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Short-term effects of a marine sanctuary on the local lobster population in the Oslo fjord, Norway

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Preface

This master thesis was written at the Norwegian University of Life Sciences by Mari Vold, student in the Natural Resources and Wildlife Management program, under supervision of Stein R. Moe, Thrond O. Haugen and Jonathan Colman. Thrond's expert guidance concerning everything related to statistics, models, plots and figures, combined with his benevolent presence during our meetings, have kept me moving forward through the semester. Stein's quick responses to my every question, his thoroughness and attention to detail has lifted the quality of this thesis considerably. Jonathan deserves every admiration for contributing extensively to the field work even with broken bones in his legs! Many volunteers have also taken part in our field work during lobster sampling in September 2020 and 2021, and December 2021. Their efforts are invaluable. A special mention to Knut and Odd, and Teyie, who always made me laugh. I heartily thank you all!

The corona pandemic loomed over the country when this thesis was initiated. The field work was not very affected by this. Working from home on a lonely project such as a master thesis, however, is no easy feat after enduring nearly two years of social restrictions and weeks and months of isolation, quarantine, and disease. Returning to the study hall felt like quite the ordeal to me. Without my classmates and friends, I would be hard pressed to find enough motivation to come back to the university and finish my degree. You gave me the reason I needed to show up. I never would have enjoyed every day of this semester as much as I did without our routinely lunchbreaks at noon, and other spontaneous breaks (hours and hours) throughout the day. A special mention to Ane and Erland. You have been my rock and family and I thank you for always being there so reliably. I would not have done it without you.

Thanks to Linnea for pushing me out of my discomfort zone and reminding me to take care of my physical health. Without you, I would sit tightly with my back ache and "take care of it later". Thanks to my classmates for making me feel like I belonged from the moment I entered NMBU. Thanks to the boys, for including me, for your enthusiasm over our common interests in nature and wildlife, and for sharing with me your nerd-level knowledge reaching far beyond the scope of our curriculum. To have such friends is a privilege.

Thanks to every teacher who has made extra efforts to get us through our classes during a pandemic. It has truly meant a lot. Thanks to my family for supporting me through my quarter-life-crisis and the final lapse of my extended education. That includes you, Embla, the most patient dog in the world. I owe you so much. I would also like to thank Leikarringen Frøy and Flatlusa spelemannslag for welcoming me into another family, Agrarmetropolens Tradenighet. They received me with open arms far outside the ordinary admission season, and despite my short student-life-expectancy. The fresh breath of music and dance has reawakened a dormant joy for life and play in me, and it has truly made me happy. With that, my greatest ambitions on my own behalf are achieved.

Now remains only the saving of Mother Earth, the love of my life and main reason why I do anything at all, whom I thank more than anything or anyone else, for my life, purpose, and all things worth fighting for. I promise to fight hard for as long as I may live.

Ås, May 2022
Mari Vold

Abstract

The European lobster (*Homarus gammarus*) population in Norway is over-fished and endangered, and marine protected areas (MPAs) are an increasingly utilized measure for protection of this species. Previous studies in Norway have shown that even small MPAs can benefit the local lobster population, and that protection responses can be detected after a short period of time, such as increased survival, population abundance and mean body size. Still, there are different demographic responses in different MPAs, which means there are regional effects that call for more investigations. This is the first study conducted in the Oslo fjord, presenting an analysis of the short-term demographic responses to protection of a new, small MPA. I have studied survival, population density and sex ratio in a fjord system, the Oslo fjord, with high pressure from fisheries, pollution, climate change and other human impacts, using mark-recapture methodology with a “before-after control-impact" design (BACI) applying robust design models. The sampling effort consisted of 3 sessions (September 2020, September 2021, and December 2021) with 20 traps x 5 days and ~24 hours soaking time. A total of 304 lobsters were captured and tagged, and 49 recaptures were registered.

Within the MPA, male survival was shown to increase with body size and was substantially higher for large body sizes relative to male survival in the control area, proving that male lobsters benefit from sex-selective harvesting protection already after just one effective protection season. Simultaneously, a high and stable survival for females in the control area showed that females benefit from fishing regulations that protect egg-bearing females. Confidence intervals were large, especially for males in the control area and females in the MPA, due to small sample sets and few recaptures.

The abundance and density of male lobsters in the MPA was much higher than in the control area after the first effective protection season, proving that fishing mortality is high in the harvested population and gives room for rapid demographic responses in a recently protected lobster population.

The body size distribution in both MPA and control area are further testimony to a high and size-specific fishing mortality in harvested areas of the Oslo fjord, showing low fractions of large males and of legal-sized females. A high fraction of small males in the MPA points to a high potential for rapid growth and increased phenotypic diversity in the protected population following protection. The results show that mean body size did not change notably for neither females, nor males, but strongly suggests that catchability for female individuals increased from September to December.

Sex ratio investigations show that there is a relatively higher share of males in the MPA after the first effective protection season, relative to the control area.

Combined, the results show that marine protected areas have short-term effects on local lobster demography, indicating that the fishing pressure in high and gives room for rapid responses in the lobster population.

Contents

Introduction

The European lobster (*Homarus gammarus*, hereafter "lobster") in Norway is over-exploited and classified as VU (vulnerable) on the Norwegian Biodiversity Information Centre's "red list" for endangered species (Tandberg, 2021). Establishment of marine protected areas (MPAs) in Norway is one of several management measures meant to secure sustainable lobster populations. Trap fishing within the MPAs is prohibited (Norwegian Fisheries Directorate, Unknown-a) Similar lobster reserves in Skagerak (Flødevigen, Bolærne and Kvernskjær) have been proven to benefit lobster populations locally, even if the reserve is small (0.5-1 km^2) (Fernández-Chacón, 2021; Moland et al., 2013). Among the positive protection effects on lobster in MPAs are increased abundance, population density and survival (especially for legal-sized lobsters (25-32 cm, (Norwegian Fisheries Directorate, Unknown-d)) and males(Fernández-Chacón, 2021)), increased mean body size (Moland et al., 2013) and restoration of sexual selection and sexually selected traits, such as large claws and bodies (Sørdalen et al., 2020).

MPAs' positive effect on lobster populations in Norwegian waters are partly explained by the residency and small home ranges of European lobsters (Moland et al., 2011). Several studies show that most lobsters move only a few kilometres during a one-year period and are often recaptured close to their primary encounter location (Huserbråten, 2013; Moland et al., 2011; Smith, 2001). Short migration distances are linked to availability of lobster habitat, and vice versa (Smith, 2001).

Lobsters suffer a high and stable mortality in areas open to harvest (Fernández-Chacón, 2021), but because of size- and sex-specific fishing regulations, survival in populations exposed to harvesting is also unnaturally dependent on body size and sex. A "legal body length" is a mortality cause to the lobster in a fished population, unlike populations protected from harvesting, where a larger body size is expected to have positive effect on survival (Fernández-Chacón et al., 2020). The sex-differentiated fishing selection in Norway stems from the protection of all females with external eggs, regardless of body size. Lobster populations in MPAs have a larger mean body size and higher phenotypic complexity than fished populations (Fernández-Chacón et al., 2020). Sexually selected traits in males (large bodies and large claws) that are insignificant in control areas, increase over time in MPAs (Sørdalen et al., 2018; Sørdalen et al., 2020).

In 2021, a new marine protected area was established in the Oslo Fjord. According to the demands set by the European Water Framework Directive (WFD) established in 2000, all Norwegian bodies of water, including fjords, must have "very good/good ecological status" (WFD 2000/60/EC). The Oslo Fjord is presently classified as having "poor ecological status" due to human impacts such as overfishing, pollution, and climate change (Norwegian Environment Agency, 2019). This is therefore an interesting site for replication studies on lobster in a marine protected area, as regional effects are shown to give different protection results in different MPAs (Fernández-Chacón, 2021). Replication studies are necessary to discover such regional effects, and this is the first study to investigate MPA effects in the Oslo Fjord. With the shortest time series possible for application of BACI and capture-mark-recapture analyses, this study aims to find short-term demographic effects of a new MPA on the local lobster population.

Given the extensive harvesting and sex-specific regulations in Norway, I expected survival to increase in the MPA after protection for both sexes, but even more for males than for females relative to areas open to harvesting outside the MPA. In the control area outside the MPA, on the other hand, survival would expectedly stay low after protection of the MPA because mortality caused by fishing should remain high.

My prediction was that the lobster population and density in the MPA would be higher after the fishing season in 2021, relative to the control area, and that the difference would be larger for males than females. I expected the control area population and densities to decrease during the fishing season in 2021.


Figure 1: Gravid female lobster sampled in the MPA on September 17th in 2021.

As mean body size for both sexes, male body size particularly, has increased in the absence of harvesting in Scandinavian MPAs similar to the MPA studied here (Moland et al., 2013), I expected to see the start of a development like this in this study as well. At the same time, I also predicted a difference in body size distribution between the MPA and control area after the first fishing season following protection, assuming that legal-sized lobsters would be taken out of the control area during the fishing season, while they would survive and remain detectable in the MPA.

As a result of sex-differentiated fishing selection, and assuming a natural sex ratio of about 1:1, I expected the sex ratio in the control area, and MPA prior to protection, to be skewed in favor of females. Protection was expected to benefit males in the MPA more than females, leading to a more balanced sex ratio within the reserve after protection had taken effect.

Materials and methods

Study species and regulations

The European lobster is a long-lived species of decapod crustacean. Age estimates up to 57 years (Sheehy et al., 1999) and sizes up to 50 cm and weights up to 8 kg are registered (Otterlei, Unknown). Lobster populations in Norway are subject to overfishing and high harvesting mortality, and lobsters are unlikely to become this large and old (Fernández-Chacón et al., 2020). According to regional fishing regulations, lobsters in the Oslo Fjord are protected from December 1st until October 1st. Fishing can be conducted during October and November, under the limitation of 10 traps for recreational fishers and 100 traps for commercial fishers. Lobsters with external eggs, and lobsters smaller than 25 cm or longer than 32 cm are protected all year long and must be released back into the fjord if caught in a trap. (Norwegian Fisheries Directorate, Unknown-d) Lobsters of 25-32 cm are hereafter denoted “legal-sized”.

Sex- and size-specific harvesting regulations can change population demography and phenotypic diversity, often selecting for conspicuous traits such as large body size or antlers (cervids) that are connected to high fitness and reproduction potential, and sexual selection (Sørdalen et al., 2018; Sørdalen et al., 2020). Female lobsters, given the opportunity in a diverse population, prefer males with larger bodies and claws over smaller males with smaller claws. A lack of large males may therefore lead to evolution towards smaller body lengths and claw lengths (Sørdalen et al., 2018; Sørdalen et al., 2020). Lobsters in Norway, males particularly, are unlikely to become fully grown because of high fishing mortality from commercial and recreational fishing. Most male lobsters are fished shortly after they reach the minimum legal size of 25 cm (Fernández-Chacón et al., 2020) and will therefore never reach the maximum legal size of 32 cm. In other words, ordinary fishing regulations are likely not enough to secure sexual selection, phenotypic diversity, and a healthy demography in a wild lobster population. The European lobster needs additional protection measures, such as MPAs. MPAs are proven to be effective since the lobster has a high site fidelity, using small home ranges of 5728-41548 m^2, mean 19879m^2 +/- 2152m^2 over 242 days of observation (The Norwegian Skagerak coast, Sept 2006 – Aug 2007), with no significant difference between sexes (Moland et al., 2011; Moland et al., 2013). Even a small MPA can therefore benefit lobster populations locally (Moland et al., 2013).

Figure 2: Norwegian nature surveillance (Statens naturoppsyn, SNO), an operational unit under the Norwegian Environment Agency, stopping by to make sure that research sampling happened in accordance with permissions. MPA, September 16th, 2021.

Study system

This study has been conducted in a newly established lobster reserve and control area nearby in Drøbaksundet, south of Oscarsborg and west of Drøbak, respectively (Figure 4). The reserve was established in 2021, and all types of fishing equipment except hook-and-line are now banned.

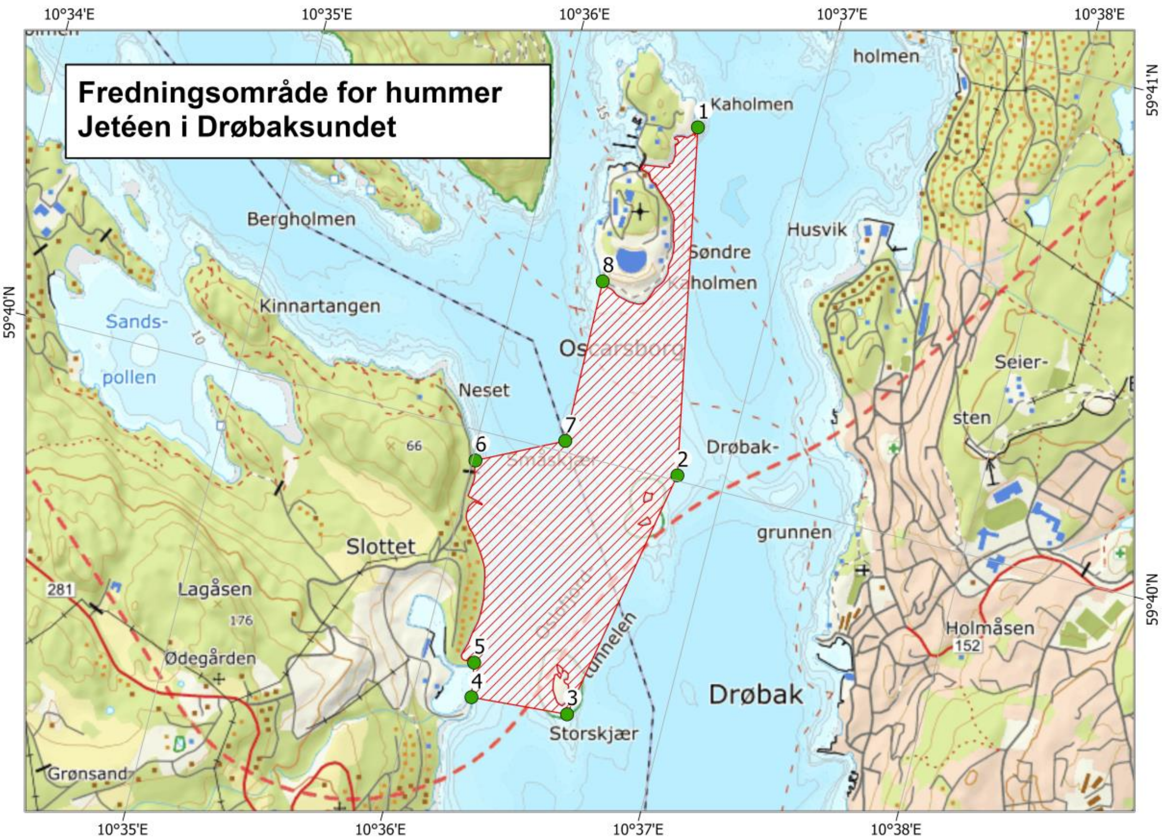

Figure 3: The marine protected area for lobster, Jetéen in Drøbaksundet (Norwegian Fisheries Directorate, Unknown-c).

Lobster sampling design

Using capture-mark-recapture methods, research sampling with traps was conducted three times, once in 2020 (17-21 September, session 1), and twice in 2021 (16-20 September, session 2; and 5-9 December, session 3).

Sampling session 1 was conducted prior to legal protection. Session 2 was conducted after protection but before the next ordinary fishing season. In other words, the legal protection of lobsters in the MPA had not yet led to a difference in human impact between the MPA and the control area. The third and final sampling session (session 3) was conducted after the ordinary fishing season, making it possible to investigate the developments in the marine protected area and the control areas, respectively, using a before-after control-impact (BACI) approach.

Table 1: Temporal sampling design. The MPA was protected between sessions 1 and 2. Lobsters in the MPA were effectively protected for the first time during the ordinary fishing season of 2021 (Ocotber 1st-November 30th). Sampling session 3 was therefore the first opportunity to discover protection-induced demographic differences between subpopulations in the MPA and control areas.

Month	J	F	M	A	M	J	J	A	S	O	N	D
2020									1			
2021									2			3

Sampling sessions   Fishing season

The trap type used for lobster sampling is a common lobster trap by Norwegian standards, such as described by the Norwegian Directorate for Fisheries (Norwegian Fisheries Directorate, Unknown-b). Trap distribution was designed using stratification (2 layers of depth intervals at 5-20 m and 20-50 m, 10 traps per layer = a total of 20 traps per area) and randomized positions within the two depth strata, with a minimum of 30 meters horizontal distance between traps were drawn using the "random-points-inside-polygon"-tool in QGIS. All escape routes from the traps were closed during sampling.

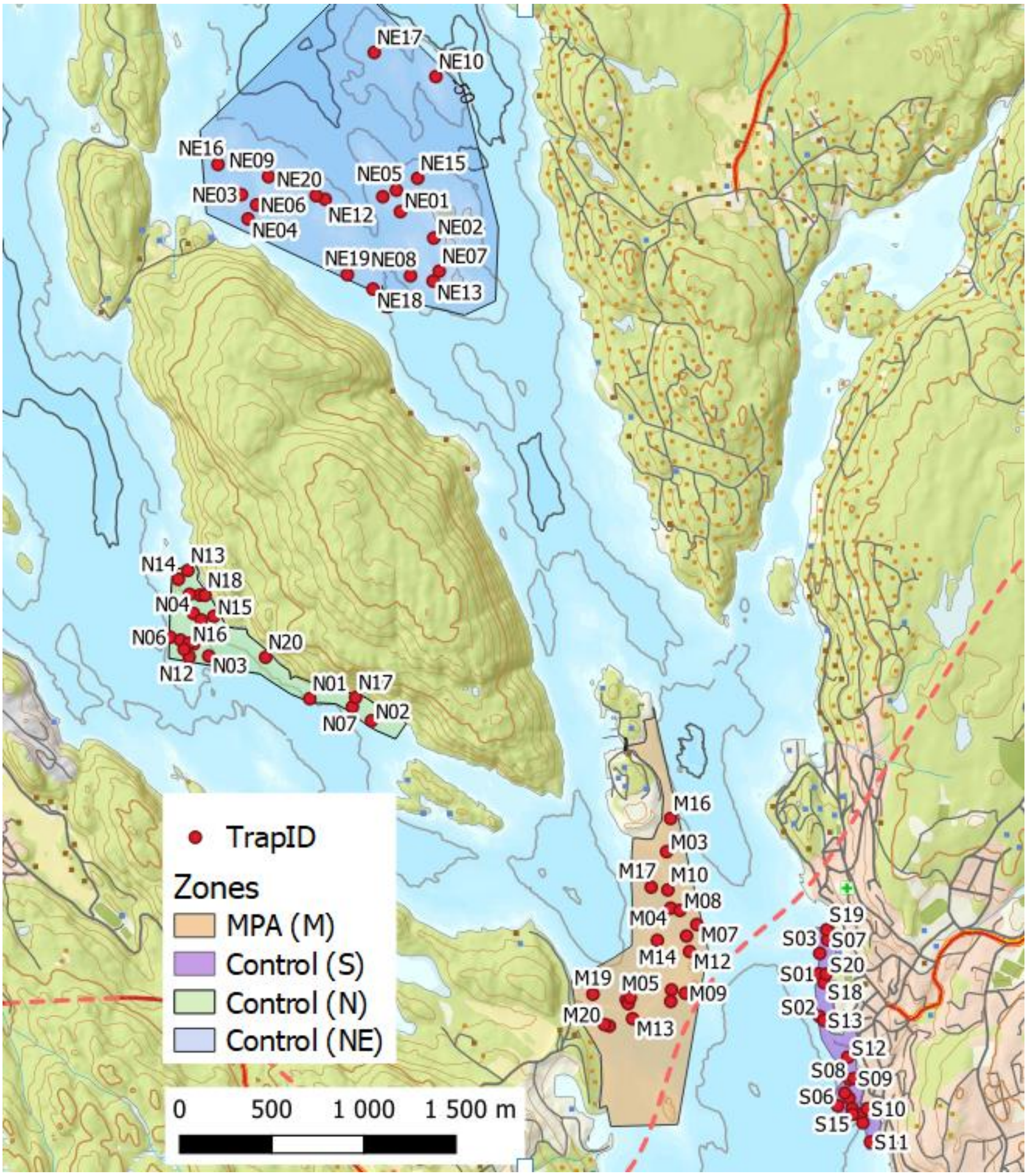

Figure 4: Map showing trap placements in the MPA and control areas. The MPA traps are denoted with an M, while control area traps are denoted with a letter pointing roughly towards the area's location in cardinal directions (S=south, N=north, NE=North-East). Data from areas N and NE were not used in the statistical analysis, as the modeling tools were unable to estimate their parameters.

Figure 5: Odd handling one of the standard lobster traps during sampling sessions. MPA, September 16th, 2021.

Every sampling session consisted of 5 days of fishing, with approximately 24 hours of soaking time for each day (i.e., a sampling effort of 20 traps x 5 days per site per sampling session). The MPA and control area were fished simultaneously, so that shared temporal effects could be accounted for. Although attempts were made to achieve consistent trap locations, traps were occasionally transported over several tens of meters at the worst because of wind drift and strong tidal currents in both MPA and control areas. Human error, such as inconsistency in field routines, combined with two non-matching location sets (boat GPS vs hand-held GPS) added further to this dilemma, which affects the precision with which we might predict area and location dependent sizes such as local lobster population density.

Capture – mark – recapture methods: Field routines

Every captured lobster's length was measured from the tip of the rostrum to the posterior margin of the telson. We determined the sex by examination of the first pair of pleopods. The lobsters were tagged with 60 mm white T-bar tags (FD-94, T-bar, Floy-tag Inc) in the thorax before we released them back into the fjord. All lobsters were handled as quickly and gently as possible, to ensure that animal welfare standards were met. Length, sex, external eggs, and recaptures were noted for each trap, date, and sampling area.

Statistical analysis

Mark-recapture data was analyzed using Huggins Robust Design models with MARK software (Huggins, 1989). Preparation of data and construction of input-file to Mark was performed in Microsoft Excel, while visual presentation of results in plots were made using R software.

The Robust Design approach allows for a simultaneous estimation of survival, S, and true capture probability, p*, recapture probability during a fishing session, c, and finally two parameters that keep track on individuals availability for capture, γ' and γ''(Figur 7). All parameters are estimated under the assumption of a demographically closed system (no net migration or mortality) during a fishing session. Owing to the few sample sessions included in this study, none of the availability-parameters could be estimated. However, all remaining parameters were estimable.

Table 2: Availability probabilities for different scenarios

	Unobservable, time i	Observable, time i
Unobservable, i+1	γ'_i	γ''_i
Observable, i+1	$1-\gamma'_i$	$1-\gamma''_i$

The capture probability allows us to estimate population abundance, N, and population density, N divided by area.

$$N = c \cdot p^*$$

Population size estimates were converted to effective population densities by assigning a maximum effective sampling area (A_e, Figure 6A) around each trap corresponding to literature-based home-range areas (HR) measured for lobster from Skagerrak area (Olsen et al., 2011). By summing up the union of the individual A_es, a total zone-specific effective sample area (totA_e) could be estimated in Qgis (Figure 6B). The effective population density could then be estimated as: N/totA_e.

A B

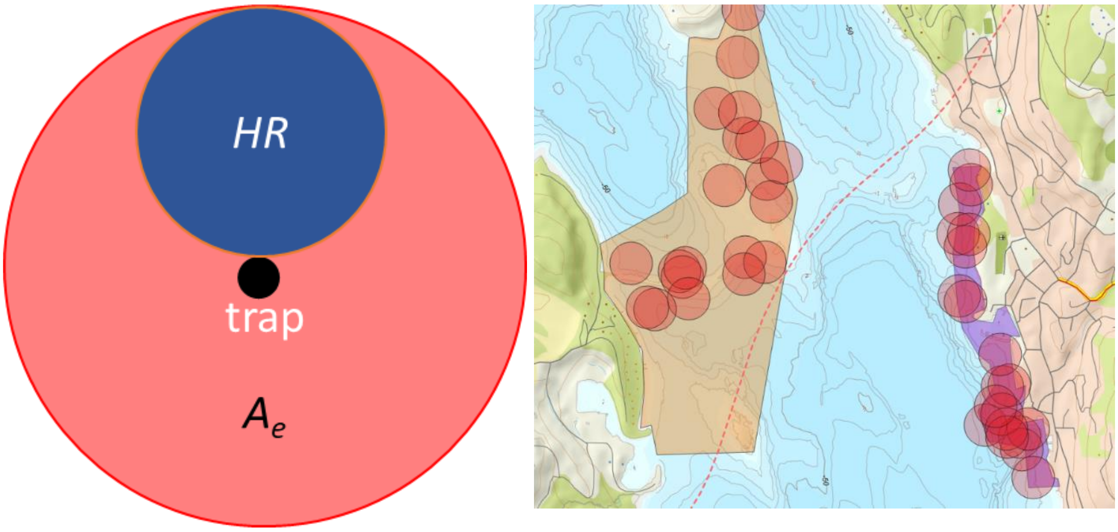

Figure 6. A. Definitions of home range areas (*HR*) and effective sample areas (A_e) for a trap. B. Distribution of trap-specific A_es from part of the MPA (M) and the control area (S).

Table 3: Effective area fished given trap locations in sampling zones.

Area name	**Total area, totA_e [m^2]**
MPA (M)	279239
Control area (S)	182228

Robust design models are dependent on recapture data, and they are sensitive to extreme values when recapture data sets are small. This leads to instabilities and non-convergent parameter estimates. Data from N and NE were therefore excluded from further statistical analysis.

The Huggins robust design parametrization

From the input file containing individual encounter histories, the five parameter types could be estimated using log likelihood method implemented in the software Mark. The set-up consisted of three sampling sessions (Sep20, Sep21, Dec21) with five encounter occasions each. This allowed for estimation of two survival estimates (Sep20-Sep21 and Sep21-Dec21), as well as true capture probability (p*) and recapture probability (c) for each sample session.

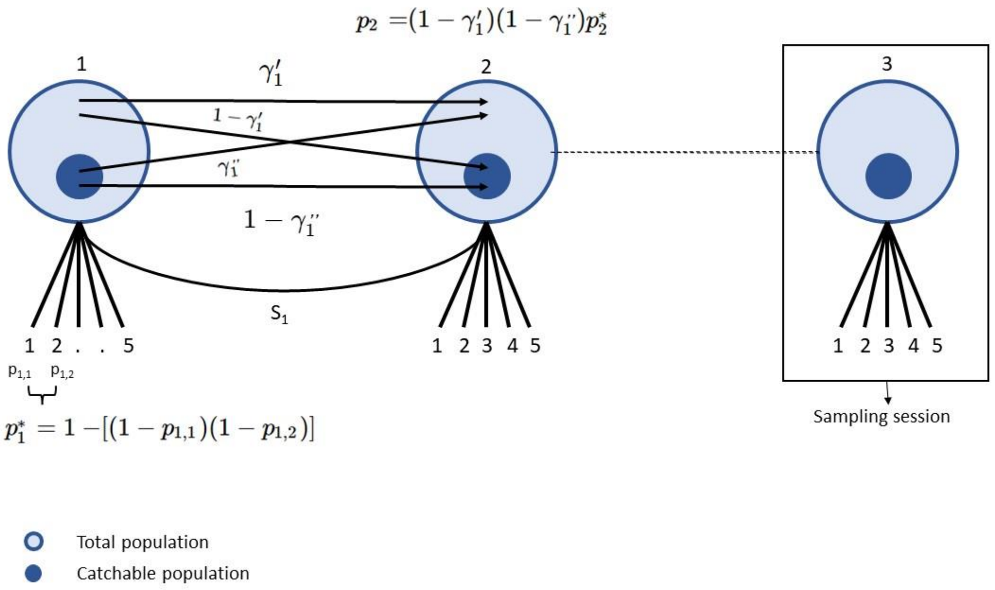

Figure 7: Parameter diagram for the Huggins robust design models.

- p*: True detection probability - needed for estimation of population size N
- γ: probability of movement between catchable subpopulation and total population
- 1-γ: probability of availability
- p: Apparent encounter probability
- S_i: Survival from session_i to session_i+1

MARK

Detection histories were created for a MARK input file using logical values (0=not encountered, 1=encountered), with one entry per day of fishing adding to total of 15 encounter possibilities (3 sessions * 5 days) for each lobster individual.
For instance, a detection history like 010001001000000 would mean the individual was encountered for the first time on day two during the first sampling session (i.e., September 2020, colored red), re-encountered on the first and fourth days during session two (i.e., September 2021, colored blue) and not encountered during session 3(i.e., December 2021, colored black). By combining all individuals' encounter histories, the likelihood of observing certain histories under various estimates of survival, detection probabilities and observabilities could be constructed in MARK. The various parameters under estimation could also be made conditional on group effects such as zone and sex and functions of individual (and external, but not applied here) covariates such as body size. This made it possible to address key hypotheses pertinent to this study, such as differential length-specific survival between sex and zones. Construction of candidate CAS models were motivated by the hypotheses formulated for this study, with focus on size, zone, and sex effects on survival. The fitted candidate models were subjected to model selection using AICc as a criterion (Akaike, 1974; Anderson, 2008).

To test for temporal or spatial change in sex-ratio between zones and capture sessions candidate generalized linear models were fitted using a binomial response where 1=females and 0=males and a

logit link function(McCullagh & Nelder, 2019). Effect tests were performed using loglikelihood-ratio tests.
In order to explore changes in size distribution between zones and capture sessions kernel-based density plots were inspected. Owing to multimodal length distributions, no formal tests were performed at this stage.

Results

A total number of 304 individual lobsters were captured and marked for the first time during our 3 sampling sessions in the MPA and control area combined (Table 4). There was an uptake in capture numbers in the MPA in session 3, compared to sessions 1 and 2, while capture numbers in the control area decreased slightly for every session (Table 5). Out of 304 sampled lobsters, 49 (~ 16 %) have been recaptured and 12 (~2.4 %) have been recaptured more than once. Put together, the 49 recaptured individuals were encountered 64 times (Table 6).

Table 4: Number of first captures in the MPA and control area.

Area	Individuals	%
MPA	192	63,16
Control area	112	36,84
SUM	**304**	**100**

Table 5: First captures divided by sampling zone and session.

Session	MPA	Control area	Total
1	57	44	101
2	45	36	81
3	90	32	122
Total	**192**	**112**	**304**

Table 6: Numbers of encounters for recaptured individuals.

Encounters per individual	Individuals	Total number of encounters	Recaptures
2	37	74	37
3	9	27	18
4	3	12	9
SUM	**49**	**113**	**64**

Survival (Huggins model)

The Huggins model selection favored a model where survival (from September 2021 to December 2021) was modelled as function zone, sex and individual length, p* and c as function of session and zone (Table 7). Gammas were modelled as constants (but no reliable estimates were provided (highlighted, Table 8). The selected survival model attained 42 % of the AICc-support amongst all fitted candidate models.

The robust design model analysis issued no convergent parameter estimates for two other control areas, N (not sampled in 2021) and NE (Figure 4) There were only 3 recaptures in total from these areas, all of them females.

Estimated survival for males in the control area were high for sizes < 25 cm. Legal-sized-male survival estimates decreased rapidly towards no survival for males longer than 32 cm (Figure 8). Out of 9 male recaptures (Table 9) from this area, three were made in December 2021 and only one of these (26 cm) was larger than 25 cm.

Estimated survival for males in the MPA ranges from ~70 % to ~80 %, positively correlated with body size (Figure 9). Out of 16 male recaptures, four were < 25 cm, eleven were legal-sized, and one was longer than 32 cm.

Survival predictions for females in the control area were close to 90 % for all body sizes (Figure 8). Out of 16 female recaptures in the control area, two were longer than 32 cm, four were shorter than 25 cm, and the rest were legal-sized. Two females have been recaptured three times each. Both were legal-sized and encountered in all three sampling sessions. 10 out of 16 recaptured females were registered with external eggs. One of these were < 25 cm, two were > 32 cm, and the rest were legal-sized.

Estimated survival for females in the MPA decreased with body size (Figure 8). Out of 8 recaptured females in the MPA, three were < 25 cm, four were legal-sized, and one was 36 cm long.

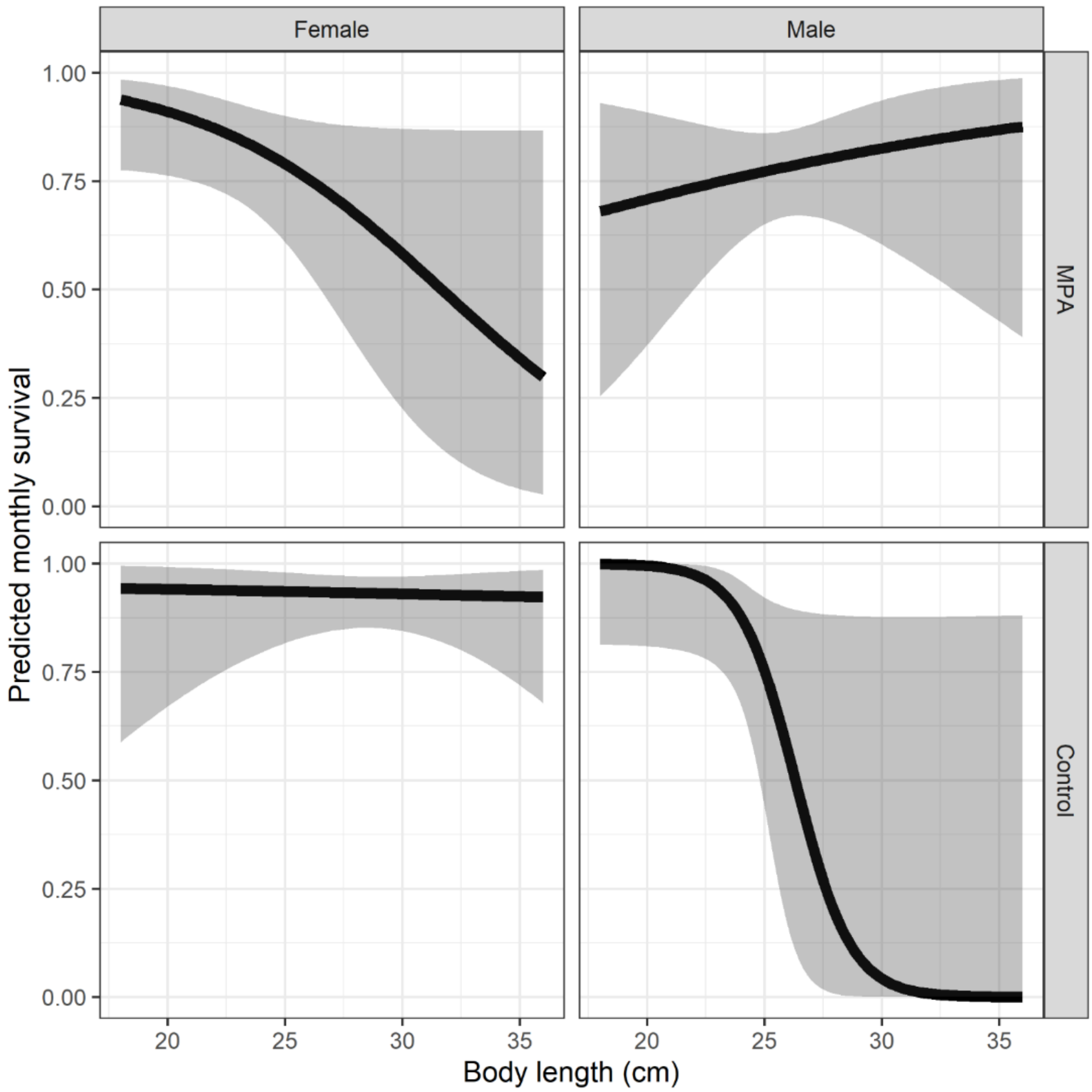

Figure 8: Monthly survival from September 2021 to December 2021 as a function of body length, with sex and sampling area as additional parameters.

Table 7. Model selection table for candidate Huggins models fitted to capture-mark-recapture lobster data from the Drøbak area from September 2020 to December 2021. Abbreviations: G=gender [M=male, F=Female], Z=Zone [C=control, MP=MPA], t=time [t1=Sep20, t2=Sep21, t3=Dec21], L = body length, L^2 = (body length) ^{2}, const=constant. M-C: Males in control zone.

Model parameters & covariates					Model selection metrics					
S	γ'	γ''	p*	c	AICc	ΔAICc	AICc Weights	Num. Par	Deviance	-2log(L)
G*Z*L	const	const	t*Z	t*Z	1524.40	0.00	0.42	20	1481.96	1481.96
G*Z*L; M-C,t2(L)	const	const	t*Z	t*Z	1525.77	1.38	0.21	21	1481.09	1481.09
G*Z*L; M-C,t2(L^2)	const	const	t*Z	t*Z	1526.14	1.75	0.17	21	1481.46	1481.46
G*Z*L; M,t2(Z*L)	const	const	t*Z	t*Z	1527.29	2.90	0.10	22	1480.34	1480.34
G*Z*L; M,t2(Z*L^2)	const	const	t*Z	t*Z	1527.58	3.19	0.08	22	1480.63	1480.63
Z*L	const	const	t*Z	t*Z	1531.42	7.02	0.01	17	1495.66	1495.66
t*G*Z	const	const	t*Z	t*Z	1533.73	9.33	0.00	21	1489.04	1489.04
t*G*Z	const	const	t*Z*G	t*Z	1536.29	11.89	0.00	21	1491.60	1491.60
F(t);M(t*Z)	const	const	t*Z*G	t*Z	1536.96	12.57	0.00	19	1496.77	1496.77
F(t);M(t*Z)	const	const	t*Z	t*Z	1538.19	13.79	0.00	19	1497.99	1497.99
t*G*Z	t*Z	Z	t*Z	t*Z	1538.26	13.87	0.00	23	1489.03	1489.03
t*G*Z	const	const	t*Z*G	t*Z	1538.83	14.44	0.00	27	1480.36	1480.36
t*G*Z	t*G*Z	G*Z	t*G*Z	t*G*Z	1723.09	198.69	0.00	110	1407.32	1407.32

Table 8. Logit parameter estimates and corresponding precision estimates (SE (=standard error) and 95 % confidence limits) for the selected Huggins model (Table 7). Abbreviations: S=Survival MPA=mpa=marine protected area. C=control area. F=female. M=male. stL=stLength. LCL=Lower Confidence Line. UCL=Upper Confidence Line. Numbers [1,2,3] = session numbers. Highlighted cells are non-converged estimates for availability.

Parameter label	Session	Zone	Sex	Parameter type	Covariate	Est	SE	LCL	UCL
S_mpa_F		MPA	F	Intercept		1.01	0.5	-0.02	2.04
S_mpa_F		MPA	F	Slope	stL	-0.74	0.4	-1.53	0.05
S_C_F		C	F	Intercept		2.65	0.51	1.66	3.65
S_C_F		C	F	Slope	stL	-0.07	0.4	-0.86	0.72
S_mpa_M		MPA	M	Intercept		1.32	0.31	0.71	1.93
S_mpa_M		MPA	M	Slope	stL	0.25	0.43	-0.6	1.09
S_C_M		C	M	Intercept		-0.21	1.18	-2.51	2.1
S_C_M		C	M	Slope	stL	-3.17	1.65	-6.4	0.07
$\gamma' = \gamma''$		MPA=C	F=M	Intercept		-12.92	NA	NA	NA
p_MPA1	1	MPA	F=M	Intercept		-2.11	0.87	-3.82	-0.4
p_C1	1	C	F=M	Intercept		-1.67	0.69	-3.01	-0.33
p_MPA2	2	MPA	F=M	Intercept		-0.76	0.33	-1.42	-0.11
p_C2	2	C	F=M	Intercept		-1.84	0.45	-2.72	-0.96
p_MPA3	3	MPA	F=M	Intercept		-2.4	0.52	-3.41	-1.39
p_C3	3	C	F=M	Intercept		-2.57	0.35	-3.25	-1.89
c_MPA1	1	MPA	F=M	Intercept		-3	0.42	-3.82	-2.18
c_C1	1	C	F=M	Intercept		-2.35	0.35	-3.03	-1.66
c_MPA2	2	MPA	F=M	Intercept		-2.61	0.35	-3.29	-1.94
c_C2	2	C	F=M	Intercept		-3.21	0.51	-4.21	-2.21
c_MPA3	3	MPA	F=M	Intercept		-3.63	0.41	-4.44	-2.82
c_C3	3	C	F=M	Intercept		-4.34	1.01	-6.32	-2.37

Table 9: Males were recaptured less often than females in control area S. Not a single male was recaptured thrice.

Recaptures in control area S					
Times captured	**Females**	**Males**	**SUM**	**Males [%]**	**Females [%]**
2	10	8	18	44,44	55,56
3	4	1	5	20,00	80,00
4	2	0	2	0,00	100,00
Total	**16**	**9**	**25**	**36**	**64**

Table 10: Males were recaptured more often than females in the MPA. Not a single female was recaptured thrice.

Recaptures in MPA					
Times captured	**Females**	**Males**	**SUM**	**Males [%]**	**Females [%]**
2	7	12	19	63,16	36,84
3	1	3	4	75,00	25,00
4	0	1	1	100,00	0,00
Total	**8**	**16**	**24**	**66,67**	**33,33**

Catchable population size and density

Population size (N) estimates for the MPA and control area were derived from the selected Huggins model, by use of the estimates for true encounter probability, p*. N estimates for the MPA were temporally variable (~ 20-120 females and ~40-150 males) with wide confidence intervals, especially for sessions 1 and 3, while N estimates for the control area were more stable with narrower confidence intervals, ranging from ~40-75 individuals.

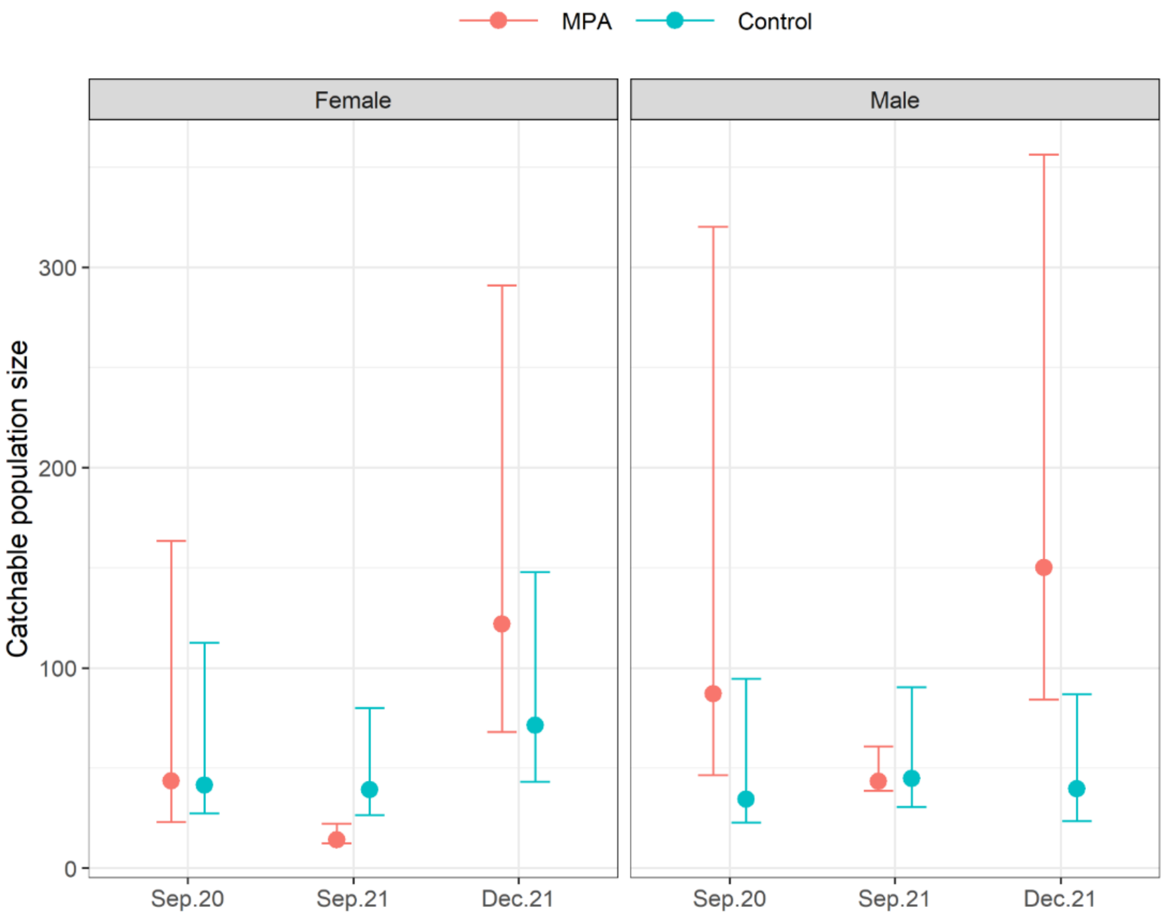

Figure 9: Population size estimates, N, divided by sex, sampling area and sampling session. Sep.20=session 1; Sep.21=session 2; Dec.21=session 3.

Population size estimates for the MPA and control area are incomparable since they are not corrected for differences in fishing efforts (trap location densities) and effective sampling area in each sampling zone. Population densities, N/da, are better for comparison and were derived from populations size estimates divided by the effective total fished area per lobster trap, $totA_e$ (Table 3).

Population density estimates in the control area range from ~0.2 individuals per 1000 m^2 (ind/da) to ~0.4 ind/da. Excluding the relatively high estimate for females during session 3 (~0.4 ind/da), control area densities range from 20-25 ind/da.

There was found no evidence that neither population size nor density decreased in the control area during the fishing season of 2021. On the contrary, density estimates for females in the control area were higher after the fishing season of 2021 than before. The density of males in the control area did not change notably. However, the density of males in the MPA was more than double the density of males in the control are in December 2021, and both male and female densities in the MPA rose from September 2021 to December 2021.

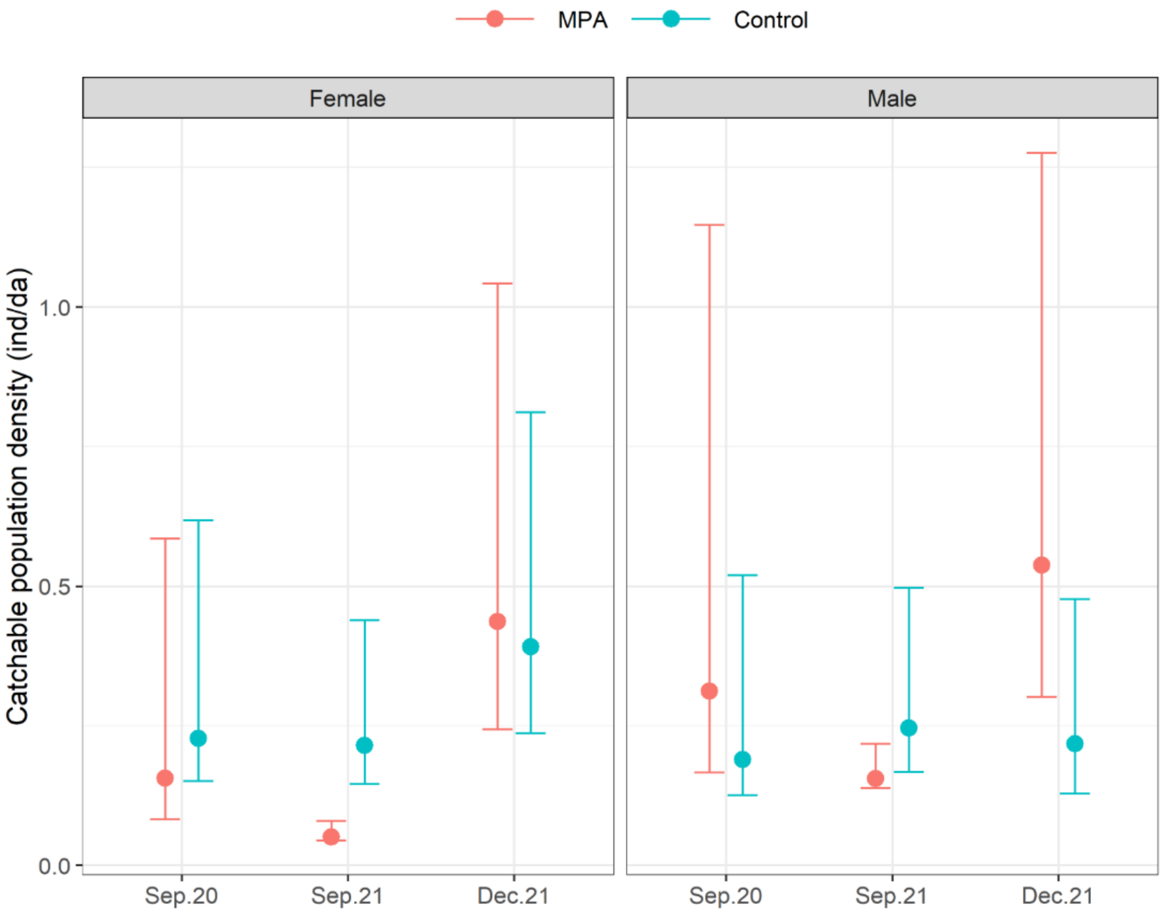

Figure 10: Population density: Catchable population divided by effectively fished area, presented as individuals per area [ind/da, 1 da=1000 m^2], for each sampling session, zone and sex.

Body size distribution

Mean male body size did not change notably in the MPA compared to the control area after one season of protection from harvesting. What was however evident was that among our sampled individuals, the mean body size of females was larger than males in every sampling zone and session. The difference was greatest in the control area during session 1 (~4 cm), when mean male L was ~25 cm and mean female L was ~29 cm. (Figure 11). Although there was a higher fraction of ~25 cm males in the MPA, relative to the control area, the same pattern can also be found prior to protection. For females, the fraction of large lobsters decreased in the MPA from September 2021 to December 2021.

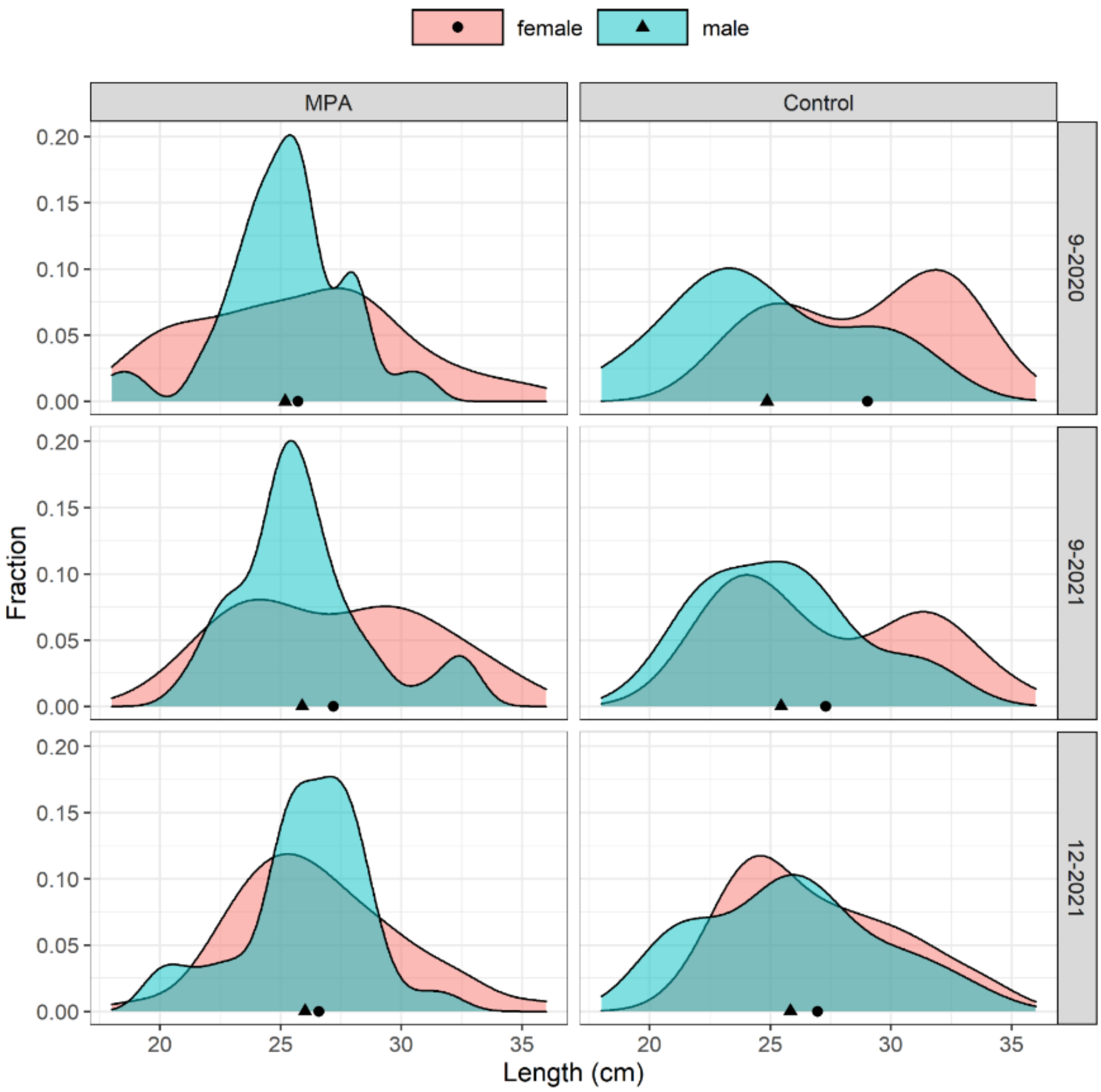

Figure 11. Sex-specific kernel density plots (smoothed histogram) of individual lengths of lobsters as function of sampling zone and session. Points represent sex-specific mean values.

Sex ratio

Although there is a higher share of females than males in the control area during session 1 and 3, the reverse is shown for session 2. (Figure 12) Combined, the available data does not indicate a significantly higher share of females than males in the control area neither before nor after the fishing season of 2021. The share of females in the MPA was low during both September sampling sessions (mating season) but increased in December. (Figure 12)

Sex ratio variability was χ^2-tested. The additive model was ranked highest, and the factorial model was ranked lowest. There was an additive significant temporal and spatial difference in sex ratios, while the factorial model was not supported by the available sample data.

Table 11: Overall sex distribution in control area and MPA

	Females	Males	SUM	% Females	% Males
MPA	71	121	192	36.98	63.02
Control area	58	52	110	52.73	47.27

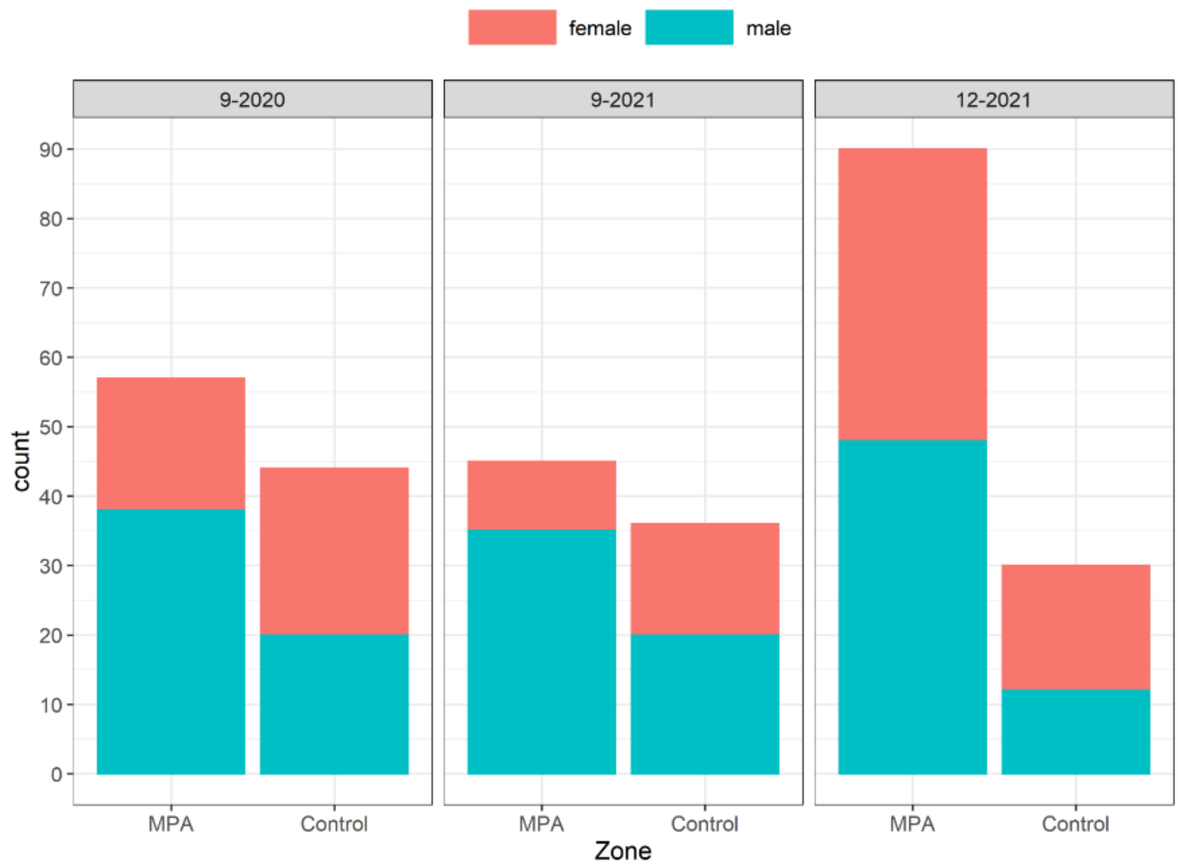

Figure 12: Number of first captures of female (red) and male (blue) lobsters, by session (chronologically) and zone.

Discussion

Male survival increased with body size in the MPA following protection, contrary to control area, in align with expectations. Contrary to expectations, predicted female survival decreased with body size from September to December 2021, and was lower than female survival in the control area. As expected, high and stable survival for females compared to males in the control area shows that protection of egg-bearing females works.

Population estimates for both females and males were higher in the MPA than in the control area after the first effective protection season, as, expected, but they were also higher after the season (December) than before (September), which means one should take care with concluding, based on these results, that the population in MPA has already become larger than that in the control area. Density estimates for both females and males were also higher in the MPA than in the control are after the first effective protection season, with a much greater difference for males (MPA vs control area) than females (MPA vs control area), as expected. Contrary to my beliefs, the results do not show an overall decrease in population densities in the control area over the fishing season in 2021, only a slight decrease for males. Female density, on the other hand, was estimated as larger after the fishing season than before, opposite to my expectations.

While there was a slight tendency to a change in body size distribution (higher fraction of legal-sized lobsters) in the MPA for both sexes, the mean body sizes were quite similar during all three sampling sessions and do not support the prediction that mean body size would be larger in the MPA compared to the control area after the first effective protection season. As expected, though, there was a larger fraction of large females compared to males in both areas, and the fraction of legal-sized lobsters was low in both areas, and lower for males than females.

Unlike my expectations, the data does not show a significantly higher share of females compared to males in either sampling area (there are only slightly more females in the control area in Sept 2020 and Dec 2021). On the contrary, the share of sampled males is much higher in the MPA in September 2020 and 2021, compared to females, and slightly higher also in December 2021. Although there is a sharp contrast in sheer numbers of lobster between the MPA and control area after the first effective fishing season, and in the change in numbers in MPA compared to control area, a X^2-test shows that this variability is additively significant, not factorially.

Survival

After only one fishing season following protection of the MPA, there was a sharp contrast between male survival estimates in the control area and the MPA. Contrary to male survival in the control area, which decreased rapidly past body lengths of 25 cm, male monthly survival increased with body size in the MPA, and there was already a wider spread in body lengths. This is evidence of the significant impact fishing has on the demography of the lobster population.

The results show, as expected, that male lobsters in the control area are targeted and selected during fishing season, rendering their survival near zero for body lengths over the protection limit of 25 cm. A dense placement of traps in the control area, combined with an apparent rise in lobster activity levels in December 2021 (indicated by increased captures in the MPA after the fishing season, table 5), should mean that surviving male lobsters in the control area were detectable during this period. As for females in the MPA (discussed below), there were few previously sampled male individuals from this area and therefore few that could be recaptured, affecting the precision of the model predictions for survival. A larger dataset/longer time series, and preferably an upgrade from T-bar tags to telemetry tags that can track movement over time, is necessary to shed further light on the parameters that affect male catchability through time and space. One cannot rule out that the large males in the control area had emigrated during the fishing season. Nevertheless, given the low male survival in the control area compared to both female survival in the same area, and male survival in the MPA, high fishing mortality seems the most likely reason why there are no surviving large males in the control area after the fishing season.

In alignment with my predictions, results from the control area imply that females benefit from the protection of gravid individuals during fishing season and are more likely to reach protected sizes >32 cm, compared to males. Female's overall survival was high, regardless of size, in the control area. Combined with egg registrations for 10/16 recaptured females, this proves that protection of gravid females is an effective management tool. Higher survival for body sizes 25-32 cm for females, compared to males, show the effect of these regulations on lobster demography and phenotypic complexity in the control area.

Contrary to my predictions, female monthly survival in the MPA was lower than in the control area and decreased with body size. Confidence intervals increase with body length, however, given the small number of recaptures that these results were based on. The small number of recaptures is connected to the surprisingly low number of detected females in the MPA during sessions 1 and 2. In other words, there were few females that could be recaptured. The statistically non-significant detection boom for females after the fishing season in 2021 shows that there were probably more detectable females in the MPA population than data from the two first sampling sessions would have suggested, but for some reason they would not enter the traps. Previous studies have shown that females displayed a lower detectability than males and lower re-catchability rates (geometric mean 0.363, vs males geometric mean 0.471) in a reserve at Kårva on the coast of Sweden (Moland, 2013). This is a suggested explanation to apparent higher annual survival rates for large females than for large males ((0.75), 0.4-0.6 for large males, in MPAs (Fernández-Chacón, 2021)). This is discussed further in the following.

Whether the short-term estimates for survival presented in this study are indicative for a long-term development in this MPA remains to be seen and warrants further research.

Catchable population size and density

Contrary to my expectations, the results indicated higher densities of lobster in both the MPA and harvested control area after the fishing season in 2021, relative to before. However, the assumption that protection from harvesting did benefit the male population in the MPA already during their first protected season is supported by the difference in predicted change in density for males in the MPA relative to the control area: The density of males in the MPA after the fishing season, compared to before, is more than doubled, while there was a slight decrease in the density of males in the control area,

The surprising increase in predicted population density after harvesting can be related to seasonal changes in activity levels which affect catchability. Catchability is highly dependent on activity levels when using a passive fishing method like baited traps, and varies with sex, age, body size and moulting stage in addition to seasonal and daily behavioural patterns (Moland et al., 2011; Smith, 2001). September is high season for mating for lobsters, and for shell-shifting in females. Females that mate during this period are shy, sheltered and provided for by their partner in his cave for as long as they are shell-less and vulnerable (Sørdalen, 2022). In this period, females have lower detectability than males and may be underrepresented in a capture-mark-recapture study. By December, females will have grown a new armor, left their mate's cave and started feeding themselves again, and activity levels will resume causing higher female catchability (Sørdalen, 2022). This seems a viable explanation for our increased population and density estimates for females after harvesting, as this development is evident in both the MPA and control area simultaneously.

It is more difficult to suggest explanations for the increased density of males in the MPA in after the fishing season compared to before. Telemetry studies from MPAs at the Skagerak coast show that all-over activity levels for lobster are higher during summer and lower during winter, correlated with temperature (Moland et al., 2011). It is possible that the large share of small males in the population (Figure 11), combined with the high frequency of shell-shifting in small lobsters (Sørdalen, 2022), causes a significant decrease in male detectability before the fishing season, as males also shed their shells during fall, but over a longer time period than females (September through November) (source). Replicated telemetry studies from this study site are necessary to discover more about temporal variations in lobster activity levels that may affect catchability, and thereby all other parameter estimates that can be modelled from sampled data (survival, population, ++).

Body size distribution

My expectation of observing early changes in mean body size in the MPA compared to the control area after the first fishing effective protection season, were not met by the results. Although more legal-sized lobsters were captured in the MPA, so were smaller lobsters: The sample from December was generally larger.

As previously discussed, size-dependent frequency of shell-shifting can lead to a lower detectability for small lobsters during shell-shifting season, compared to larger lobsters. This can explain the observed decreasing fraction of larger females in the MPA and control area from before the fishing season (coinciding with shell-shifting season) to after the fishing season (shell-shifting over).

There is an initial difference in body size distribution between MPA (large share of small males) and control area (low share of small males) which cannot be explained by isolating sex-wise or seasonal variation in behavior alone. There could be a habitat-dependency here, that has yet to be investigated.

Future studies that compare habitat qualities, combined with telemetry studies for detailed data on a lobster's movement and preferred habitat throughout a year can secure a more representative lobster data set and would be most useful. Such studies aside, an extended time series to the present sampling design for similar studies to this one might also disclose more information relevant to this topic.

Sex ratio

There is a higher relative proportion of males in the MPA, compared to the control area after the first effective protection season, as expected.

To my initial surprise, a low share of females was captured in the MPA during both fishing sessions prior to effective protection, compared to males. In the control area, where I expected an uneven sex distribution in favor of females, the female to male ratio was closer to 1:1 but increased slightly after the fishing season in 2021. Given the previously discussed sex-, size- and season-dependent detectability in lobster, the low detection of females in the MPA seems less surprising in retrospect. On the flip side, one could have expected a higher proportion of males in the control area during September sampling session, in the hypothetical absence of high, gender selective fishing mortality: If the detectability of males were higher than that of females, and the proportions of males and females were equal, it must logically mean that the sampled male fraction should be higher than the female fraction. Evidence to the opposite suggests that the real, but hitherto unobserved, sex ratio indeed favors females in the harvested population of the control area. As previously mentioned, though, the difference in sex ratio between the MPA and control area before protection went into effect, points towards habitat dependent differences in demography, which I was unable to disclose in this study.

Results from a χ^2-test showed a slight decrease in sex ration for males in the control area, but this was not a statistically significant interaction. It is however possible that protection of the MPA will lead to increased fishing pressure and mortality in the control area, assuming that fishers will move spatially instead of reducing their fishing efforts. A longer time series (and again, telemetry studies) can help in disclosing such developments in the future.

Conclusion

Marine protected areas have short term effects on lobster demography, such as increased survival for legal-sized males and increased body size diversity in the male fraction of the population, compared to harvested populations.

All parameter estimates are dependent on catchability dependent samples from the lobster population, and catchability varies with sex, age, size, time, space and habitat. Telemetry studies and habitat investigations are necessary to disclose the local implications of this on the lobster population.

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