i>
	Bolærne	0.04	0.02	2.91	0.0038
	log CL: MPA	-0.18	0.04	-4.45	<0.001
	Kvernskjær: MPA	-0.02	0.02	-1.28	<i>0.2010</i>
	Bolærne: MPA	-0.04	0.02	-2.46	0.0143

Appendix 5 – Model diagnostics

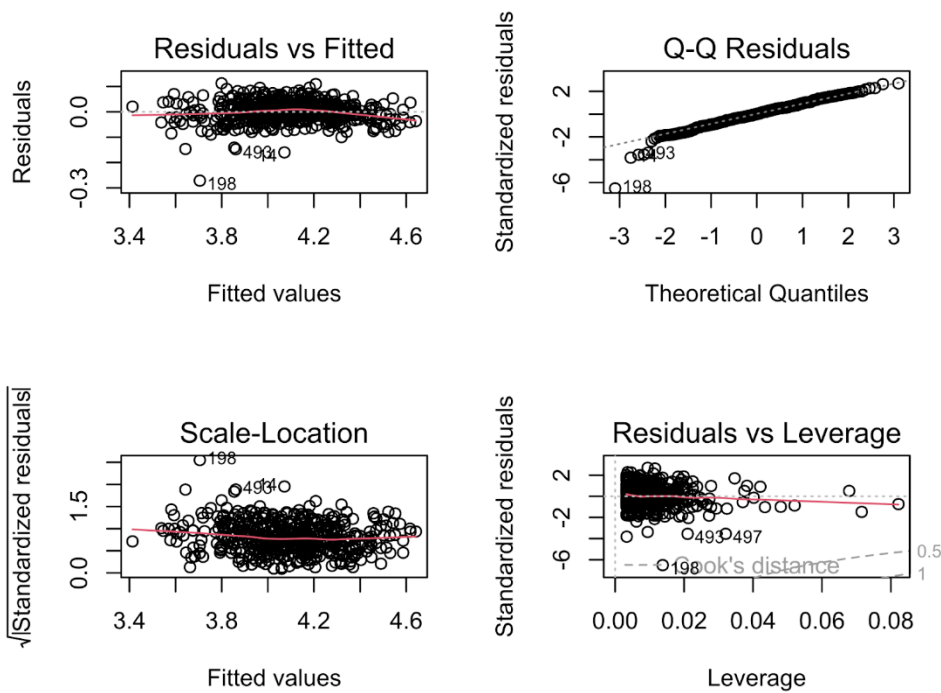


Figure A4: Model diagnostics to check for homoscedasticity and normality of residuals of the temporal model $\log AW \sim \log TL + \text{status} + \text{yp} + \log TL : \text{status}$.

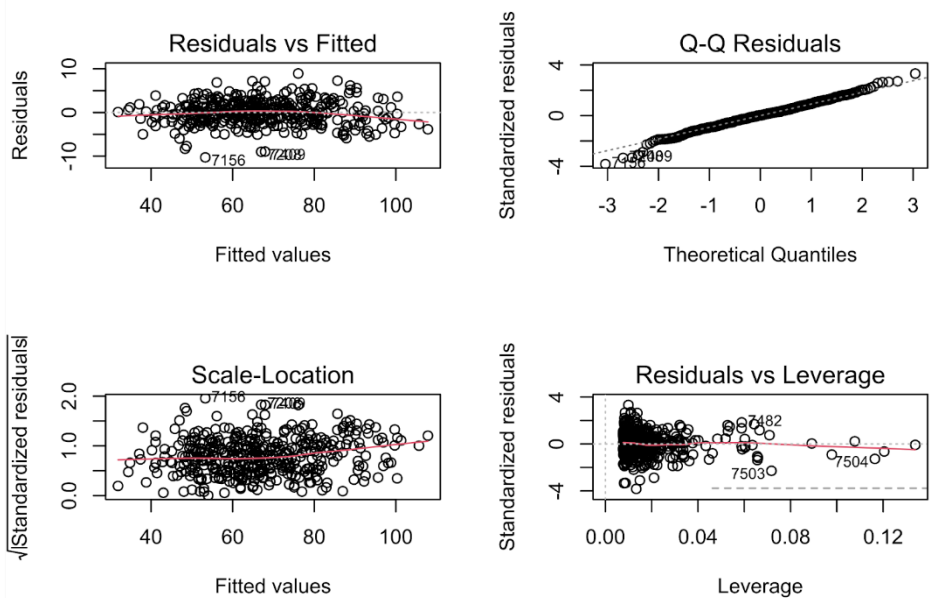


Figure A5: Model diagnostics to check for homoscedasticity and normality of residuals of the model $\log AW \sim \log TL + \text{status} + \text{area} + \text{status} : \text{area} + \text{status} : \log TL$.

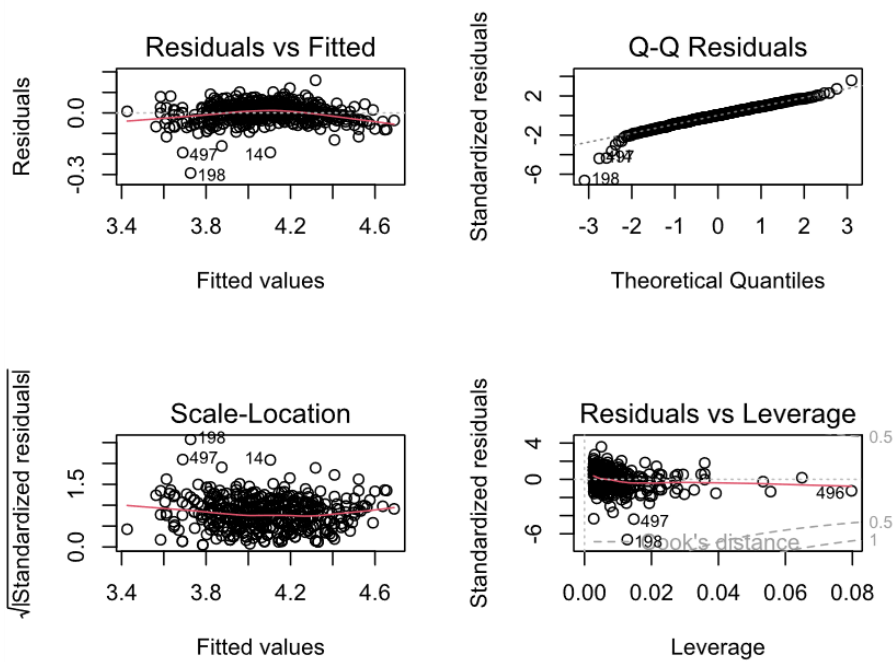


Figure A6: Model diagnostics to check for homoscedasticity and normality of residuals of the temporal model $\log AW \sim \log CL + \text{status} + \log CL:\text{status}$.

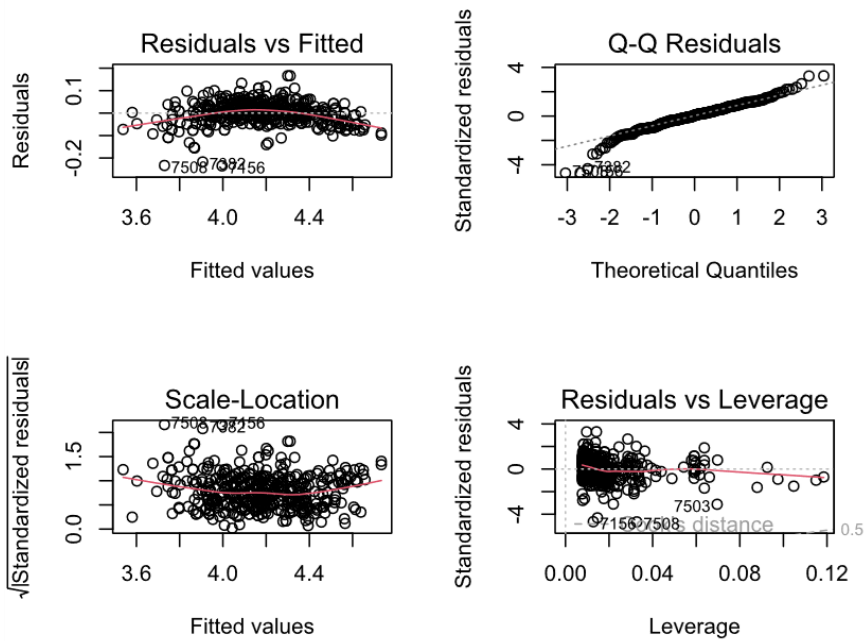


Figure A7: Model diagnostics to check for homoscedasticity and normality of residuals of the model $\log AW \sim \log CL + \text{status} + \text{area} + \text{status}:\text{area} + \text{status}:\log CL$.

Appendix 6 – Estimates of mean individual egg carrying capacity

Table A5: Mean individual egg carrying capacity in female lobsters (*H. gammarus*) with range through all years based on the model $F_{CL} = 0.0045 * CL^{3.2214}$. Percent diff represents change in mean individual egg carrying capacity from 2007 (first year of protection) in control areas and MPAs. Positive change since 2007 in bold.

Year	F _{CL} control	% diff	F _{CL} MPA	% diff
2007	9 283 (6 079–19 025)		10 156 (6 079–22 443)	
2008	7 658 (6 079–15 050)	-17.5	9 905 (6 079–39 483)	-2.5
2009	8 435 (6 079–17 459)	-9.1	10 129 (6 079–28 331)	-0.3
2010	8 783 (6 079–33 589)	-5.4	10 774 (6 079 – 27 630)	6.1
2011	8 585 (6 079–23 671)	-7.5	10 831 (6 079 – 40 380)	6.6
2012	9 039 (6 079–24 302)	-2.6	12 124 (6 079 – 36 876)	19.4
2013	8 840 (6 079–31 260)	-4.8	12 241 (6 079 – 46 055)	20.5
2014	9 468 (6 079–18 493)	2	13 276 (6 079 – 32 800)	30.7
2015	9 512 (6 079–25 598)	2.5	13 699 (6 079 – 43 153)	34.9
2016	9 787 (6 079–20 121)	5.4	15 589 (6 079 – 41 290)	53.5
2017	9 805 (6 079 – 29 045)	5.6	15 018 (6 079 – 36 876)	47.9
2018	10 315 (6 079 – 27 630)	11.1	15 422 (6 079 – 49 088)	51.9
2019	9 679 (6 079 – 25 598)	4.3	15 500 (6 079 – 56 698)	52.6
2020	9 394 (6 079 – 29 771)	1.2	17 146 (6 079 – 51 186)	68.8
2021	9 313 (6 079 – 30 509)	0.3	16 900 (6 582 – 56 698)	66.4
2022	9 798 (6 079 – 35 206)	5.5	16 171 (6 079 – 49 088)	59.2
2023	10 623 (6 327 - 31 260)	14.4	17 728 (6 327 - 56 698)	74.6

Table A6: Mean individual egg carrying capacity in female lobsters (*H. gammarus*) through all years based on the model $F_{CL} = 0.0045 \cdot CL^{3.2214}$. Percent diff represents change from mean individual egg carrying capacity the year before in control areas and MPAs in Flødevigen, Kvernskjær, and Bolærne. MPAs were implemented in 2006, so this table shows the development in individual egg carrying capacity 17 years after protection. Positive percentage change marked in bold.

Year	Flødevigen MPA		Kvernskjær MPA		Bolærne MPA	
	Mean	% diff	Mean	% diff	Mean	% diff
2007	11129		9633		10163	
2008	11076	-0.5	9045	-6.1	10205	0.4
2009	11915	7.6	9719	7.5	9600	-5.9
2010	12349	3.6	9818	1.0	10834	12.9
2011	11117	-10.0	10655	8.5	10954	1.1
2012	13590	22.2	12644	18.7	11084	1.2
2013	14754	8.6	11976	-5.3	11305	2.0
2014	13926	-5.6	12547	4.8	13552	19.9
2015	15169	8.9	13214	5.3	13344	-1.5
2016	18060	19.1	15325	16.0	14371	7.7
2017	15268	-15.5	14531	-5.2	15439	7.4
2018	16846	10.3	15898	9.4	13793	-10.7
2019	18562	10.2	14531	-8.6	14072	2.0
2020	18280	-1.5	17199	18.4	16096	14.4
2021	17408	-4.8	15932	-7.4	17659	9.7
2022	19503	12.0	15754	-1.1	14803	-16.2
2023	17464	-10.5	17119	8.7	18359	24.0
Year	Flødevigen control		Kvernskjær control		Bolærne control	
	Mean	% diff	Mean	% diff	Mean	% diff
2007	9247		9289		9303	
2008	8488	-8.2	7468	-19.6	7157	-23.1
2009	9272	9.2	8203	9.8	8547	19.4
2010	9339	0.7	7970	-2.8	9541	11.6
2011	8624	-7.7	8313	4.3	9616	0.8
2012	9898	14.8	8881	6.8	9124	-5.1
2013	9042	-8.6	8705	-2.0	9059	-0.7
2014	9939	9.9	8858	1.8	10158	12.1
2015	10469	5.3	9163	3.4	9585	-5.6
2016	11084	5.9	9194	0.3	10620	10.8
2017	10999	-0.8	9297	1.1	10382	-2.2
2018	10752	-2.2	8974	-3.5	11992	15.5
2019	9742	-9.4	8855	-1.3	10816	-9.8
2020	9818	0.8	8688	-1.9	10324	-4.5
2021	8754	-10.8	9392	8.1	9624	-6.8
2022	10838	23.8	9571	1.9	9276	-3.6
2023	12129	11.9	9610	0.4	11415	23.1

