



Demographic responses to protection from harvesting in a long-lived marine species

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ABSTRACT

Marine protected areas (MPAs) are usually considered to have positive effects on the recovery of over-exploited populations. However, resolving the extent to which MPAs function according to their conservation goals requires that essential demographic information such as individual survival and population size are quantified. To this end, we analyzed a 16-year replicated mark-recapture study on European lobster (*Homarus gammarus*, $n = 8793$) conducted at several protected and unprotected sites in southern Norway, quantifying the impact of MPAs on local population dynamics by means of a “before-after control-impact” study approach (BACI). Lobster survival and abundance were estimated by applying multi-state and robust design models to the mark-recapture data. These models revealed underlying positive responses to protection. Annual survival rates and population abundances reached higher values in the MPAs, compared to the unprotected sites (abundance range: MPAs = 96–1172, control areas = 92–747). In general, female survival was higher than male survival (range of survival: male = 0.13–0.75, female = 0.37–0.85), while larger males benefited more from protection compared to smaller males (range of increase in survival after protection: big = 100–125%, small = 55–101%). We also detected regional differences in demographic responses to protection, as not all MPAs showed the same changes in abundance over time. Our results show that MPAs can reach conservation goals by increasing the local survival and abundance of lobster, but they also highlight demographic differences between sexes and geographic areas that are worth considering for the management and design of both current and future MPAs.

1. Introduction

Worldwide, the conservation and management of fisheries has put the focus on marine protected areas (MPAs) as a tool to improve the abundance, diversity and productivity of organisms (Lester et al., 2009; Lubchenco et al., 2003). In Northern Europe, MPAs are increasingly being used as a fisheries management tool (Denny and Babcock, 2004; Fenberg et al., 2012; Pastoors et al., 2000), but extensive data collections for a scientific evaluation of MPAs are generally rare. As a result, the success of MPAs as means to enhance populations of target species has been questioned (Florin et al., 2013).

Establishment of MPAs, along with long-term investment in appropriate monitoring programmes, may be good examples of adaptive management, a strategy put forward as a way of managing natural resources in the face of uncertainty (Holling, 1978; Walters, 1986). An

adaptive approach involves exploring alternative ways to meet management objectives and predict the outcomes of alternatives based on the current state of knowledge. For example, exploring how the population structure (i.e. males and females of different size classes), abundance or vital rates of a target species within an area of interest respond to different levels or modes of harvesting. In marine systems, such knowledge is often incomplete and ecological uncertainty therefore represents a key obstacle for management.

A good understanding of MPA-effects on the demography of harvested species can only be achieved through the analysis of extensive empirical data collected by monitoring populations over time and under different modes of management (Babcock et al., 2010; Baskett and Barnett, 2015). Long-term mark-recapture monitoring programs can provide the high-resolution of individual data required to estimate key demographic rates and to understand local population dynamics

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(Fernández-Chacón et al., 2013). Such studies are likely to generate ecological knowledge useful for applied purposes, such as how population size or vital rates of an exploited species within an area of interest respond to changes in harvest levels (e.g., Fernández-Chacón et al., 2015). However, because not all individuals alive in a population are always found (i.e., detection is “imperfect”), mortality, emigration and recapture failure can be confounded on some occasions, making raw encounter data an unreliable measure of both individual- and population status. Therefore, to robustly estimate key vital rates from encounter data we need statistical approaches accounting for detectability, such as capture–recapture models (Lebreton et al., 1992; Williams et al., 2002). By separating biological- (i.e., survival and/or dispersal rates) from observational processes (i.e., recapture probability), these models allow assessing the influence of external factors on population parameters, enabling us to investigate demographic responses to environmental change.

In this study, we analyzed extensive mark-recapture data on European lobster (*Homarus gammarus*) collected along the Norwegian Skagerrak coast to assess the influence of three MPAs on the abundance and individual vital rates of this intensively harvested and depleted species (Kleiven et al., 2012). To do so, we used capture-recapture models to quantify variation in survival and abundance between different size-categories and sexes as well as between protected and unprotected areas, while also accounting for detectability, size class transitions (i.e. growth) and temporary movement. Already, the Skagerrak MPAs have seen increased lobster catch-per-unit-effort (a proxy for abundance) and mean body size compared to neighboring areas where harvesting is allowed (Fernández-Chacón et al., 2020; Moland et al., 2013a). Also, several years of capture-recapture monitoring of European lobster within a coastal MPA in western Sweden revealed that demographic responses to protection can differ between sexes (Moland et al., 2013b). However, robust quantitative information on annual vital rates for different sexes and size classes inside vs. outside MPAs, as well as direct estimates of both total and sex-specific population abundance are still lacking.

We hypothesized that full protection from fisheries would lead to improved survival and increased abundance of lobster. Specifically, we predicted survival of large individuals of both sexes to increase inside MPAs after MPA implementation, compared to harvested sites. We also predicted an increase in abundance of lobsters inside MPAs across our three study areas. Broadly, we aimed to: i) separate the underlying demographic processes (i.e. individual survival, growth and temporary movements) driving local population responses to protection from harvesting and ii) to provide novel and reliable demographic information (i.e. population size estimates, temporary emigration probabilities, sex and size-specific survival rates) for the purpose of improving our general knowledge of how MPAs affect the demography of target species, and to guide future management decisions.

2. Materials and methods

2.1. Study species

The European lobster is a long-lived decapod crustacean of significant ecological and commercial importance, distributed from the north of Norway to Morocco in North Africa (Triantafyllidis et al., 2005). Longevity spans several decades, during which large specimen may grow to attain weights up to 10 kg. Average age of large (150–170 mm CL) male and female specimen has been estimated as high as 31 and 54 years, respectively (Sheehy et al., 1999). Based on data from wild caught females, size at 50% maturity (i.e., when 25% of females are ovigerous to account for biennial spawning) in Skagerrak is 79–80 mm CL (≈ 23 cm TL) (M. Ulmestrand, Swedish University of Agricultural Sciences, unpublished data).

European lobster prefers rocky habitat at depths down to 60 m (Galparsoro et al., 2009). The species is considered site-attached and

acoustically tagged individuals displayed limited home ranges in shorter term studies, e.g. <0.04 km² during a period of 318 days (Moland et al., 2011) <0.64 km² during a period of less than 2 months (Wiig et al., 2014) and <0.01 km² for a period spanning several months including spring and autumn study periods (Skerritt et al., 2015). However, exceptions include movement up to tens of km (see e.g., Huserbråten et al., 2013; Thorbjørnsen et al., 2018). Newly hatched larvae undergo four molt stages during 13 to 35 days in the plankton prior to settlement (Schmalenbach and Franke, 2010). The dispersal potential is thus considerable at the pelagic larval stages and connectivity in Skagerrak is considered high based on molecular work (Huserbråten et al., 2013).

In Norway, landings of European lobster decreased dramatically (90%) between 1960 and 1980, indicating a collapse (Agnalt, 2008). However, Kleiven et al. (2012) documented that official landing data does not reflect stock development due to unreported recreational and commercial catches. Therefore, catch rate (CPUE), which has decreased by 65% from the 1950s to 2000s (Pettersen et al., 2009), should be considered as a better indication of stock status. In Norway, lobsters are legally caught from 1 October to 30 November in traps fitted with two circular escape vents measuring 60 mm in diameter. Effort is limited to 10 and 100 traps for recreational and commercial fishers, respectively. In 2008, minimum legal size was increased from 24 to 25 cm total length and a ban on capture and trade with ovigerous females was introduced. In 2017, a slot limit with maximum legal size at 32 cm total length was introduced in Skagerrak (east of Lindesnes – the southern cape of Norway). Recreational fishers outnumber commercial participants in the fishery which has long traditions in coastal communities. A recent strip transect study conducted in western Skagerrak found that 65% of deployed lobster traps belonged to recreational fishers (Kleiven et al., 2011). Although considered depleted throughout its range, the species continues to support economically important fisheries in certain areas, mainly in Ireland and UK.

2.2. Study system

Located on the Norwegian Skagerrak coast, the MPAs included in this study were established to generate knowledge on the development of lobster populations in areas unaffected by extractive fishing (Pettersen et al., 2009). All capture of lobster has been effectively banned in the MPAs since September 2006 through gear restrictions, with only hook and line fishing allowed (Moland et al., 2013a). Policing of the MPAs are based on collaboration between the Directorate of Fisheries, the Coast Guard and local police.

The three MPA sites studied, listed from west to east in Skagerrak, are: (1) Flødevigen (N 58° 25', E 8° 45'), (2) the Bolærne archipelago at the mouth of the Oslo fjord (N 59° 13', E 10° 31'), and (3) the small island Kvernskjær (N 59° 02', E 10° 58') in the Hvaler archipelago (Fig. 1). Control areas open to lobster fishing are located adjacent to these and separated from MPAs by distances of 1700, 850 and 2250 m (from MPA center to control area center) in Flødevigen, Bolærne and Hvaler, respectively (Fig. 1). At each location, the MPAs and control areas are of approximately equal size (≈ 1 , ≈ 0.7 and ≈ 0.5 km² in Flødevigen, Bolærne and Hvaler, respectively).

2.3. Sampling design

An annual standardised research trapping survey, including capture-mark-recapture, was conducted inside the proposed MPA areas during three consecutive years prior to designation (2004–2006). In 2006, in the last sampling season prior to implementation of the MPAs, adjacent control areas were designated and included in the survey (2006–2019). Thus, as of 2006, the assessment program was designed as a BACI Paired Series approach (Stewart-oaten et al., 1986). In this design the MPA and control areas are sampled at the same times so that shared temporal effects can be accounted for. Lobsters were sampled using standard ‘parlour’ traps (900 × 450 × 400 mm with 120 mm entrances) baited

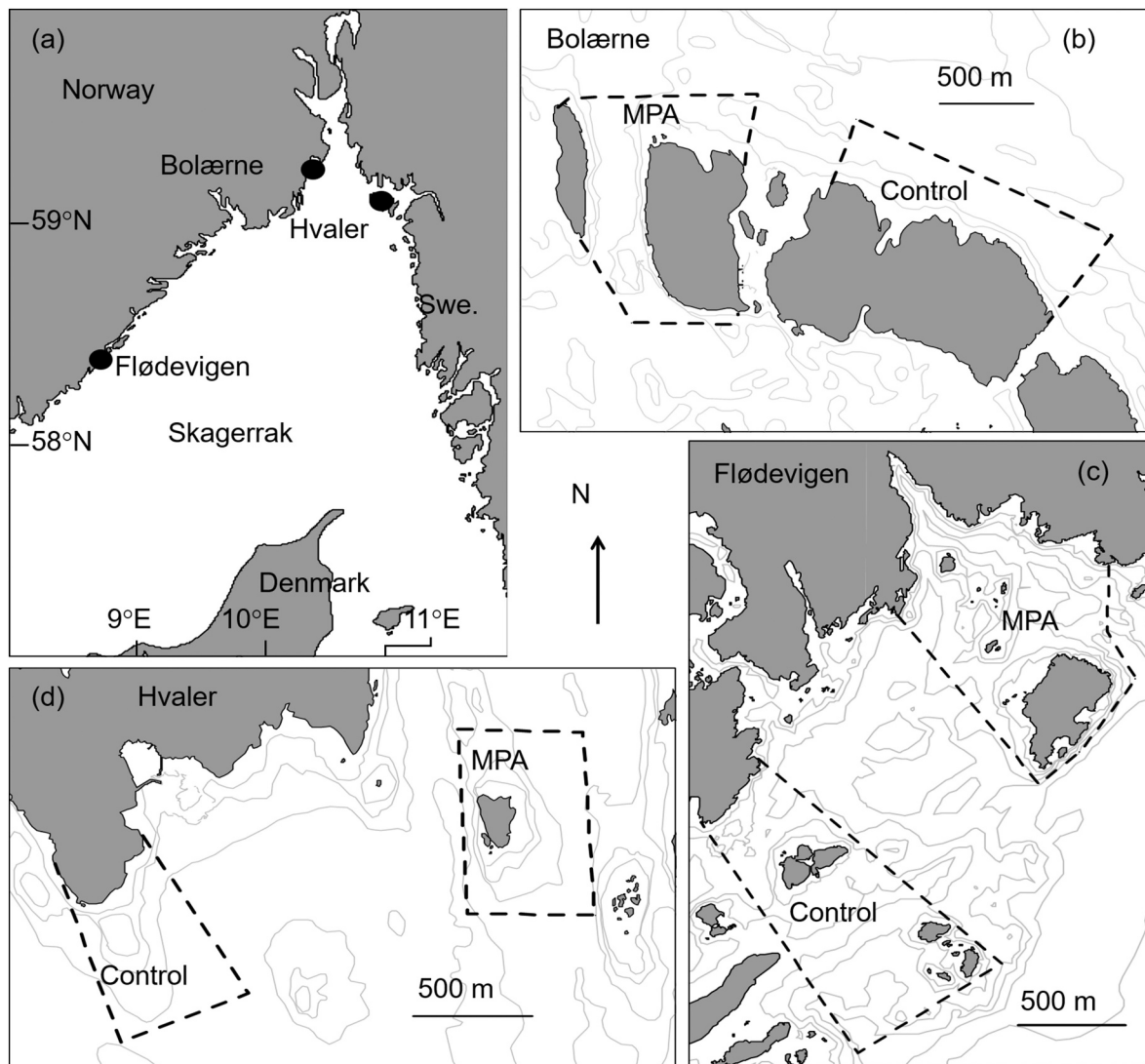


Fig. 1. Clockwise from top: (a) dark circles showing the location and delineation of original MPA and control area pairs in Skagerrak, (b) the Bolærne MPA and control area, (c) the Flødevigen MPA and control area, and (d) the Hvaler MPA and control area. Dashed lines in panels b to d represent the maritime boundaries (extent lines) of each MPA and Control area.

with frozen mackerel (*Scomber scombrus*). Single traps were deployed at 10–30 m depth throughout the areas sampled. The standardised annual sampling effort (100 traps day⁻¹) was spread over four days using 50 traps in each region (25 traps simultaneously in MPA and control area) in each year, with approximately 24 h soak time. Sampling was conducted between 20 August and 10 September in each year, during the same week in each region in each year, and simultaneously inside MPA and control area in each year since inclusion of control areas.

Lobsters were measured and tagged immediately upon capture and released at the site of capture. Total length (TL) was measured to the nearest mm from the tip of the rostrum to the posterior margin of the telson. Sex was determined by examination of the first pair of pleopods. All lobsters caught were tagged with individually numbered T-bar anchor tags (TBA2, 45 × 2 mm, Hallprint Pty. Ltd., Holden Hill, South Australia) with printed information about the ongoing project. Tags were inserted in the ventral musculature between cephalothorax and abdomen, to the right side of the midline using a standard tag applicator. Placing the tag in this area ensures its retention through multiple molts.

2.4. Data analysis

Mark-recapture data from the lobster surveys were analyzed following a Robust Design approach (Pollock, 1982) distinguishing primary (annual) sampling seasons and secondary sampling occasions (repeated surveys within season). Under this framework, populations are assumed to be open to gains and losses during the time interval between primary occasions, whereas they are assumed to be closed within annual surveys due to the short time interval (e.g. 24 h) between secondary trapping sessions. With the aim of investigating both open and closed population parameters, data was analyzed in 2 steps: first, using data from the primary occasions only, we constructed multistate models in program E-SURGE to model annual recapture probabilities (p) and survival rates (S) of lobsters in our study system. Second, using data from both the primary and secondary sampling occasions, we constructed Robust Design (RD) models in program MARK to estimate lobster population sizes (N) for each year, location and sex. Although RD models can also estimate S , in our case we investigated survival dynamics first, using multistate models, and focused the second step of the mark-recapture analysis on other parameters of interest (see below).

Prior to any analysis of mark-recapture data, a Goodness-of-fit (GOF) test has to be conducted to check if the encounter data meets the assumptions of a “global” departure model, most commonly a Cormack-Jolly-Seber (CJS) model with full time-dependence in survival and recapture probabilities (see Lebreton). To our best knowledge, there are no specific GOF tests for RD models and to evaluate the fit of a CJS model may be inappropriate in this case. Nevertheless, GOF tests for multistate models do exist, so in the case of the multistate survival analysis, a global departure model was evaluated, namely the Arnason-Schwarz (AS) model (Pradel et al., 2003). This general model considers full time, state (size class) and group (sex) interactions in model parameters. GOF testing was performed using U-CARE (Choquet et al., 2009), a statistical program that helps users to detect sources of lack of fit in mark-recapture data (mainly caused by differences in survival and recapture probabilities among individuals) and to redefine the structure of the departure model to accommodate these heterogeneities. Although data stratification in different groups or individual states may already solve goodness-of-fit problems, we still applied an overdispersion coefficient or \hat{c} (calculated as the sum of chi-square results for each test divided by the total number of degrees of freedom) to correct for remaining sources of lack of fit when performing the statistical analyses in program E-SURGE.

2.5. Modelling of survival (S) and recapture probability (p)

For the aims of this analysis, mark-recapture data on lobster was summarized in different individual encounter history datasets, one for each study site. Local survey data was pooled into one (primary) record per year (11 records in the case of lobster MPAs and 9 in the case of control areas), showing, for each primary occasion, whether the individual was encountered (“1”) or not (“0”). In this case, encounters (“1”) were reclassified, taking into account the total body length of the individual, defining two types of encounters or “events”: lobster measuring 25 cm or more (“1”) and lobster measuring less than 25 cm of total length (“2”). Each individual encounter history was also assigned to a sex category using a binary code (“10” = male, “01” = female) included after the sequence of individual records.

These encounter histories were analyzed by constructing multi-state models in program E-SURGE (Choquet and Nogue, 2010). This program allows defining a model pattern to link our field records (events) to the corresponding individual states through a series of steps based on transition matrices. In our case, encounter events 1 and 2 (see above) were directly linked to two model states: “alive with legal size” (LL) and “alive with sublegal size” (LS). Recorded non-detections (event “0”) can be potentially related to any possible state, including an additional “dead” state (\dagger), which is not observable and its corresponding recapture probabilities are structurally zero in our modelling (see Appendix A for supporting information).

By allowing individuals to move within a finite set of states between capture occasions, multi-state models allow the estimation of three types of parameters: survival (S), transition (Ψ) and recapture probabilities (p) (Lebreton and Pradel, 2002). Transition probabilities are conditional on survival, and in order to obtain separate estimates for each parameter, we took advantage of the process-decomposition tool implemented in program E-SURGE. In the case of transition probabilities, only body growth transitions ($\Psi_{LS \rightarrow LL}$) were explicitly estimated; transitions from legal to sublegal size states were treated as impossible and fixed to zero in our modelling.

Data from each study site was analyzed independently. In each analysis, model construction followed a sequential approach departing from a general model with full time and state interactions in survival (S) and recapture probabilities (p) that was subsequently simplified with the aim to improve model parsimony. Model selection was based on the Akaike information criterion (AIC) and we considered as our best model (i.e. the most parsimonious structure) the one showing the lowest AIC value of the set (Burnham and Anderson, 1998). Models differing in less

than 2 points of AIC ($\Delta AIC < 2$) were considered statistically equivalent. We focused our modelling on survival and recapture parameters, starting with p and removing state (body size), time and sex effects until the most parsimonious structure for p was found. Then, we retained this structure in the subsequent modelling of survival probabilities (S). State, sex and time effects were tested on S by combining constancy (“.”), additivity (“+”) or interaction (“*”) between effects until the most parsimonious structure for survival was found. In the case of data from the lobster MPAs, temporal trends in survival and the existence of 2 periods (before and after MPA implementation) with different but constant survival probabilities were also tested. Body growth transitions ($\Psi_{LS \rightarrow LL}$) were always kept constant to avoid unnecessary increases in the number of estimable parameters and model combinations.

This modelling approach does not distinguish local mortality from permanent emigration, so the obtained survival estimates are “apparent” and could be biased low if emigration from the study area was high. Previous studies conducted in Skagerrak have shown that European lobsters can be resident with limited home ranges (Moland et al., 2011), so biases in local survival rates caused by permanent emigration are expected to be low. Nevertheless, movements of lobsters in the form of temporary emigration from the study area were taken into account in the estimation of local population sizes (see below).

2.6. Estimation of population size (N)

Population abundance was estimated by applying Robust Design (RD) models to complete individual encounter histories including within-year surveys. RD models use the information contained in both the primary and secondary sampling sessions to provide estimates of annual population size (N), in addition to annual survival (S) and two detection parameters: survey-specific capture (c) and recapture (r) probabilities, which describe the likelihood of newly encountering and re-encountering a lobster in a given secondary sampling occasion (note that the p estimated in the first survival analysis is conceptually different and it reflects detection probability for the entire primary period). RD models also include extra parameters describing the “availability” of the individuals for capture (Kendall et al., 1997), in particular a probability of becoming unavailable to capture or to emigrate from the study area in a given year (γ'') and a probability of staying away of the study area, once having dispersed (γ'). We constructed RD models in program MARK, primarily to estimate abundance but also to test new hypotheses regarding movement patterns and individual responses to trapping by means of the additional parameters provided in this modelling framework. For each site, we conducted three independent RD analyses: one for each sex and one using all individual records (ignoring sex). Dynamic (size) states were not included at this stage to keep a reasonable number of estimable parameters. Survival parameters were kept either constant or time-dependent, reflecting the best structure selected in previous survival analyses. In contrast, different constraints and model structures were tested on movement (γ'' and γ') and detectability parameters (c and r): following Kendall et al. (1997) we constructed different models for the γ parameters based on plausible hypotheses about the movement patterns of lobsters: no temporary emigration ($\gamma'' = \gamma' = 0$), random temporary emigration ($\gamma'' = \gamma'$) and Markovian temporary emigration ($\gamma'' \neq \gamma'$). In the case of c and r parameters we followed the closed population modelling approach described in Otis et al. (1978) and checked for a behavioral response of lobsters to trapping by contrasting a null constant model with identical capture and recapture probabilities between secondary sessions ($c = r$) against an alternative one considering constant but different values for each parameter ($c \neq r$). Model selection in program MARK was based on AIC. Models differing by $\Delta AIC < 2$ were considered statistically equivalent. The abundance parameter (N) was not included explicitly in the model structure and was calculated as a derived parameter. N estimates were model-averaged in program MARK. To quantify the statistical significance of the differences in abundance between control and reserve areas, we

fitted a GLMM (Generalized Linear Mixed Model) with year and site as fixed effects and an autoregressive-moving average (ARMA) to correct for autocorrelation using the function 'gls' in R-package 'nlme' (Pinheiro et al., 2019).

3. Results

A total of 8793 lobsters were tagged in the MPAs and control areas during the study period, with 5264 individuals being recaptured at least once. The number of sampled individuals differed among locations, with less recaptures obtained at the control areas compared to the MPA sites (Table 1), but the proportion of sexes in the samples of marked and recaptured lobsters was similar (% marked: male = 49.6, female = 50.4; % recaptured: male = 49.4, female = 50.5). Results of the multistate GOF test conducted in U-CARE showed that the departure model fitted our data adequately (i.e. all total c -hat values were ≤ 1 ; Table B, Appendix B), thus indicating that overdispersion was absent, with no need to apply a correction coefficient when conducting the survival analyses in E-SURGE.

3.1. Survival dynamics, body growth and recapture probabilities

Annual survival of lobster was affected by individual sex and size class (state), with either one or both effects appearing among the top ranked models ($\Delta AIC < 2$) of all study sites (Table 2). At the MPAs, the best model structure always considered size and sex effects on survival as well as a temporal effect, either in the form of additive time effects or 2 time-periods. Survival models including size and sex interactions were well supported at all control areas (Table 2), and so were additive time effects (except for Bolærne; Table 2).

The comparison of mean survival values obtained from models specifically contrasting the before-after scenario (two separate time periods) showed a general increase in survival after protection in all MPAs, with significantly higher post-protection values compared to neighboring control areas (i.e. no overlap in 95% C-I, Fig. 2). In general, small-sized individuals showed higher survival rates than bigger ones: at the control areas, mean survival of legal-sized (bigger) lobster was usually below 0.5, with the lowest values corresponding to males (Fig. 2). In the MPAs, mean survival of big males increased 125.2%, 101.2% and 99.8% at Flødevigen, Bolærne and Hvaler sites, respectively. Female survival was usually higher than that of males under both protected and unprotected contexts (Fig. 2) increasing, in the case of big females, by 78.5%, 61.5% and 57.1% at Flødevigen, Bolærne and Hvaler MPAs, respectively.

The probability of small lobsters growing to attain legal size (state transition) changed between regions, with higher values ($\pm SE$) at Flødevigen (MPA = 0.79 ± 0.07 ; control = 0.82 ± 0.04) and lower, but similar values at Hvaler and Bolærne archipelagos (ranging from 0.53 ± 0.05 to 0.65 ± 0.08). As in the modelling of survival, models with sex and size interactions on p were usually well supported (Table 2). Sex- and size-specific recapture probabilities obtained at each location pointed to a higher detectability of males compared to females, with big females showing the lowest detection rates (see Fig. C and additional information in Appendix C).

Table 1

Total number of male and female lobsters that were tagged and recaptured (at least once) at the sampling sites during the study years. Size ranges (minimum and maximum total length of the sampled individuals) are also given for each site.

Location	Area	Male			Female		
		Marked	Recaptured	Size range (cm)	Marked	Recaptured	Size range (cm)
Flødevigen	MPA	625	297	[15.2–42.5]	688	372	[13.1–42.2]
	Control	302	164	[16–34.5]	316	182	[14.7–35]
Bolærne	MPA	1102	553	[14.5–40.8]	1047	620	[16.6–39.5]
	Control	666	417	[16.2–36.2]	558	372	[15.3–37.5]
Hvaler	MPA	799	610	[16.5–38]	812	431	[14.3–42.4]
	Control	868	562	[13.4–37.8]	1010	684	[15.6–42.8]

3.2. Trapping responses, temporary emigration and changes in population size

Behavioral responses to trapping (i.e. significant differences between first capture (c) and recapture (r) probabilities within the sampling season; $c \neq r$) were detected at three of the six study sites: one control site (Hvaler), and two MPAs (Flødevigen and Bolærne; see AIC of tested $c \neq r$ model structure in Table 3). At these MPAs, r values were slightly lower than c ones (Flødevigen: $c = 0.062 \pm 0.005$, $r = 0.051 \pm 0.004$; Bolærne: $c = 0.068 \pm 0.004$, $r = 0.057 \pm 0.004$), whereas at Hvaler control area, r values were much higher, indicating higher probability of recapture after 1st capture ($c = 0.083 \pm 0.005$, $r = 0.164 \pm 0.016$). The Markovian movement hypothesis received good statistical support in the modelling of Flødevigen lobster data (high ranked at the MPA and best supported at the control area; Table 3), but results were inconclusive regarding the existence of temporary emigration at the remaining sites, with random or markovian movements being as well supported as the 'no movement' hypothesis ($\Delta AIC < 2$; Table 3). Results from Flødevigen showed that lobster had a lower probability to emigrate compared to the probability of remaining outside the study area after dispersal ($\gamma'' < \gamma'$), with lower emigration estimates for the MPA ($\gamma''_{MPA} = 0.16 \pm 0.07$) than for the control area ($\gamma''_{control} = 0.59 \pm 0.09$). Site-specific analyses focusing on one sex yielded similar model selection results (see Tables D1 and D2 in Appendix D).

Derived estimates of population size (N) showed temporal changes in abundance at all sites during the study period (Fig. 3). Overall, the highest N estimates were obtained within protected areas (Fig. 3). Total abundance levels increased after protection at Flødevigen and Bolærne regions, with larger populations at the MPAs compared to the corresponding control areas after 2006 (Fig. 3). Such differences in total N between paired sites at Flødevigen and Bolærne were statistically significant ($p < 0.05$; Table E, Appendix E). At Hvaler, both areas (MPA and control) showed similar total abundance estimates, with no significant differences in N between protected and fished area ($p > 0.05$; Table E, Appendix E). Mean and maximum N values were higher for females (mean $N_{females}$: 277.93; range $N_{females}$ [min-max]: 75.42–696.68) than for males (mean N_{males} : 151.26; range N_{males} [min-max]: 24.25–556.60). Females showed significantly higher abundances at the Flødevigen MPA compared to the corresponding control area (Fig. 3 and Table E). Female abundance at Bolærne and Hvaler did not differ significantly between protected and fished areas ($p < 0.05$; Table E). In the case of males, abundance estimates were significantly higher at Bolærne and Flødevigen MPAs, compared to their corresponding control areas, but differences were not significant between Hvaler sites (Fig. 3 and Table E).

4. Discussion

A novel two-step analytical approach was applied to 16 years of mark-recapture data on European lobster collected inside and outside replicated northern European MPAs, before and after MPA implementation. This study design allowed us to quantify the long-term demographic responses of this species to protection from harvesting. The implementation of no-take marine MPAs benefited lobster survival and resulted in significantly higher abundances inside MPAs in two out of

Table 2

Summary of model selection results obtained for the multi-state analyses conducted at each study site, showing AIC and Δ AIC values for all model structures tested on detection (p) and survival (S) probabilities (see Appendix A for further details on model selection results, including deviance and number of parameters for each model). The best models in each modelling step are underlined, whereas statistically equivalent models for survival (i.e. those with Δ AIC <2) are shown in **bold**. Models including trend or period effects on survival were only tested in the analysis of MPAs data.

Modelling of p	Flødevigen				Bolærne				Hvaler			
	MPA		Control		MPA		Control		MPA		Control	
	AIC	Δ AIC	AIC	Δ AIC	AIC	Δ AIC	AIC	Δ AIC	AIC	Δ AIC	AIC	Δ AIC
Size * sex * t	5174.97	72.07	1574.50	88.35	7599.03	66.88	3173.82	88.42	7937.21	73.34	5453.40	42.64
Size * sex + t	<u>5148.56</u>	<u>45.66</u>	1538.36	52.21	7573.53	41.38	5012.81	1927.41	7916.40	52.53	5431.78	21.02
Size * sex	5171.04	68.14	1527.35	41.20	<u>7564.40</u>	<u>32.25</u>	<u>3126.29</u>	<u>40.89</u>	7913.90	50.04	<u>5423.77</u>	<u>13.01</u>
Size * t	5163.46	60.56	2425.09	938.94	7607.71	75.56	3172.82	87.41	9721.16	1857.29	5446.83	36.07
Sex * t	5155.48	52.58	1557.84	71.69	7581.39	49.24	3169.88	84.47	10021.00	2157.13	5447.96	37.20
Size	5182.26	79.36	<u>1525.95</u>	<u>39.80</u>	7589.26	57.11	3151.78	66.38	7929.68	65.82	5436.33	25.57
Sex	5167.65	64.75	1531.87	45.72	7568.81	36.65	3145.56	60.16	7916.31	52.44	5436.66	25.90
Size + t	7360.38	2257.49	1537.39	51.24	7599.65	67.50	3162.73	77.33	7923.31	59.44	5444.92	34.16
Sex + t	7230.44	2127.54	1542.75	56.60	7577.42	45.27	3154.76	69.36	<u>7908.44</u>	<u>44.57</u>	5443.49	32.73
(.)	5180.37	77.48	1529.93	43.78	7587.38	55.23	3157.48	72.08	7928.09	64.22	5447.50	36.74
t	5155.13	52.23	1541.47	55.32	7596.02	63.86	3167.41	82.01	7919.36	55.49	5455.54	44.78

Modelling of S	Flødevigen				Bolærne				Hvaler			
	MPA		Control		MPA		Control		MPA		Control	
	AIC	Δ AIC	AIC	Δ AIC	AIC	Δ AIC	AIC	Δ AIC	AIC	Δ AIC	AIC	Δ AIC
Size * sex * t	5148.56	45.66	1525.95	39.80	7564.40	32.25	3126.29	40.89	7908.44	44.57	5423.77	13.01
Size * sex + t	6824.92	1722.02	1486.81	0.66	7532.15	0.00	3097.14	11.74	7885.71	21.84	5410.76	0.00
Size * sex	<u>5107.11</u>	<u>4.22</u>	1494.11	7.97	7549.30	17.14	3085.40	0.00	<u>7872.56</u>	<u>8.70</u>	5430.10	19.34
Size * t	5152.64	49.74	1500.73	14.58	7593.78	61.62	3133.07	47.67	7951.44	87.57	5417.93	7.17
Sex * t	5114.26	11.36	1518.61	32.47	7554.25	22.10	3110.24	24.83	7902.23	38.37	5534.91	124.15
Size	6206.34	1103.44	1491.60	5.45	7590.90	58.75	3113.20	27.80	7936.84	72.97	5442.27	31.51
Sex	5105.15	2.25	1502.82	16.67	7556.36	24.21	3086.54	1.14	10159.01	2295.14	5542.16	131.40
Size + t	5144.27	41.37	1486.15	0.00	7578.39	46.23	3121.99	36.59	7932.51	68.64	5437.20	26.44
Sex + t	5116.41	13.51	1503.15	17.01	7539.02	6.87	3100.01	14.61	7893.89	30.03	5528.81	118.05
(.)	5132.58	29.68	1501.43	15.28	7592.00	59.85	3115.04	29.63	7961.89	98.02	5553.11	142.35
t	5143.92	41.02	1502.01	15.86	7578.36	46.21	3124.98	39.58	7955.81	91.94	5537.70	126.94
Best S * 2 T	<u>5102.90</u>	<u>0.00</u>			7541.46	9.30			<u>7863.87</u>	<u>0.00</u>		
Best S + trend	5144.65	41.75			7551.14	18.99			7872.23	8.36		

three MPA-Control area pairs. These results are unbiased by the imperfect detection (capture probability) or movement of individuals. The ecological and management implications of our results are discussed below.

During the 16-year study period, annual survival of European lobster remained low and fairly stable in areas open to harvest in Skagerrak. In contrast, substantially higher survival rates of both male and female lobsters were recorded inside MPAs after protection, with a maximum increase of 125% for large males. This increase in survival of legal-sized lobsters suggests that local protection from harvesting is indeed effective. Previous studies conducted within the same MPA network have reported increases in catch-per-unit-effort and mean body size of the individuals within the MPAs, consistent with the survival benefit reported here (Huserbråten et al., 2013; Moland et al., 2013a). Also, previous acoustic telemetry studies conducted at the Flødevigen and Hvaler MPAs (Huserbråten et al., 2013; Moland et al., 2011) and recent studies on harvest selection (Fernández-Chacón et al., 2020) have revealed an overall high survival of tagged lobster under protection, but estimates of sex- and size-specific vital rates, and knowledge of their spatial and temporal dynamics were still missing. Comparable estimates are also provided by a mark-recapture study conducted at a Swedish MPA (Moland et al., 2013b), in which the authors report an increasing trend in survival within the MPA, including sex effects on both survival and detectability. The model results and parameter estimates reported in Moland et al. (2013b) are in accordance with our findings, with females showing high survival rates but low detectability compared to males. Interestingly, a recent experiment on freshwater crayfish (*Cherax destructor*) found that catchability was higher for males compared to females, and that females were also shyer, less active and slower growing (Biro and Sampson, 2015). Similarly, for European lobsters,

males could suffer higher mortality from being more active, engaging in aggressive behavioral interactions and exposing themselves to trap fisheries (Debusse et al., 2003; Skerritt et al., 2015; Wiig et al., 2014). Behavioral differences aside, the general higher survival levels of females compared to males in our study system could also be linked to existent sex-biased harvest regulations, as egg-bearing females were given full protection at all sites, including control areas. Unlike survival, we did not find any consistent pattern between MPAs and control areas in the probability of growing from small to big size class, although we did see regional variation that might reflect existing spatial heterogeneity in the availability of resources for lobsters.

The survival estimates reported in this study shed light on the potential longevity of this harvested species. Sheehy et al. (1999) estimated that the average age of large European lobsters was 31 and 54 years for males and females respectively, while the estimated maximum ages of the largest lobsters were 42 and 72 years respectively. In our study, the annual survival probability of large females within the MPAs was about 0.75, while the survival of large males was in the range of 0.4–0.6. Our result qualitatively matches that of Sheehy et al. (1999), showing that males have lower survival and therefore shorter expected life spans. Quantitatively, on the other hand, it would be extremely unlikely for lobsters to reach an age of 40–70 years given the survival estimates reported here. Possibly, the lobster population in Norway has evolved a different life history compared to the population in the UK studied by Sheehy et al. (1999), the former being heavily depleted by selective fishing for decades. Alternatively, our survival estimates could be biased low due to our multi-state analyses confounding permanent emigration and mortality.

The robust design models indicate that tagged lobsters did not move or had low probability of leaving a study site in a given year. This

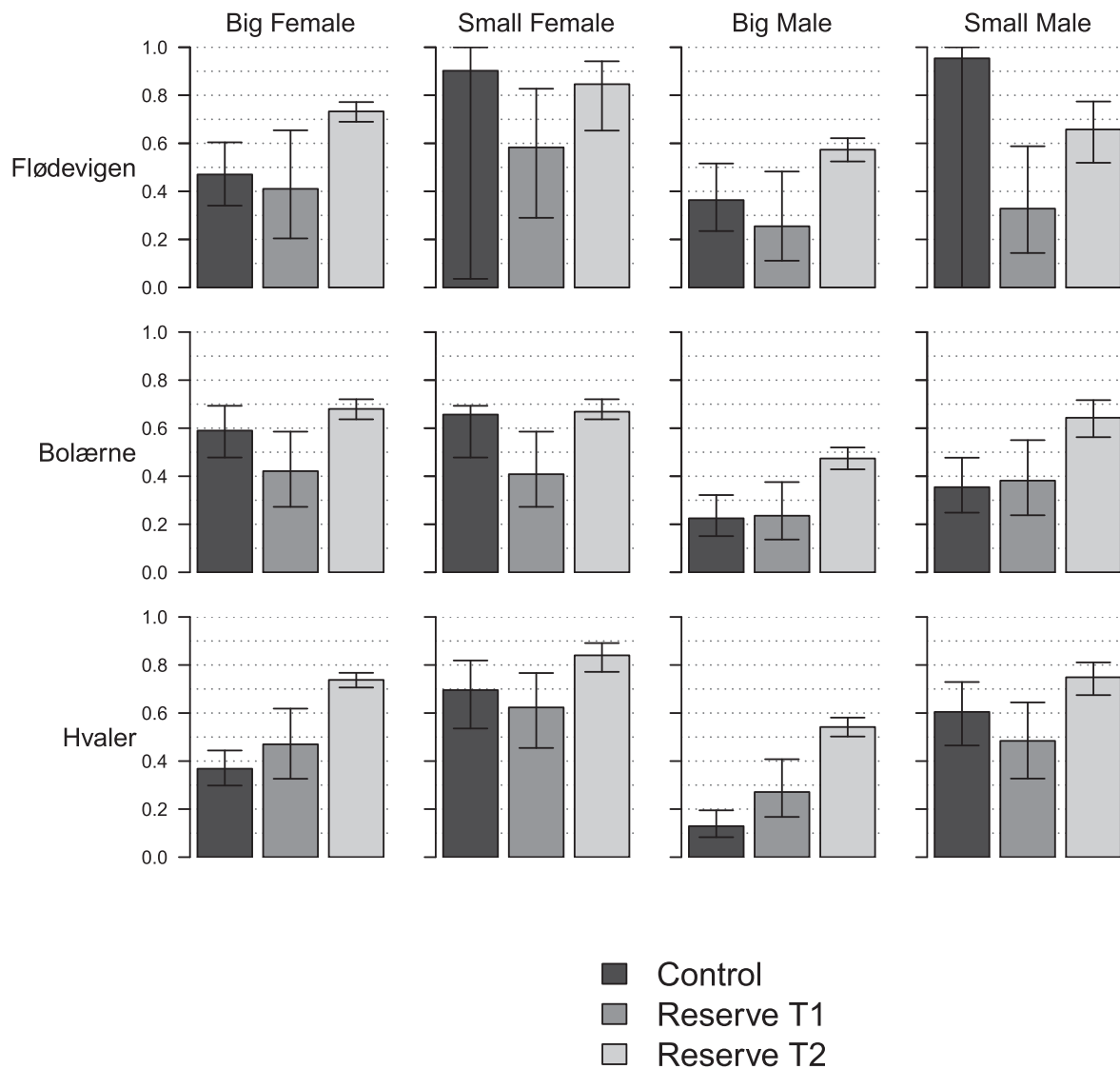


Fig. 2. Mean apparent survival rates of European lobster (bars = 95% confidence intervals) for each study site, sex and size class categories. Survival values for the MPAs (“Reserves” in the figure) are also split in two time periods: before (T1: years 2004–2006) and after protection (T2: years 2006–2019). All estimates were extracted from constant models including sex (Male, Female) and size-state (Big, Small) effects on the survival parameter. Estimates for the MPAs were extracted from similar models including a period effect on their structure (for a list of all survival models, see Table 2).

suggests that our survival estimates are indeed unbiased and also that European lobsters are stationary animals showing high fidelity to the tagging- and release sites most of the time, and that dispersal is dominated by larval drift rather than adult movement (see also, Ellis et al., 2014; Huserbråten et al., 2013). Interestingly, the estimated probability of leaving the Flødevigen MPA was low compared to the probability of leaving the neighboring control area. From an ecological perspective this is somewhat surprising, given that density-dependent processes (competition for resources) are likely to be intensified inside MPAs where population densities are higher, leading to increased spillover to neighboring areas (Goñi et al., 2010). On the other hand, our result is consistent with a recent hypothesis suggesting that spillover fisheries will select against movement out of MPAs, favoring stationary individuals that remain within MPA boundaries (Villegas-Ríos et al., 2017).

Contrary to survival, which improved after protection and always remained higher at the MPAs compared to control areas, lobster abundance did not always follow the same pattern. While lobster abundance at Flødevigen and Bolærne MPAs have remained significantly above those at control sites for many years, the Hvaler MPA-control pair have

largely overlapped. While we do not yet understand the underlying drivers causing this regional variation in dynamics, local habitat features and space availability are likely to play a role. For instance, the Hvaler MPA is small and relatively isolated by deep areas of soft bottom, and also had the lowest estimated population size among the studied MPAs. Sex-specific patterns of abundance seemed to reflect survival results, as a lower abundance of males in general is consistent with their lower survival rates compared to females. Also, some annual changes in abundance occurred in synchrony between MPA and control areas, potentially reflecting environmental variation acting over large spatial areas.

In summary, this study provides novel information on underlying demographic changes associated with the protection of a long-lived and overharvested marine species, the European lobster. We identified common patterns but also spatial differences in demographic responses to MPA establishment, and concluded that MPAs can benefit local population development via improved survival, especially by larger individuals. However, not all sites are equal and despite receiving full protection some may not reach expected conservation goals due to space and/or habitat constraints. Together, these findings can assist future

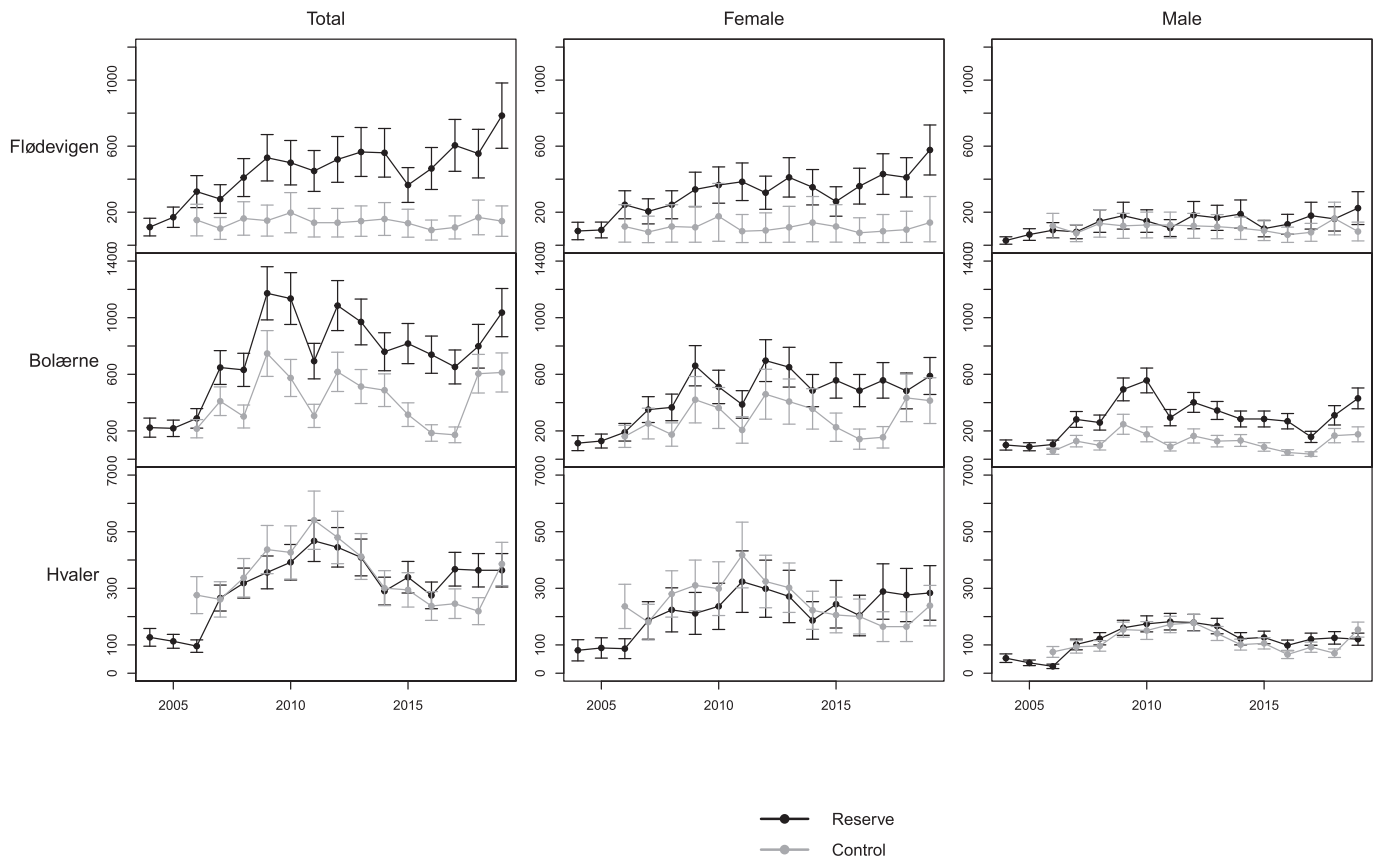


Fig. 3. Annual abundance (N_t) of lobster at each MPA (“Reserve”, in the figure) and control area estimated for each year of study (2004–2019). Total and sex-specific N_t estimates were obtained as derived parameters from the Robust Design analyses conducted in program MARK (see *methods*). To allow direct comparison, temporal abundances obtained at each MPA and control area pairs were plotted together. No sampling occurred at control areas prior to 2006.

Table 3

Robust design model selection results obtained for each study site, showing AIC and Δ AIC values for all model structures tested on secondary detection (c and r) and movement (γ) parameters (see Appendix B for site-specific model selection results obtained for each sex). Detection parameters were modelled first and the resulting lowest AIC model was then used for testing movement hypotheses (see *methods*). The final retained models in each modelling step are underlined, whereas statistically equivalent movement models (i.e. those with Δ AIC < 2) are shown in **bold**.

	Flødevigen				Bolærne				Hvaler			
	MPA		Control		MPA		Control		MPA		Control	
	AIC	Δ AIC	AIC	Δ AIC	AIC	Δ AIC	AIC	Δ AIC	AIC	Δ AIC	AIC	Δ AIC
Detection												
$(c = r)$	-2902.26	16.47	<u>-910.48</u>	0.76	-10,040.71	2.66	<u>-4156.65</u>	0.00	-6308.57	0.00	-8182.60	32.81
$(c \neq r)$	<u>-2916.66</u>	2.07	-910.07	1.17	<u>-10,043.36</u>	0.00	-4155.75	0.91	-6307.99	0.58	<u>-8214.78</u>	0.62
Movement												
$(\gamma'' = \gamma' = 0)$	-2916.66	2.07	-910.48	0.76	<u>-10,043.36</u>	0.00	<u>-4156.65</u>	0.00	<u>-6308.57</u>	0.00	<u>-8214.78</u>	0.62
$(\gamma'' = \gamma')$	<u>-2918.73</u>	0.00	-910.48	0.76	<u>-10,043.36</u>	0.00	-4154.61	2.05	<u>-6306.75</u>	1.82	<u>-8215.40</u>	0.00
$(\gamma'' \neq \gamma')$	<u>-2918.35</u>	0.38	<u>-911.24</u>	0.00	-10,039.49	3.87	-4152.56	4.09	-6305.03	3.54	-8213.40	2.00

management actions and improve the design of future MPAs.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2021.109094>.

CRedit authorship contribution statement

We declare that all authors included in the present work have all significantly contributed to produce the submitted manuscript. Dr. Esben Moland Olsen, Dr. Halvor Knutsen and Dr. Even Moland designed

the field study and collected the individual data analyzed in the present manuscript. Dr. Lucie Buttay prepared the capture-recapture datasets, developing an R code for detecting errors (e.g., misspelled IDs or wrong length measurements) or inconsistencies (e.g., changes in sex assignment) in the field data before the analyses were performed. Dr. Albert Fernández Chacón, first author, analyzed the capture-recapture data and wrote the manuscript. All authors contributed to generate a first draft of the manuscript with their inputs on introduction, study area/species and discussion sections, as well as in the design of figures and tables. All

authors continued contributing to produce revised versions of the manuscript by helping to complete response letters to referees and by editing, when necessary, the main text, figures and tables.

Declaration of competing interest

The authors declare that no conflicts of interests are associated with the research work submitted here.

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