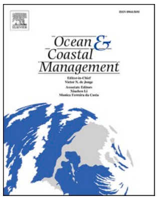
Ocean and Coastal Management 261 (2025) 107535

Contents lists available at ScienceDirect

Ocean and Coastal Management

journal homepage: www.elsevier.com/locate/ocecoaman



Lobster-specific MPA offers little refuge for fish: Long-term closure does not compensate for insufficient size

Diana Perry *, Andreas Wikström, Håkan Wennhage, Mattias Sköld, Andreas Sundelöf

Institute of Marine Research, Department of Aquatic Resources, Swedish University of Agricultural Sciences (SLU), Lysekil, Sweden

ARTICLE INFO

Keywords:
Marine protected area (MPA)
European lobster (*Homarus gammarus)*
Long-term closure effects
Species assemblage
Labridae
Gadidae

ABSTRACT

Small marine protected areas (MPAs) have proven effective at increasing the size and abundance of specific species, not least of which is the European lobster *Homarus gammarus*. However, the benefits of closure for the marine community as a whole are not as well established and vary considerably by location. Kåvra, a partially protected area (PPA) on the Swedish west coast, closed to nearly all forms of fishing for over three decades has shown a strong increase in size and abundance of lobster since the areas establishment. In this study we show continuously increasing positive effects on the lobster population with higher catch per unit effort, and an approximately eight-times higher total reproductive potential within the PPA compared to fished reference areas. However, no effects of closure were seen on the fish assemblage. Single small-scale MPAs can be an effective conservation method for specific species like European lobster, thus contributing to genetic diversity, and the reproductive capacity of intensively fished species. However, without careful consideration of the intended management outcome, single small MPAs alone are often not a sufficient strategy for increasing fish abundances to protect depleted stocks.

1. Introduction

Marine protected areas (MPAs) are a marine management and conservation strategy that have been increasing in spatial coverage, particularly in coastal areas over the last few decades (Wood et al., 2008), with the European Commission setting a 30% protection target for the sea in the EU in 2022. The implementation of MPAs as a tool for ecosystem based management is typically intended as a way of offsetting the effects of human induced changes to marine ecosystems resulting from various pressures such as fishing and habitat alteration (Gaines et al., 2010). MPAs may have many different levels of protection including seasonal access closures, seasonal fishing closures, fishing gear restrictions, as well as the complete restriction of resource harvesting called no-take zones (NTZ) (Lubchenco et al., 2003). Often, a single MPA can have a zonation of different types/levels of restrictions with the intention to balance the cultural and economic needs of the surrounding communities, maintain sustainable harvesting and fishing practices, and ensure the protection of marine species and ecosystems (Green et al., 2013). Ideally, MPA establishment should be implemented with very clear goals (Grorud-Colvert et al., 2021), and each of the various strategies of protection should be designed and implemented with a specific intention in mind, such as the protection or recovery of specific species or habitats.

Typically, the larger the area that is protected, specifically the larger the NTZ area is, or the more it encompasses the full movement patterns of the species within the reserve boundaries, the more successful the MPA is at protecting and conserving the species within (Baskett and Barnett, 2015; Fovargue et al., 2018). However, smaller sized MPAs have also proven to be an effective management tool, particularly when designed as a network where multiple smaller sized MPAs are placed strategically within a larger area (Lubchenco et al., 2003). In an evaluation of 10 small MPAs in Australia Turnbull et al. (2018) found that the success of a small MPA in increasing biodiversity and biomass was dependent upon the location of the MPA, that the area has full protection (i.e. a NTZ) and importantly, that the local society is involved and supports the protection of the area. Thus, the effectiveness of an MPA depends on a design with clear conservation targets to allow for the selection of the location and level of protection while involving the local community and stakeholders.

Another important aspect of designing the MPA and determining the

---

* Corresponding author.
E-mail address: diana.perry@slu.se (D. Perry).

https://doi.org/10.1016/j.ocecoaman.2024.107535
Received 14 September 2024; Received in revised form 11 November 2024; Accepted 22 December 2024
Available online 16 January 2025

desired management result is taking into account the differences in response to protection measures for different species. Larval dispersal, age and size structure, species habitat preference and movement patterns, and generation time are some of the traits that influence how species respond to MPA closures. When creating an MPA for the conservation of harvested species in particular, it is also important to consider including critical habitats such as spawning, feeding, and nursery grounds (Green et al., 2013). Green et al. (2013) demonstrate that age at maturity plays a very important role in species recovery time, particularly for species subjected to heavy exploitation/harvesting. Furthermore, longer lived species potentially take decades to show stable population abundance increases, because increases in biomass typically proceed increases in abundances given that abundance depends on increased reproduction and processes spanning generations (Baskett and Barnett, 2015). These findings demonstrate the importance of long-term closure and that the effectiveness of the MPA may take decades to determine, with longer living, more transient species showing oscillations in population abundance for many years/decades after area closure (Micheli et al., 2004; Molloy et al., 2009; White et al., 2013).

Kåvra, a partially protected area (PPA) on the west coast of Sweden has banned lobster fishing since 1989 (Øresland and Ulmestrand, 2013), and restricted all other types of fishing except hook-and-line (which is very limited) as a response to the all-time low numbers of the European lobster, *Homarus gammarus,* in the 70s and 80s (Sundelöf et al., 2013), making Kåvra one of the oldest PPAs in Europe. Kåvra was mainly protected as a reference area for research to study the development of the lobster population biology in the absence of harvesting (Moland et al., 2013b) and was intended to increase the biological knowledge of the species. As such, it has been very successful in increasing size and abundance of lobster within the boundaries of the PPA, however, additional effects on the fish community have not previously been thoroughly evaluated. An evaluation of the catch data from closure in 1989 until 2007, showed that the density of lobster within Kåvra continued to increase during the first 17 years, while the lobster numbers in the surrounding fished areas showed a decline (Moland et al., 2013b). Adult lobster are extremely restricted in movement and therefore an increase in density within the PPAs boarders does not lead to a significant spill-over effect in other areas, with mark-recapture studies in Kåvra showing that only 1.4 percent out of thousands of tagged individuals were recaptured farther than 1 km from the PPAs boundaries (Øresland and Ulmestrand, 2013). High adult lobster residency rates have also been documented in Norway (Huserbråten et al., 2013). The increase in numbers and size of females within Kåvra has resulted in an estimated 3.5 times higher egg production rate compared to a similarly sized unprotected area (Bergström et al., 2007). Interestingly, Molloy et al. (2009) showed that a general response of fish species to area closure, regardless of whether the area was closed specifically for protection of that species, indicated that species that are commercially exploited show a clear positive response to protected areas, particularly long-term closer areas. However, non-fished species had a much weaker, if any, response to protection. On the Swedish west coast, in addition to the lobster fishery, there is a newly established commercial wrasse fishery (Bourlat et al., 2021) which began in 2010 (Andersson et al., 2021b). Therefore, following Molloy et al.*'s* review, an PPA such as Kåvra may be expected to show positive results within the parks boundaries for wrasse fishes and some gadoid species that have traditionally been exploited. Such patterns were seen in another small reserve on the Swedish west coast, Vinga, for wrasse and cod species, however the initial population increase response of Atlantic cod following closure was no longer observed approximately 10 years later (Kraufvelin et al., 2023).

The aim of the current study was to evaluate the effectiveness of a long-term (>3 decades) fisheries closure on increasing the abundances of mobile marine organisms within the Kåvra PPA boundaries. This was done to determine if differences in size, species diversity, and/or abundance could be found between the PPA and reference areas with the assumption that if differences existed they would be more pronounced for more stationary species, and those targeted by fisheries. Observation of the species assemblages were done by fishing using lobster pots and fyke nets in 2017 and 2018 within Kåvra PPA, as well as two fished reference sites outside the PPA. This follow up study was conducted nearly three decades after the initial closure of the fisheries in Kåvra and provides valuable information on the effectiveness of long-term closure as a marine management strategy.

2. Methods

2.1. Study location and design

The study was conducted at three locations in the archipelago on the Swedish west coast outside Lysekil (Fig. 1). The marine protected area Kåvra (58.33N; 11.63E) was compared with two adjacent reference areas, St Kornö (58.29N; 11.37E) and Långö (58.25N; 11.38E), two areas fished commercially and recreationally targeting lobsters and brown crab using crustacean pots, and wrasses using wrasse pots and fyke nets (Bourlat et al., 2021). Kåvra, closed to lobster fishery and all other fishing except for hook-and-line since 1989, is a small PPA of approximately 2.1 km^2 with a water depth ranging from 0 to 30 m. The hook-and-line fishing, targeting primarily mackerel with occasional bycatch of gadoids, is strictly recreational and the fishing pressure is low enough that it is assumed not to significantly impact the fish community. Compliance to the fishing regulations in the Kåvra PPA is considered good as the area is well known and respected in the local fishing community, and controlled both by inspectors and the Swedish coast guard. The marine coastal area studied for the St Kornö reference site is 2.5 km^2 in size and located 2.3 km south of the PPA Kåvra. Långö reference site has an area of 2.3 km^2 and is located 6.7 km south of Kåvra. St Kornö and Långö are both assigned as reference sites in this study given that they are similar to the Kåvra PPA with regards to depth, substrate, size and topography.

2.2. Fishing gear

All fishing was conducted in the month of August for both 2017 and 2018 and total fishing effort did not vary between the three locations (ANOVA $p = 0.30$). The fyke nets used in the study were structured with a double-codend with 3 chambers and 7 hoops, the largest measuring 30 cm, with a 6 m leader, a mesh size of 10 mm in the codend, and 15 mm in the leader. In Kåvra 110 fyke net stations were sampled, 108 in Långö and 108 in St. Kornö. Stations for fyke net sampling were randomized to the extent possible within each site on, or in close proximity to, hard bottom between 0 and 20 m depths. Average soak time for each station was 23.6 h, with a minimum of 18.3 and a maximum of 28.3 h.

Lobster pots were also deployed targeting European lobster, which were 92 cm long, 45 cm wide, 40 cm high, structured with two entrances (one on each side; diameter 120 mm) to the baited chamber. All pots had a mesh size of 50 mm and were baited with mackerel or herring. The pots were randomly set (within the substrate and depth requirements) on hard bottoms at depths from 5 to 30 m, with the total number of stations for both years being 133 in Kåvra, 134 in Långö, and 131 in St Kornö. The average soak time for each station was 45.2 h (24–96 h). Fyke net and lobster pot stations were only visited once, with no revisiting of stations between years 2017–2018.

All lobsters were recorded, including information on carapace length and sex. Fish caught were identified and individually measured (length in cm). All other catches were identified and number of individuals per species were recorded. Fish and invertebrates were handled with care and released back in the water at the place of capture. Additionally, data from the time of PPA closure in 1989–2007 were used to calculate the historical lobster average size per sex in Kåvra (both fyke net and pot data were used during early survey fishing; these data are referred to as

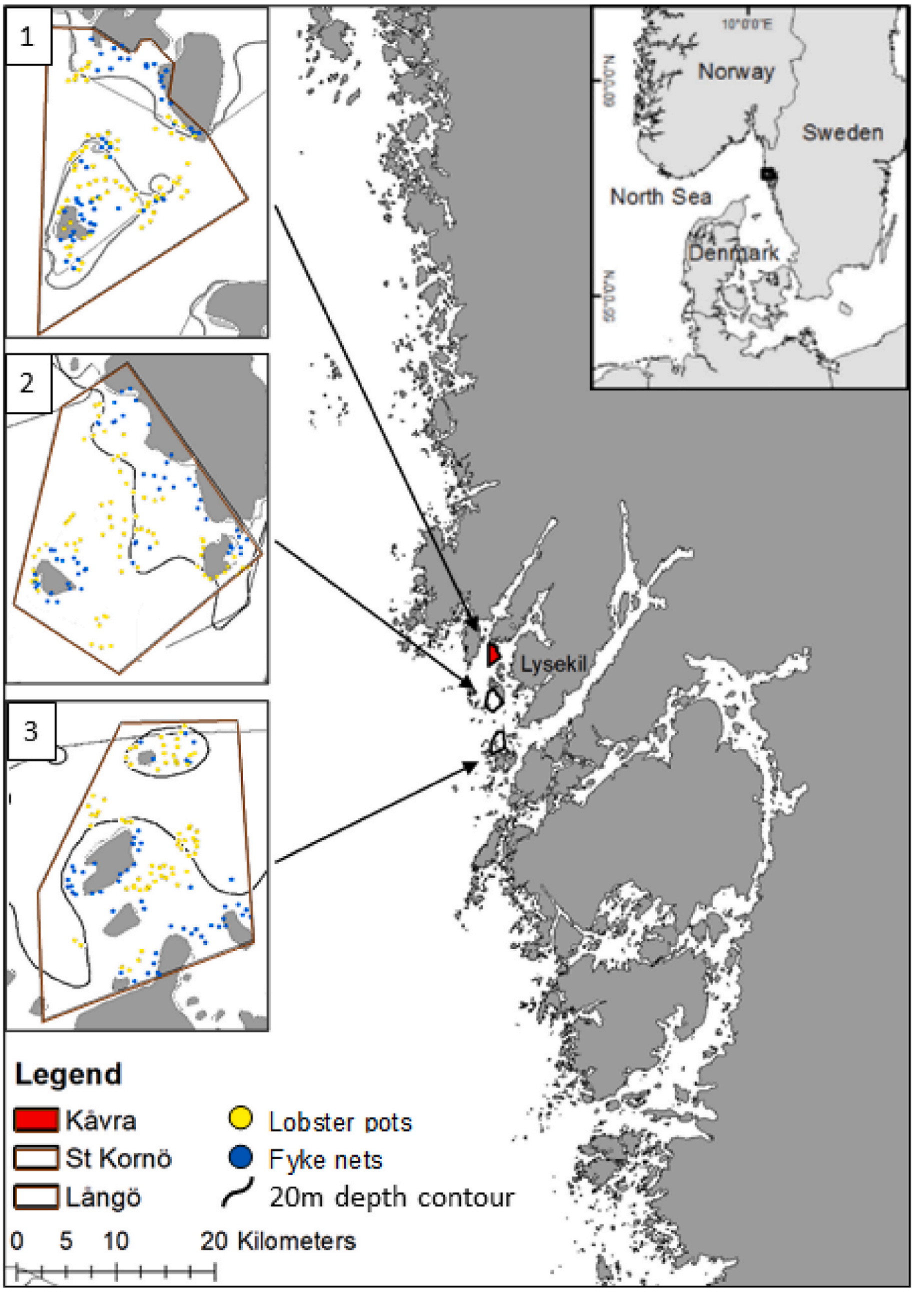


Fig. 1. Map of the study area along the west coast of Sweden. Kåvra PPA (top −1) marked in red has been closed to fishery for since 1989. The reference areas Stora Kornö (middle −2) and Långö (bottom −3) are being used as fishing grounds for both commercial and recreational fishers targeting lobster and wrasses. The yellow circles represent the positions sampled with lobster pots and blue circles represent positions sampled with fyke nets. The black curved line represents the 20 m depth contour with the area towards the gray shaded land from the line ≤20 m. The depth contour is provided by © The Swedish Maritime Administration.

"early period" hereafter) used for Fig. 6.

2.3. Statistical analysis

Multivariate analyses were performed using the Primer 7 software (v.7.0.22, Plymouth Marine Laboratory). Differences in species composition per site were assessed for the fyke net data using non-parametric permutational multivariate analysis of variance (PERMANOVA (Anderson et al., 2008),) with the Bray-Curtis similarity index on fourth root transformed data. Patterns for the 0–6 m and 6–20 m fyke net data, including the main species contributing to the dissimilarity, were visualized using constrained ordination based on Bray-Curtis dissimilarity measures with Canonical analysis of principle coordinates (CAP).

The eleven species identified as contributing to differences between sites were further analyzed for catch per unit effort per 24 h (CPUE/day) for fyke net data. The eleven species were *Symphodus melops*, *Taurulus bubalis*, *Pollachius virens*, *Labrus bergylta*, *Homarus gammarus*, *Gobius niger*, *Gadus morhua*, *Ciliata mustela*, *Centrolabrus exoletus*, *Carcinus maenas*, and *Cancer pagurus*. Additional statistical analyses were performed using STATISTICA 64 version 13. Additionally, CPUE per pot per 24 h was calculated for *Cancer pagurus*, *Carcinus maenas*, and *Homarus gammarus*. For fish within the Labridae and Gadidae families comparisons between mean lengths per site were also performed using the one-way ANOVA and Kruskal-Wallis non-parametric analysis of variance. Fish from these two families were selected for analysis because they were the two most abundant fish families caught, as well as containing species of commercial interest for fisheries.

An additional calculation for *H. gammarus* was performed to convert

CPUE from numbers to weights in kg for males (m) and females (f). Size composition varies greatly between fished and protected areas and catch in weight captures both number and size of catch. The relationship between carapace length and weight varies also between males and females and, therefore, CPUE is effected by the number of individuals caught per sex. CPUE/kg was calculated using equations (1) and (2), respectively, where W is weight in kilograms and CL is carapace length in millimeters (Sundelöf et al., 2015).

$$W_m = 0.000376987 \times CL^{3.1488} \qquad \text{Eq. 1}$$

$$W_f = 0.001949666 \times CL^{2.7775} \qquad \text{Eq. 2}$$

Potential egg production is a proxy for reproductive potential for *H. gammarus* and was calculated using methods established by Ulmestrand (2003) and Sundelöf et al. (2015), where the proportion berried (PB) females are calculated using carapace length (CL) with a = 37.62, b = 0.48, and c = 0.01 (equation (3)), where only females with a CL > 74 mm were considered mature and included in the calculation. Then the number of potential eggs "y" (fecundity) were calculated using linear regression (equation (4)) where CL is the carapace length value in millimeters per individual because the number of eggs is directly related to the size of the female. Reproductive potential (RP) was then calculated by multiplying the PB by y and then subsequently multiplying RP by the number of individuals caught to determine reproductive potential of the individuals assessed per area (Kåvra, Långö, and St Kornö). Thus, reproductive potential accounts for both the total number of captured female individuals, as well as the size per individual female as a relative measure to compare the assessed areas.

$$\mathrm{PB} = \frac{1}{1 + e^{(a - b^{*}CL)}} \Big/ e^{(c^{*}CL)} \qquad \text{Eq. 3}$$

$$\mathrm{y} = 372.09^{*}\mathrm{CL} - 22598 \qquad \text{Eq. 4}$$

3. Results

3.1. Species assemblage

When evaluating the entire marine community within the PPA and reference areas using both gear types 23 families were observed under the 2017-18 fishing period, from 3 different group classifications including crustaceans, bony fishes, and sea stars, of which 14 families were fish. There were 4954 individuals caught from 18 different families in the PPA, while for the two reference areas there were 5150 individuals from 21 families caught in Långö and 5674 individuals from 19 families in St Kornö (Supplementary Material Table 1).

Analysis of the species composition for the fyke net data at 0–6 m was analyzed using PERMANOVA, and showed a difference in species catch per site (**p = 0.036**), with the pairwise post-hoc tests indicating significant differences between the Kåvra PPA and the reference site St. Kornö (Kåvra-Långö p = 0.080, Kåvra-St. Kornö **p = 0.012**, Långö-St. Kornö p = 0.395). The PERMANOVA analysis for the fyke net data from 6 to 20 m also showed a significant difference in species catch per site (**p = 0.002**) with a pairwise post-hoc test indicating differences between all pairs of sites (Kåvra-Långö **p = 0.040**, Kåvra-St. Kornö **p = 0.017**, Långö-St. Kornö **p = 0.0034**). The pot data failed to meet the assumption criteria and therefore no PERMANOVA test was performed. The canonical analysis of principle coordinates (CAP) plot visualizes the dissimilarities between the Kåvra PPA, Långö, and St. Kornö (Fig. 2).

When reviewing the fish assemblage caught within the three sites the fish families found in the highest total abundances were Labridae, Gadidae, Cottidae, Anguillidae, Lotidae, and Gobiidae. All of these six families had a total of greater than 50 individuals observed during the 2017-18 seasons, though the Labridae family was caught in 15-20-fold greater numbers compared to all of the other most abundant fish families. Eleven species were identified from the CAP analysis (Fig. 2) which were further investigated for comparisons of catch per unit effort per 24 h (CPUE/day). For the fyke net data differences between CPUE/fyke net/day were calculated using general linear models (GLM). The resulting significance values per species were as follows: for *Symphodus melops* (p > 0.05), *Carcinus maenas* (p = 0.051), *Centrolabrus exoletus* (**p = 0.01**), *Cancer pagurus* (p > 0.05), *Gadus morhua* (**p = 0.018**), *Pollachius virens* (p > 0.05), *Homarus gammarus* (**p<0.001**), *Ciliata mustela* (**p = 0.028**), *Gobius niger* (p > 0.05), *Labrus bergylta* (**p = 0.002**), and *Taurulus bubalis* (p > 0.05). For the species showing significant differences between sites Tukey HSD post-hoc analyses were performed. The post-hoc results for *C. exoletus* showed that there was a significantly larger CPUE/fyke net/day in St. Kornö compared to Kåvra (**p = 0.006**). For *C. mustela* there was also a significantly larger CPUE/fyke net/day in St. Kornö compared to Kåvra (**p = 0.039**). For *G. morhua* there was a significantly larger CPUE/fyke net/day in Långö compared to St. Kornö (**p = 0.020**) but no difference between the reference sites and the PPA. For *H. gammarus* there was a significantly larger CPUE/fyke net/day in Kåvra compared to both Långö and St Kornö (**p<0.001** and **p<0.001**, respectively). For L. *bergylta* there was a significantly larger CPUE/fyke net/day in St. Kornö compared to Kåvra (**p = 0.001**).

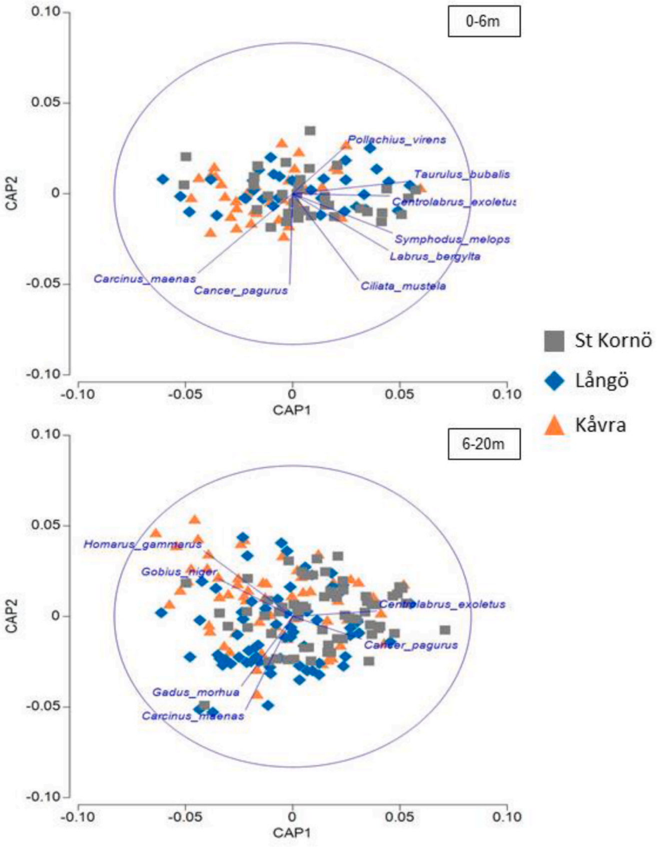


Fig. 2. Canonical analysis of principle coordinates (CAP) using constrained ordination based on dissimilarity measures for the fyke net data for 0–6 m (top panel) and 6–20 m (bottom panel). The Kåvra PPA is shown in orange (triangles), Långö in blue (diamonds), and St. Kornö in gray (squares).

The CPUE/day per lobster pot GLM analysis showed significant differences for all three crustacean species analyzed, *Cancer pagurus* (**p<0.001**), *Carcinus maenas* (**p = 0.009**), and *Homarus gammarus* (**p<0.001**) (Fig. 3). The Tukey HSD post-hoc analyses showed significantly lower CPUE/pot/day for *C. pagurus* in Kåvra compared to the two reference sites, **p<0.001** for Långö and **p<0.001** for St. Kornö as well. The post-hoc results for *C. maenas* showed a significantly higher CPUE/pot/day in Långö compared to both Kåvra and St. Kornö, **p = 0.019** and **p = 0.024**, respectively. For *H. gammarus* the post-hoc results showed a

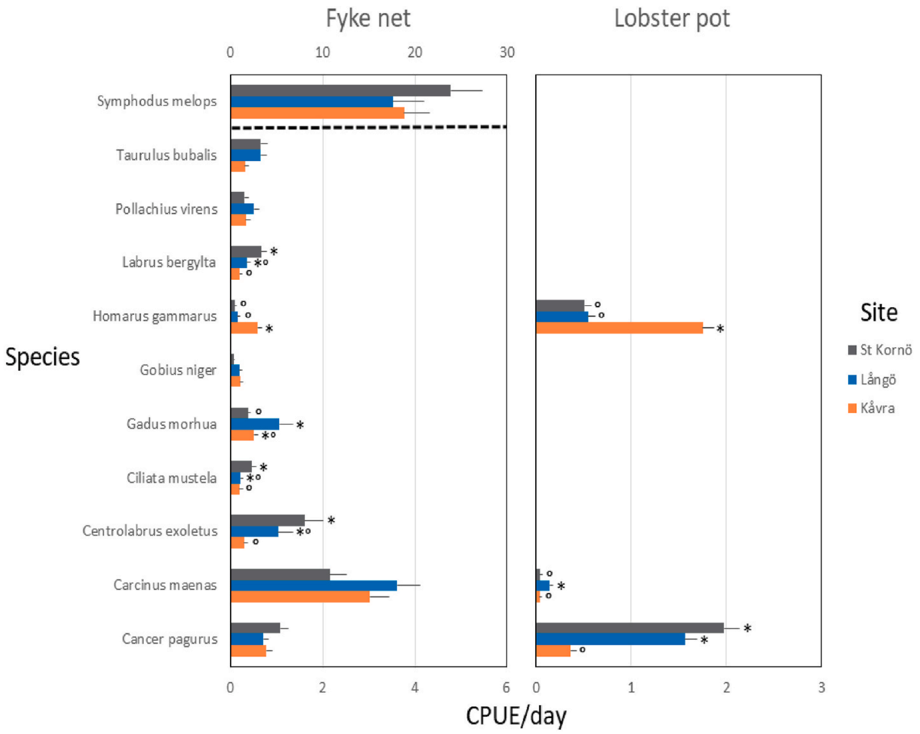


Fig. 3. The catch per unit effort (CPUE) per day (24hrs) per site is shown for the 10 species identified in the CAP analysis as driving differences between sites, Kåvra PPA (orange), Långö (blue), and St. Kornö (gray). The species shown are *Symphodus melops*, *Taurulus bubalis*, *Pollachius virens*, *Labrus bergylta*, *Homarus gammarus*, *Gobius niger*, *Gadus morhua*, *Ciliata mustela*, *Centrolabrus exoletus*, *Carcinus maenas*, and *Cancer pagurus*. CPUE/day for fyke nets is shown in the left panel while CPUE/day for lobster pots is shown on the right. *Note* that for the fyke net data there are two different scales denoted with the thick dashed black line with the top (0–30) related to the CPUE/day for *Symphodus melops*, while all other species below the dashed line in the fyke net panel relate to the scale on the bottom (0–6). Significant differences ($p \leq 0.05$) for the post-hoc results for a single gear type within species comparisons are denoted with a symbol (*°) where having the same symbol indicates no significant difference. *Note* also that the lobster pots did not catch the 7 non-crustacean species in numbers large enough to include on the CPUE/day graph.

significantly higher CPUE/pot/day in Kåvra as compared to both Långö and St. Kornö, **p<0.001** and **p<0.001**, respectively.

The most abundant family caught in the PPA, as well as the two reference sites, were wrasses (Labridae). Four wrasse species were caught within the PPA, whereas both reference sites had five species. For all sites, the most abundant fish was the corkwing wrasse, *Symphodus melops*. The mean length per site was analyzed for all Labridae species caught with greater than 5 individuals per site. The mean length of *C. rupestris* was found to be greatest in the reference area Långö when compared to Kåvra and St Kornö, while the mean length of *S. melops* was greatest in St Kornö compared to Kåvra and Långö (Table 1).

The second most abundant fish family was Gadidae with six species caught, though only a single individual *Trisopterus esmarkii* was caught in Långö and none in Kåvra or St. Kornö. Of all cod fishes *Gadus morhua* was caught in the largest numbers and was the only gadoid species analyzed showing significant differences in mean length between sites, with significantly larger individuals caught in St. Kornö as compared to those in the other reference area Långö. No differences in mean length were found among *G. morhua* in the PPA and the two reference sites (Table 1).

There were 13 benthic invertebrate species from 9 different families caught during the 2017-18 seasons (Table S1). Of which 10 were species of crustaceans and three were sea stars. Of all the benthic species caught only three were seen in numbers greater than 35 individuals per site and

Table 1

Labridae and Gadidae species mean size (cm) per site from fyke net data ± standard deviation (SD). The number of individuals caught is listed under (n). P-values were listed as "Not applicable" (N/A) when a One-way ANOVA/Kruskal-Wallis test was not performed because one or more site(s) had n < 5.

		KÅVRA		LÅNGÖ		ST KORNÖ		
Family	**Species**	**Avg. size ± SD**	**n**	**Avg. size ± SD**	**n**	**Avg. size ± SD**	**n**	**p-value**
Labridae	*Centrolabrus exoletus*	9.9 (±1.2)	31	10.0 (±1.4)	104	9.8 (±1.5)	172	>0.05
	Ctenolabrus rupestris	9.8 (±1.2)	1588	10.0 (±1.2)	1757	9.9 (±1.1)	1563	**<0.001***
	Labrus bergylta	16.6 (±5.3)	21	15.1 (±4.0)	39	15.6 (±5.5)	71	>0.05
	Labrus mixtus	N/A	0	18.9 (±2.6)	16	17.5 (±4.3)	6	N/A
	Symphodus melops	12.2 (±2.4)	1985	12.2 (±2.2)	1806	12.4 (±1.9)	2516	**<0.001⁂**
Gadidae	*Gadus morhua*	21.4 (±9.2)	56	17.9 (±8.4)	112	23.6 (±9.3)	40	**= 0.001†**
	Merlangius merlangus	10.2 (±2.2)	6	11.1 (±1.5)	27	12.0	1	N/A
	Pollachius pollachius	12.7 (±1.9)	9	18.9 (±8.6)	7	18.4 (±7.5)	8	>0.05
	Pollachius virens	12.3 (±1.7)	38	13.2 (±3.4)	53	14.7 (±4.9)	32	>0.05
	Raniceps raninus	19.2 (±4.6)	6	20.0 (±4.4)	4	20.3 (±2.0)	6	N/A
	Trisopterus esmarkii	N/A	0	9.0	1	N/A	0	N/A

*post-hoc results Långö-Kåvra $p < 0.001$, Långö-St Kornö $p < 0.001$ ⁂post-hoc results St Kornö-Kåvra $p < 0.001$, St Kornö-Långö $p < 0.001$ †post-hoc results Långö-St Kornö $p = 0.002$.

they were all crustaceans. An in depth analysis of *H. gammarus* pot data is detailed in the following section.

3.2. PPA focal species- *Homarus gammarus*

There were a total of 758 *H. gammarus* individuals caught during the two fishing seasons in 2017 and 2018, with 479 caught within the PPA, and 145 and 134 from the reference sites Långö and St. Kornö, respectively, using both gear types. The average catch per unit effort (CPUE) in kg per trap for *H. gammarus* in the Kåvra PPA was 1.52 kg in 2017 and 2.18 kg in 2018, while it was only 0.12 kg in the reference site Långö in 2017 and 0.41 kg in 2018. The second reference site St. Kornö had a CPUE in kg per trap of 0.16 kg in 2017 and 0.27 kg in 2018 (Fig. 4A). The average reproductive potential of lobsters per km^2, estimated from the number of eggs produced, was highest in Kåvra, with an average of approximately 2900 (±492 SD) eggs produced per mature female per year in 2017, and 2730 (±759 SD) in 2018. The reference site Långö had an estimated reproductive potential per km^2 of approximately 1630 (±942 SD) eggs produced in 2017 and 1560 (±721 SD) in 2018, while St. Kornö had the lowest average egg production per km^2 at nearly 1200 (±882 SD) in 2017 and approximately 1150 (±898 SD) in 2018 (Fig. 4B). Consequently, the total reproductive potential (as calculated by the number of eggs produced) by the sampled individuals per year was nearly seven times higher in Kåvra compared to Långö and almost nine times higher compared to the other reference site St. Kornö.

When reviewing the average size per sex within Kåvra using survey data from 1989 to 2007, and 2017 and 2018 there is a general trend in increasing size for both males and females until the end of the early period in 2007, with the average size in 2007 being 97.5 mm for females and 104.4 mm for males, respectively. The 2017-18 data shows a continued increase in the average size of both males and females from the end of the early period in 2007; an increase that is even greater than that expected from the linear regression of the earlier period data (Fig. 5).

For the period 2017–2018 using both gear types, lobsters were larger in carapace length (CL) in the PPA (range 52–175 mm CL) than the two reference sites (57–117 mm CL in Långö and 60–117 mm CL in St. Kornö) (Fig. 6). The maximum size, measured as carapace length, caught within the PPA was 175 mm, while the two reference sites both had a maximum recorded carapace length of 117 mm. The Kruskal-Wallis test for comparisons of lobster size, calculated from the size of all individuals per site, between Kåvra and the reference sites shows a significant difference with larger individuals caught within the PPA $H(2) = 201.93$, $p < 0.0001$. Additionally, the post-hoc test shows a significant difference of the PPA compared to both the reference sites, $p < 0.001$ for Långö and $p = 0.004$ for St. Kornö, however, lobsters in the two reference sites do not differ from one another in size.

4. Discussion

The Kåvra PPA was established in 1989 and since the closure of the site to fishing there has been a consistent and clear increase in size of lobster caught within Kåvra (Moland et al., 2013b; Øresland et al., 2018; Øresland and Ulmestrand, 2013; this study), however the PPA did not show significantly larger CPUE/day or mean length for any other species analyzed. We also found that the PPA had much higher catch rates, and a total reproductive potential nearly eight times higher than that found in the reference sites for *Homarus gammarus*. The higher reproductive potential is a result of the greater numbers and larger female lobsters within the PPA. Notably, the pots used for sampling lobster in 2017 and 2018 are size-selective, and may bias catches away from both the smallest and largest individuals, indicating that the maximum size of lobsters in the area could be even higher (Øresland et al., 2018).

Rapid and continued response to closures with increased size of the European lobster, *H. gammarus*, has been shown in Norway as well (Knutsen et al., 2022), though these PPAs were implemented 15 years after Kåvra. The Norwegian MPAs have been shown to increase the size, thereby even rebuilding phenotypic complexity, of the lobsters within the MPAs which then provides protection from harvest selection (Fernández-Chacón et al., 2020). This buffering against harvest selection is important given that harvesting of *H. gammarus* may change mating behavior, and could lead to fisheries-induced evolution towards smaller body size (Sørdalen et al., 2018). Sørdalen et al. (2022) also show that closure reduces the fisheries induced slow-growth selection meaning that lobster grow faster within the protected areas, an additional reason for the rapid recovery of *H. gammarus* populations in reserves. There is also evidence that there has been an ecological spillover effect of the Norwegian reserves with increased lobster biomass near reserve boundaries (Thorbjørnsen et al., 2018), however, adult lobsters display restricted movement and high residency. Despite the limited adult dispersal, a high level of gene flow has been shown in Skagerrak (Ellis et al., 2017), indicating the importance of larval drift (Huserbråten et al., 2013). However, Øresland and Ulmestrand (2013) noted that there was high retention of the deep water mass around Kåvra, not

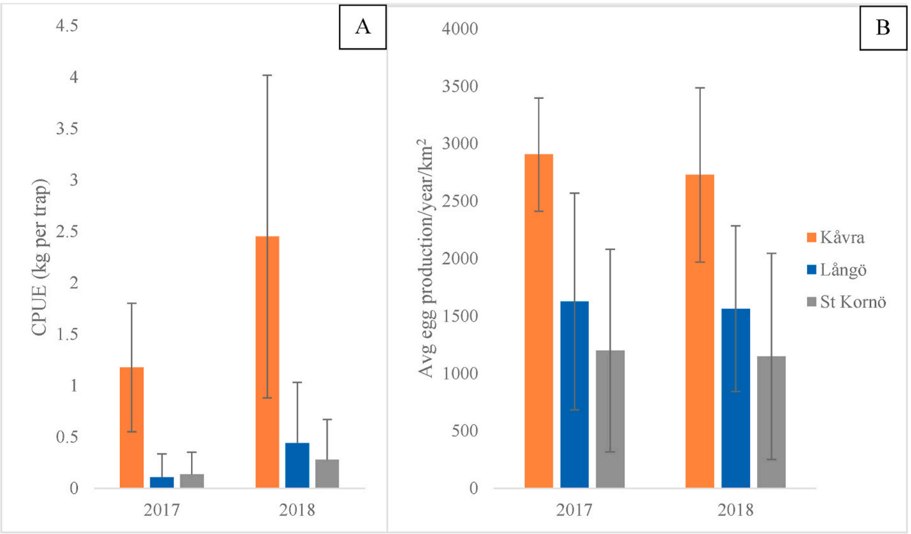


Fig. 4. A) Average catch per unit effort (CPUE) in kg per trap of *Homarus gammarus* in 2017-18. B) Average predicted egg production (±SD) per mature female per year and location as related to the total number of mature females. Kåvra is shown in orange, Långö in blue and St Kornö in gray.

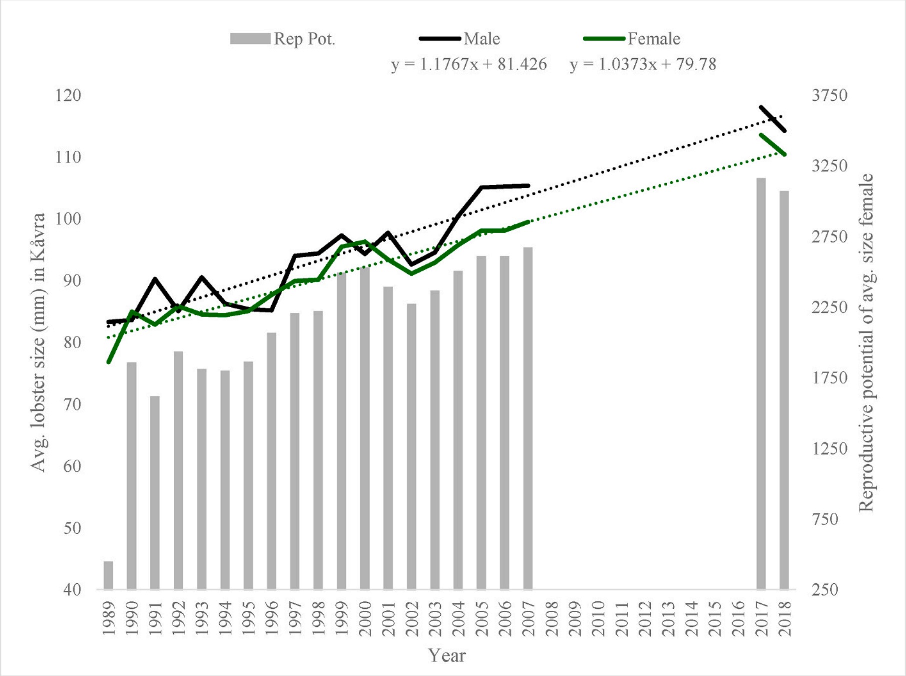


Fig. 5. Average size, measured in millimeter carapace length, of male (black) and female (green) *Homarus gammarus* within Kåvra PPA from time of closure in 1989 until 2018. Dashed black and green lines denote the linear model fitted to data for the years 1989–2007 and extrapolated to the years 2017–2018 when the PPA was revisited. Linear regression equations shown for male and female average size over years. Figure modified from Bergström et al., 2022).

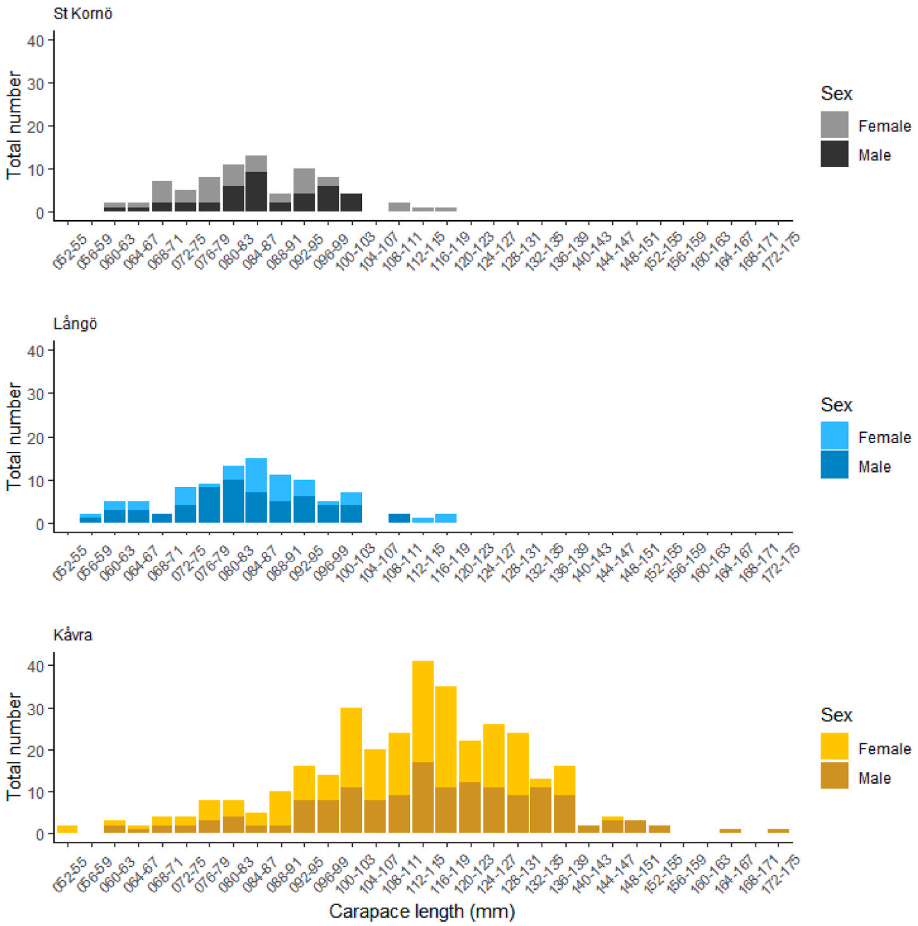


Fig. 6. Carapace size distribution (mm, shown on x-axis) for the three study locations, Kåvra (orange-bottom), Långö (blue-middle) and St. Kornö (gray-top) for males and females. The dashed black line represents the allowable minimum size catch restriction >90 mm. Figure modified from Bergström et al. 2023).

expanding more than approximately 16 km^2, which they suggest would lead to a relatively localized outflow of larvae from the Kåvra PPA.

While the PPA has been very effective for increasing the lobster population within the sites borders, this study did not find any indications of positive closure effects on the fish assemblage even though the area has been restricted to fishing for over 3 decades. In fact, the current results showed the opposite; while differences in species catches existed between sites, both higher catch rates (*L. bergylta*, *C. mustela*, and *C. exoletus*) and larger individuals (*C. rupestris* and *S. melops*) were seen in the references areas compared to the PPA (except for *H. gammarus*). Given the importance of life-history traits on the success of MPAs for particular species (Claudet et al., 2010) it may be expected that the Kåvra PPA, due to the very small size, would not be sufficient for increasing the abundance or biomass of mobile species such as cod fishes (Sköld et al., 2022). However, there is evidence of small reserves showing positive effects also on more resident temperate species (e.g. Halvorsen et al., 2017; Sköld et al., 2022). Certain fish species found in the area, such as members of the Labridae family, are highly residential (Halvorsen et al., 2021), and are targeted by the fishery for exportation to be used in aquaculture in Norway (Bourlat et al., 2021). Therefore, they could be expected to show increases in abundance as a result of the protection from fishing, however the current study found no such effects. This is in contrast to results seen in Norway where MPAs have led to increases in the abundance also of other targeted species like cod and different species of wrasse (Halvorsen et al., 2017; Moland et al., 2013a).

Although the current study did not find the same response to closure for the wrasse fishes as is seen in Norway, it is not currently possible to determine if this lack of difference is a result of there being no effect of the Kåvra PPA for this fish family, or if it is due to low fishing pressure meaning that the wrasse populations are stable and not decreasing in the region as a results of the fishing pressure. For perspective, the Norwegian wrasse fishery is older, has more active fishers, and has catch rates much higher than those found in Sweden; the Norwegian Fiskeridirektoratet issued a quota of 4 million wrasse to be caught in 2022 (https://www.fiskeridir.no/Yrkesfiske/Tema/Leppefisk/Leppefisk-reguleringa-2022) along the Norwegian Skagerrak coast, while the Swedish fishery in Skagerrak is estimated to have removed approximately 1 million wrasse per year from 2013 to 2018 (Bourlat et al., 2021). Additionally, the ineffectiveness of Kåvra at increasing the abundance of non-target species such as Atlantic cod may be related to the collapsed coastal stocks on the Swedish west coast, and the critical state of the population (Andersson et al., 2021a; Svedäng and Bardon, 2003), making recovery difficult despite a number of different management actions to reduce fishing mortality of cod on the Swedish west coast over the last decades. Similarly the PPA Vinga farther south from Kåvra on the Swedish west coast showed an initial increase in number and size of cod within the borders of the closed site, however nearly a decade after closure no differences could be detected compared to the reference sites (Bergström et al., 2016, 2022).

Interestingly, while Kåvra PPA shows strong positive effects on the lobster population and no effects on the fish community, lower total numbers of the brown crab *Cancer pagurus*, are found in the PPA compared to the reference sites Långö and St Kornö. A gear specific analysis of the data, however, shows that this pattern is quantitatively modified when reviewing the fyke net data, a gear that is not baited and therefore may catch species differentially from pots. Given the selectivity of the two gear types and the contrasting results of the fyke net compared to the pot data it is difficult to determine from the current data whether the similar CPUE of *C. pagurus* in Kåvra in fyke nets is in fact a gear effect or reflects true abundances of brown crab. It has been speculated that the presence of lobsters deter brown crabs from entering pots, thus seemingly reducing densities of brown crab. However, although absolute differences in abundance of lobster and brown crab may be difficult to assess by fishing gear, Øresland et al. (2018) used scuba diving observations which described strong differences in abundance of brown crab inside and outside Kåvra. Negative effects of protection in MPAs due to species interactions and predation have also been documented elsewhere (Micheli et al., 2004). While *C. pagurus* numbers seem to have an inverse relation to *H. gammarus* numbers with higher crab densities found in locations with lower lobster densities, the same relationship was not found with the European green crab, *C. maenas*. A lower abundance of *C. maenas* within an PPA has been documented in another no-take site along the Swedish west coast, which was attributed to top-down control resulting from the increased abundance of fish and *H. gammarus* (Kraufvelin et al., 2023).

While the Kåvra PPA is a highly effective lobster protection area no benefits to the fish community were found despite decades of fishing exclusion. These results are contradictory to many shown previously, where an increase in annual fish density of approximately 5% within reserve boundaries have been observed (reviewed by (Molloy et al., 2009)). This may be due to Kåvra's small size given the mobility of the fish assemblage, even if some species and families such as Gobiidae and Labridae are highly resident. Alternatively, it may be an indication that these species are not depleted enough to show population declines and have high abundances throughout the region. Another reason for the lack of effects on abundance of some other species with larger geographic ranges occurring in this study (e.g., cod, pollock) may be that the populations are highly depleted and a small scale PPA in such cases provides insufficient protection for recovery. This has been shown for the highly exploited cod in Kattegat, farther south on the Swedish west coast, where the NTZ established was smaller than what was originally proposed by scientists and it has been concluded that the NTZ is insufficient in size for protecting and rebuilding the cod stock (Sköld et al., 2022). Even if small reserves may be limited in the extent of protection for mobile species (Turnbull et al., 2018), there is still much evidence showing the effectiveness for certain target species, such as *H. gammarus* in Kåvra and Norwegian MPAs (Knutsen et al., 2022; Moland et al., 2021; Sørdalen et al., 2022). Additionally, there has been considerable discussion and support for the idea of networks of small reserves as a valuable management strategy both for enhancing fisheries and for conservation benefits (Berkström et al., 2021; Fovargue et al., 2018; Gaines et al., 2010; Green et al., 2013; Halvorsen et al., 2021; Synnes et al., 2023). For networks to be successful, species movements, migrations and connectivity (such as gene flow, and larval dispersal) should be considered, and it is critical to have a clearly defined objective for the management area. For Kåvra it seems the necessary requirements are only fulfilled for lobster.

4.1. A small PPA in a larger context – implications for MPA design

MPAs and in particular NTZs can be effective conservation measures improving important biological variables such as species densities, biomasses, body sizes, and richnesses (Langlois et al., 2021) and have been shown to be economically beneficial in terms of increasing fisheries profits outside the reserve boundaries (Bostedt et al., 2020; Fenberg et al., 2012). The success of MPAs as a conservation strategy intended to protect marine biodiversity has been considered to rely on five key features related to the area being a no-take zone, well enforced, over 10 years old, larger than 100 km^2, and surrounded by deep water or areas of sand (Edgar et al., 2014). For MPAs with only one or two of these key factors, Edgar et al. (2014) found that the majority of MPAs were not ecologically distinguishable from fished areas. Considered in such context, the Kåvra PPA only loosely meets three of these measures of success, as it only allows hook-and-line fishing which is considered to be minimal, compliance to the closure is considered to be good, and the area benefits strongly from long-term closure given that it has been closed since 1989. However, the area is only approximately 2 km^2 and a small portion of it is accessible from land, though only a small island. In fact, it is the very small size of the area that the authors believe is the reason for the lack of effects seen on the community in general. While there is evidence of small no-take areas successfully increasing marine organism abundance and biomass, these areas are typically within a larger network of no-take zones (Lubchenco et al., 2003), a key feature lacking for Kåvra (Bergström et al., 2022; Berkström et al., 2021). The level of exploitation prior to MPA closure and in the surrounding area also play a significant role in the success of the NTZ (Claudet et al., 2010) with non-fished species showing less or no response to MPA closure (Edgar et al., 2014). Interestingly, Denny et al. (2004) show that both the abundance and biomass of the fisheries targeted snapper, *Pagrus auratus,* increased significantly only after the shift in management from a PPA to a NTZ, which gives evidence of the ineffectiveness of a partially protected area for a mobile exploited species. On the Swedish west coast where the Kåvra PPA is located, overfishing has been linked to stock depletions, particularly for Atlantic cod and other gadoids, and other ecological effects (Baden et al., 2012; Cardinale and Svedäng, 2004; Sköld et al., 2022).

5. Conclusion

In summary, while the Kåvra PPA has yielded strong positive effects on the target species *H. gammarus*, the results of the current study clearly indicate that little to no positive effects can be seen on the marine community as a whole. For improved conservation status to be achieved, it is recommended that management increase the number of NTZ in the area in order to create an MPA network to improve ecological connectivity, as well as greatly increase the size of Kåvra and any other future MPAs in the area, measures which have been shown globally to improve MPA success (Claudet et al., 2008; Edgar et al., 2014; Fenberg et al., 2012; Green et al., 2013; Micheli et al., 2004; Moland et al., 2021). This long-lived species, after more than three decades is still increasing in size and number within the area. Additionally, the PPA as a reference area has provided an excellent opportunity to increase biological knowledge on lobster biology by providing baseline information on an unfished population. The use of small PPAs may also contribute by reducing genetic effects which helps avoid fisheries induced evolution in lobster. In order to establish population wide effects and sustainable management not only of lobster but other species as well, single small area PPAs alone are insufficient, and additional management and protection measures must also be implemented. We propose that any NTZ must consider and find balance between the size of the protected area, life-history traits of the target species, and the level of depletion surrounding the area. Within the analyzed areas in this study we conclude that there is a mismatch between these three factors. Several historically important commercial fish stocks in Sweden and the wider Skagerrak region are decreasing and it is therefore of critical importance that management measures are implemented which successfully rebuild stocks and protect biodiversity (e.g. Baden et al., 2012; Cardinale et al., 2023; Cardinale and Svedäng, 2004; Jonsson et al., 2016; Svedäng and Bardon, 2003). With the European Commission's goal of increasing the number of MPAs to a 30% protection target in the EU studies such as this one are necessary for highlighting the significance of creating MPAs large enough, and within a protection network encompassing migration and larval dispersal in order to ensure successful protection of marine biodiversity.

CRediT authorship contribution statement

Diana Perry: Writing – review & editing, Writing – original draft, Visualization, Formal analysis. **Andreas Wikström:** Writing – review & editing, Writing – original draft, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization. **Håkan Wennhage:** Writing – review & editing, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Mattias Sköld:** Writing – review & editing, Visualization, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Andreas Sundelöf:** Writing – review & editing, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Ethics

The capture and release of all species was carried out under the permission of the Swedish Board of Agriculture Dnr 5.8.18–07717/2017.

Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors recognize the invaluable contribution of Mats Ulmestrand in the design and collection of the early period data from 1989 to 2007. The authors would also like to thank Peter Jakobsson for more than 30 years of skilled work, as well as Baldvin Thorvaldsson and Maria Ovegård for valuable assistance in the field. Thank you to Martin Gullström for his willingness to discuss statistical methodology. The authors are very grateful for the valuable feedback provided by reviewers which significantly improved the manuscript. The work was financed by the Swedish Agency for Marine and Water Management (SwAM) (contract 2378–20) and the European Maritime and Fisheries Fund (contracts 2020–1492 and 2020–1493 to SwAM).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ocecoaman.2024.107535.

Data availability

Data will be made available on request.

References

Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA + for PRIMER: Guide to Software and Statistical Methods.

Andersson, E., Högvall, J., Larsson, R., 2021a. Kusttrålundersökningen 2021: Expeditionsrapport. Lysekil.

Andersson, E., Wikström, A., Wennhage, H., 2021b. Svenskt Fiske Efter Läppfisk För Export Som Putsarfisk. Lysekil.

Baden, S., Emanuelsson, A., Pihl, L., Svensson, C., Åberg, P., 2012. Shift in seagrass food web structure over decades is linked to overfishing. Mar. Ecol. Prog. Ser. 451, 61–73. https://doi.org/10.3354/meps09585.

Baskett, M.L., Barnett, L.A.K., 2015. The ecological and evolutionary Consequences of marine reserves. Annu. Rev. Ecol. Evol. Syst. 46, 49–73. https://doi.org/10.1146/annurev-ecolsys-112414-054424.

Bergström, U., Ask, L., Degerman, E., Svenson, A., Ulmestrand, M., 2007. Efekter av fredningsområden på fisk och kräftdjur i svenska vatten. Fisk. Inf. 2, 1–36.

Bergström, U., Berkström, C., Sköld, M., Börjesson, P., Eggertsen, M., Fetterplace, L., Florin, A.-B., Fredriksson, R., Fredriksson, S., Kraufvelin, P., Lundström, K., Nilsson, J., Ovegård, M., Perry, D., Sacre, E., Sundelöf, A., Wikström, A., Wennhage, H., 2022. Long-term effects of no-take zones in Swedish waters. https://doi.org/10.54612/a.10da2mgf51.

Bergström, U., Sköld, M., Wennhage, H., Wikström, A., 2016. Aqua Reports 2016 : 20 Ekologiska Effekter Av Fiskefria Områden I Sveriges Kust- Och Havsområden. Swedish University of Agricultural Sciences.

Berkström, C., Wennerström, L., Bergström, U., 2021. Ecological connectivity of the marine protected area network in the Baltic Sea, Kattegat and Skagerrak: current knowledge and management needs. Ambio. https://doi.org/10.1007/s13280-021-01684-x.

Bostedt, G., Berkström, C., Brännlund, R., Carlén, O., Florin, A.B., Persson, L., Bergström, U., 2020. Benefits and costs of two temporary no-take zones. Mar. Policy 117, 103883. https://doi.org/10.1016/j.marpol.2020.103883.

Bourlat, S.J., Faust, E., Wennhage, H., Wikström, A., Rigby, K., Vigo, M., Kraly, P., Selander, E., André, C., 2021. Wrasse fishery on the Swedish West Coast: towards ecosystem-based management. ICES J. Mar. Sci. 1–12. https://doi.org/10.1093/icesjms/fsaa249, 2010.

Cardinale, M., Svedäng, H., 2004. Modelling recruitment and abundance of Atlantic cod, Gadus morhua, in the eastern Skagerrak-Kattegat (North Sea): evidence of severe depletion due to a prolonged period of high fishing pressure. Fish. Res. 69, 263–282. https://doi.org/10.1016/j.fishres.2004.04.001.

Cardinale, M., Zimmermann, F., Søvik, G., Griffiths, C.A., Bergenius Nord, M., Winker, H., 2023. Spatially explicit stock assessment uncovers sequential depletion of northern shrimp stock components in the North Sea. ICES J. Mar. Sci. 80, 1868–1880. https://doi.org/10.1093/icesjms/fsad111.

Claudet, J., Osenberg, C.W., Benedetti-Cecchi, L., Domenici, P., García-Charton, J.A., Pérez-Ruzafa, Á., Badalamenti, F., Bayle-Sempere, J., Brito, A., Bulleri, F., Culioli, J. M., Dimech, M., Falcón, J.M., Guala, I., Milazzo, M., Sánchez-Meca, J., Somerfield, P. J., Stobart, B., Vandeperre, F., Valle, C., Planes, S., 2008. Marine reserves: size and age do matter. Ecol. Lett. 11, 481–489. https://doi.org/10.1111/j.1461-0248.2008.01166.x.

Claudet, J., Osenberg, C.W., Domenici, P., Badalamenti, F., Milazzo, M., Falcón, J.M., Bertocci, I., Benedetti-Cecchi, L., García-Charton, J.A., Goni, R., Borg, J.A., Forcada, A., De Lucia, G.D., Pérez-Ruzafa, Á., Afonso, P., Brito, A., Guala, I., Diréach, L. Le, Sanchez-Jerez, P., Somerfield, P.J., Planes, S., 2010. Marine reserves: fish life history and ecological traits matter. Ecol. Appl. 20, 830–839. https://doi.org/10.1890/08-2131.1.

Denny, C.M., Willis, T.J., Babcock, R.C., 2004. Rapid recolonisation of snapper Pagrus auratus: sparidae within an offshore island marine reserve after implementation of no-take status. Mar. Ecol. Prog. Ser. 272, 183–190. https://doi.org/10.3354/meps272183.

Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T.F., Berkhout, J., Buxton, C.D., Campbell, S. J., Cooper, A.T., Davey, M., Edgar, S.C., Försterra, G., Galván, D.E., Irigoyen, A.J., Kushner, D.J., Moura, R., Parnell, P.E., Shears, N.T., Soler, G., Strain, E.M., Thomson, R.J., 2014. Protected areas with five key features. Nature 506, 2016–2020. https://doi.org/10.1038/nature13022.

Ellis, C.D., Hodgson, D.J., Daniels, C.L., Collins, M., Griffiths, A.G.F., 2017. Population genetic structure in European lobsters: implications for connectivity, diversity and hatchery stocking. Mar. Ecol. Prog. Ser. 563, 123–137. https://doi.org/10.3354/meps11957.

Fenberg, P.B., Caselle, J.E., Claudet, J., Clemence, M., Gaines, S.D., Antonio García-Charton, J., Gonçalves, E.J., Grorud-Colvert, K., Guidetti, P., Jenkins, S.R., Jones, P. J.S., Lester, S.E., McAllen, R., Moland, E., Planes, S., Sørensen, T.K., 2012. The science of European marine reserves: status, efficacy, and future needs. Mar. Policy 36, 1012–1021. https://doi.org/10.1016/j.marpol.2012.02.021.

Fernández-Chacón, A., Villegas-Ríos, D., Moland, E., Baskett, M.L., Olsen, E.M., Carlson, S.M., 2020. Protected areas buffer against harvest selection and rebuild phenotypic complexity. Ecol. Appl. 30, e02108. https://doi.org/10.1002/eap.2108.

Fovargue, R., Bode, M., Armsworth, P.R., 2018. Size and spacing rules can balance conservation and fishery management objectives for marine protected areas. J. Appl. Ecol. 55, 1050–1059. https://doi.org/10.1111/1365-2664.13043.

Gaines, S.D., White, C., Carr, M.H., Palumbi, S.R., 2010. Designing marine reserve networks for both conservation and fisheries management. Proc. Natl. Acad. Sci. U. S. A. 107, 18286–18293. https://doi.org/10.1073/pnas.0906473107.

Green, A., White, A., Kilarski, S., 2013. Designing marine protected area networks to achieve fisheries, biodiversity, and climate change objectives in tropical ecosystems: a practitioner guide. Nat. Conserv. USAID Coral Triangle Support Partnersh. viii+ 35.

Grorud-Colvert, K., Sullivan-Stack, J., Roberts, C., Constant, V., Horta E Costa, B., Pike, E. P., Kingston, N., Laffoley, D., Sala, E., Claudet, J., Friedlander, A.M., Gill, D.A., Lester, S.E., Day, J.C., Gonçalves, E.J., Ahmadia, G.N., Rand, M., Villagomez, A., Ban, N.C., Gurney, G.G., Spalding, A.K., Bennett, N.J., Briggs, J., Morgan, L.E., Moffitt, R., Deguignet, M., Pikitch, E.K., Darling, E.S., Jessen, S., Hameed, S.O., Di Carlo, G., Guidetti, P., Harris, J.M., Torre, J., Kizilkaya, Z., Agardy, T., Cury, P., Shah, N.J., Sack, K., Cao, L., Fernandez, M., Lubchenco, J., 2021. The MPA guide: a framework to achieve global goals for the ocean. Science 373, 1215. https://doi.org/10.1126/science.abf0861.

Halvorsen, K.T., Larsen, T., Browman, H.I., Durif, C., Aasen, N., Vøllestad, L.A., Cresci, A., Sørdalen, T.K., Bjelland, R.M., Skiftesvik, A.B., 2021. Movement patterns of temperate wrasses (Labridae) within a small marine protected area. J. Fish. Biol. 99, 1513–1518. https://doi.org/10.1111/jfb.14825.

Halvorsen, K.T., Larsen, T., Sørdalen, T.K., Vøllestad, L.A., Knutsen, H., Olsen, E.M., 2017. Impact of harvesting cleaner fish for salmonid aquaculture assessed from replicated coastal marine protected areas. Mar. Biol. Res. 13, 359–369. https://doi.org/10.1080/17451000.2016.1262042.

Huserbråten, M.B.O., Moland, E., Knutsen, H., Olsen, E.M., André, C., Stenseth, N.C., 2013. Conservation, spillover and gene flow within a network of northern European marine protected areas. PLoS One 8, 1–10. https://doi.org/10.1371/journal.pone.0073388.

Jonsson, P.R., Corell, H., André, C., Svedäng, H., Moksnes, P.O., 2016. Recent decline in cod stocks in the North Sea-Skagerrak-Kattegat shifts the sources of larval supply. Fish. Oceanogr. 25, 210–228. https://doi.org/10.1111/fog.12146.

Knutsen, J.A., Kleiven, A.R., Olsen, E.M., Knutsen, H., Espeland, S.H., Sørdalen, T.K., Thorbjørnsen, S.H., Hutchings, J.A., Fernández-Chacón, A., Huserbråten, M., Villegas-Ríos, D., Halvorsen, K.T., Nillos Kleiven, P.J., Langeland, T.K., Moland, E., 2022. Lobster reserves as a management tool in coastal waters: two decades of experience in Norway. Mar. Policy 136. https://doi.org/10.1016/j.marpol.2021.104908.

Kraufvelin, P., Bergström, L., Sundqvist, F., Ulmestrand, M., Wennhage, H., Wikström, A., Bergström, U., 2023. Rapid re-establishment of top-down control at a no-take artificial reef. Ambio 52, 556–570. https://doi.org/10.1007/s13280-022-01799-9.

Langlois, T.J., Wakefield, C.B., Harvey, E.S., Boddington, D.K., Newman, S.J., 2021. Does the benthic biota or fish assemblage within a large targeted fisheries closure differ to surrounding areas after 12 years of protection in tropical northwestern Australia? Mar. Environ. Res. 170, 105403. https://doi.org/10.1016/j.marenvres.2021.105403.

Lubchenco, J., Palumbi, S.R., Gaines, S.D., Andelman, S., 2003. Plugging a hole in the ocean: the emerging science of marine reserves. Ecol. Appl. 13, 3–7. https://doi.org/10.1890/1051-0761(2003)013[0003:pahito]2.0.co;2.

Micheli, F., Halpern, B.S., Botsford, L.W., Warner, R.R., 2004. Trajectories and correlates of community change in no-take marine reserves. Ecol. Appl. 14, 1709–1723. https://doi.org/10.1890/03-5260.

Moland, E., Fernández-Chacón, A., Sørdalen, T.K., Villegas-Ríos, D., Thorbjørnsen, S.H., Halvorsen, K.T., Huserbråten, M., Olsen, E.M., Nillos Kleiven, P.J., Kleiven, A.R., Knutsen, H., Espeland, S.H., Freitas, C., Knutsen, J.A., 2021. Restoration of abundance and dynamics of coastal fish and lobster within northern marine protected areas across two decades. Front. Mar. Sci. 8, 1–12. https://doi.org/10.3389/fmars.2021.674756.

Moland, E., Olsen, E.M., Knutsen, H., Garrigou, P., Espeland, S.H., Kleiven, A.R., André, C., Knutsen, J.A., 2013a. Lobster and cod benefit from small-scale northern marine protected areas: inference from an empirical before-after control-impact study. Proc. R. Soc. B Biol. Sci. 280, 1–9. https://doi.org/10.1098/rspb.2012.2679.

Moland, E., Ulmestrand, M., Olsen, E.M., Stenseth, N.C., 2013b. Long-term decrease in sex-specific natural mortality of European lobster within a marine protected area. Mar. Ecol. Prog. Ser. 491, 153–164. https://doi.org/10.3354/meps10459.

Molloy, P.P., McLean, I.B., Côté, I.M., 2009. Effects of marine reserve age on fish populations: a global meta-analysis. J. Appl. Ecol. 46, 743–751. https://doi.org/10.1111/j.1365-2664.2009.01662.x.

Øresland, V., Oxby, G., Oxby, F., 2018. A comparison of catches of the European lobster (Homarus gammarus) in a lobster reserve using traditional pots and scuba diving technique. Crustaceana 91, 1425–1432. https://doi.org/10.1163/15685403-00003848.

Øresland, V., Ulmestrand, M., 2013. European lobster subpopulations from limited adult movements and larval retention. ICES J. Mar. Sci. 70, 532–539. https://doi.org/10.1093/icesjms/fst019.

Sköld, M., Börjesson, P., Wennhage, H., Hjelm, J., Lövgren, J., Ringdahl, K., 2022. A no-take zone and partially protected areas are not enough to save the Kattegat cod, but enhance biomass and abundance of the local fish assemblage. ICES J. Mar. Sci. 79, 2231–2246. https://doi.org/10.1093/icesjms/fsac152.

Sørdalen, T.K., Halvorsen, K.T., Harrison, H.B., Ellis, C.D., Vøllestad, L.A., Knutsen, H., Moland, E., Olsen, E.M., 2018. Harvesting changes mating behaviour in European lobster. Evol. Appl. 11, 963–977. https://doi.org/10.1111/eva.12611.

Sørdalen, T.K., Halvorsen, K.T., Olsen, E.M., 2022. Protection from fishing improves body growth of an exploited species. Proc. R. Scociety B 289, 1–10. https://doi.org/10.1098/rspb.2022.1718.

Sundelöf, A., Bartolino, V., Ulmestrand, M., Cardinale, M., 2013. Multi-annual fluctuations in reconstructed historical time-series of a European lobster (Homarus gammarus) population disappear at increased exploitation levels. PLoS One 8. https://doi.org/10.1371/journal.pone.0058160.

Sundelöf, A., Grimm, V., Ulmestrand, M., Fiksen, Ø., 2015. Modelling harvesting strategies for the lobster fishery in northern Europe: the importance of protecting egg-bearing females. Popul. Ecol. 57, 237–251. https://doi.org/10.1007/s10144-014-0460-3.

Svedäng, H., Bardon, G., 2003. Spatial and temporal aspects of the decline in cod (Gadus morhua L.) abundance in the Kattegat and eastern Skagerrak. ICES J. Mar. Sci. 60, 32–37. https://doi.org/10.1006/jmsc.2002.1330.

Synnes, A.W., Olsen, E.M., Jorde, P.E., Knutsen, H., Moland, E., 2023. Contrasting management regimes indicative of mesopredator release in temperate coastal fish assemblages. Ecol. Evol. 1–14. https://doi.org/10.1002/ece3.10745.

Thorbjørnsen, S.H., Moland, E., Olsen Huserbråten, M.B., Knutsen, J.A., Knutsen, H., Olsen, E.M., 2018. Replicated marine protected areas (MPAs) support movement of larger, but not more, European lobsters to neighbouring fished areas. Mar. Ecol. Prog. Ser. 595, 123–133. https://doi.org/10.3354/meps12546.

Turnbull, J.W., Esmaeili, Y.S., Clark, G.F., Figueira, W.F., Johnston, E.L., Ferrari, R., 2018. Key drivers of effectiveness in small marine protected areas. Biodivers. Conserv. 27, 2217–2242. https://doi.org/10.1007/s10531-018-1532-z.

Ulmestrand, M., 2003. Reproduction of female lobsters (Homarus gammarus) on the Swedish west coast. In: Comeau, M. (Ed.), Workshop on Lobster (Homarus Americanus and H. Gammarus) Reference Points for Fishery Managment. Can. Tech. Rep. Fish. Aquat. Sci. Tracadie-Sheila, New Brunswick, p. 2506 vii + 39pp.

White, J.W., Botsford, L.W., Hastings, A., Baskett, M.L., Kaplan, D.M., Barnett, L.A.K., 2013. Transient responses of fished populations to marine reserve establishment. Conserv. Lett. 6, 180–191. https://doi.org/10.1111/j.1755-263X.2012.00295.x.

Wood, L.J., Fish, L., Laughren, J., Pauly, D., 2008. Assessing progress towards global marine protection targets: shortfalls in information and action. Oryx 42, 340–351. https://doi.org/10.1017/S003060530800046X.