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Original Article

Fish community dynamics in a coastal no-take marine protected area compared to a harvested area before and after protection from fishing

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An ecosystem's ability to maintain key functions during environmental change is largely determined by its biodiversity. We compared fish species composition, richness, diversity, catch per unit effort (CPUE), and fish size between a 1.5 km^2 no-take marine protected area (MPA) and a nearby fished area on the southern Norwegian coast annually for one decade (2011–2021), including before-protection status. In total, >26 thousand fish representing 31 species were sampled using a beach seine. No significant effect of protection was detected on either species richness, diversity, or evenness. For selected species of small-bodied intermediate predators, there was a significant decline in mean body size in the MPA area compared to the fished area, indicative of a response to protection involving trophic interactions. No significant effect of the MPA was detected on either CPUE or body size of Atlantic cod (*Gadus morhua*), a top predator mainly captured at the juvenile stage by our sampling. The limited responses seen in this study may be linked to the small size of the MPA compared to the dispersal and movement capabilities of species such as the cod.

Keywords: atlantic cod, baci, beach seine, biodiversity, conservation, mpa, trophic interactions.

Introduction

Aquatic ecosystems dominated by humans are experiencing an increased loss of biodiversity with expected negative consequences for ecosystem functions, services, and resilience in the face of future environmental change (Worm *et al*., 2006; Magurran *et al*., 2015). In particular, fisheries may strongly impact fish dynamics and have been been associated with the collapse of some fish populations (Myers *et al*., 1996; Cook *et al*., 1997). Fisheries are typically selective and usually target large individuals, as well as specific species, during certain times of the year (Zhou *et al*., 2010). Such fishing pressures may act on fish growth and behavioural traits, and result in changes to fish life histories and productivity, as well as depletion of fish abundance (Rowe and Hutchings, 2003; Olsen *et al*., 2005; Uusi-Heikkilä *et al*., 2008). Also, selective fisheries can set the stage for trophic cascades and indirect changes to biodiversity involving, for instance, relaxed pressure from harvested top predators on smaller intermediate predators (Östman *et al*., 2016). That said, all ecosystems change and with or without human impact there will be turnover in both the presence and abundance of species. When protecting biodiversity, this baseline turnover should be considered (Magurran, 2016).

An increasing number of marine protected areas (MPAs) have been established for the purpose of restoring depleted populations, protecting habitats, maintaining and restoring ecosystems, and promoting integrated coastal management (Grorud-Colvert *et al*., 2021). A no-take MPA refers to a specific geographic area in the ocean where no harvesting is allowed. Such no-take areas have been shown to positively affect abundance and biomass of harvested fish populations (Lester *et al*., 2009). Also, there is growing evidence for the potential of MPAs to mitigate fisheries-induced selection (Baskett and Barnett, 2015; Sørdalen *et al*., 2022). Protection from fishing is expected to restore the natural size structures of harvested fish as more individuals survive to reach larger sizes (Fernández-Chacón *et al*., 2020). Over time, this can lead to increased reproductive output since larger individuals tend to be more fecund and also produce offspring of higher quality (Barneche *et al*., 2018). On the other hand, body size at age may decline in MPAs if growth is increasingly density-dependent, when populations recover towards their carrying capacity (Taylor and McIlwain, 2010). Last, individuals and species with restricted home ranges may benefit more from protection by spending a higher proportion of their time within MPA borders (Villegas-Ríos *et al*., 2021). Consequently, the responses to MPAs can be shaped by which species were harvested before the establishment, which species have characteristics that promote greater responses to protection, trophic cascades, as well as MPA compliance by stakeholders.

In this study, we assessed the impact of protection from fishing on a coastal fish community in a region known for intense and size-selective fishing of top predators such as the Atlantic cod (*Gadus morhua*) (Fernández-Chacón *et al*., 2017). Coastal zones include some of the world's most productive ecosystems and support a wide range of organisms with foraging opportunities, nursery grounds, and shelter from predation, but are also among the most depleted marine systems due to overfishing and other human influences (Jackson *et*

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al., 2001). Some species live permanently in coastal habitats, while others may be present as juveniles or migrate seasonally or diurnally among different habitats (Pihl and Wennhage, 2002). This will result in a dynamic species composition related to season, time of day and habitat type (Freitas *et al.*, 2021).

Intensive harvesting and the collapse of top predators such as the Atlantic cod populations in northern European coastal systems has been linked to a potential weakening of top-down control and ongoing trophic cascades influencing the state of seagrass and seaweed habitats (Baden *et al.*, 2010; Norderhaug *et al.*, 2021). In some systems, small-bodied coastal predators such as wrasses, sticklebacks, and gobies represent an important intermediate trophic level connecting benthic grazers and zooplankton with larger piscivores fish, and a mesopredator release may follow the depletion of top predators (Östman *et al.*, 2016). Understanding such wider effects of human pressures requires detailed knowledge about coastal fish communities. To this end, MPAs represent potentially valuable field experiments on human impacts such as harvesting, in addition to their basic value for fisheries management and conservation.

We quantified and compared the composition of fish species and sizes inside a coastal no-take MPA to a nearby fished area across one decade, including before-protection samples. The MPA covers 1.5 km^2 and is a strict no-take area where all harvesting of marine resources is forbidden. It was established with the aim of restoring a local population of Atlantic cod, and is centred around a verified cod spawning site in the inner part of a small fjord in southern Norway (Ciannelli *et al.*, 2010; Knutsen *et al.*, 2010). Juvenile and mature cod are present in the MPA during all seasons, along with other potential top predators such as pollock (*Pollachius pollachius*) and anadromous brown trout (*Salmo trutta*), and the MPA will cover at least part of their typical home ranges (Freitas *et al.*, 2021; Thorbjørnsen *et al.*, 2021; Villegas-Ríos *et al.*, 2021). The MPA also holds important nearshore nursery- and feeding habitats including mudflats, seagrass, and seaweed (Knutsen *et al.*, 2010; Freitas *et al.*, 2021). Bottom trawling is not allowed in shallow inshore habitats, but demersal fishes such as the Atlantic cod are still targeted by both commercial- and recreational fishers, including the MPA study fjord before protection was established (Knutsen *et al.*, 2010). These fisheries are technically diverse and involve the use of fixed gears such as nets and traps, as well as hook and line (Fernández-Chacón *et al.*, 2017). Local populations of cod are in a depleted state and the intensity of fishing has not been sustainable (Fernández-Chacón *et al.*, 2017; Rogers *et al.*, 2017), while there are also signs of improved survival of cod inside coastal MPAs (Fernández-Chacón *et al.*, 2015; Villegas-Ríos *et al.*, 2022). Less is known about how inhore fisheries impact other species, although they will clearly capture a variety of gadids, flatfishes, smaller pelagic species and anadromous trout. Also, a commercial fishery for live wrasses such as the goldsinny (*Ctenolabrus rupestris*) has developed since the 1990s because of their role as cleaner-fish in the salmonid aquaculture industry (Halvorsen *et al.*, 2017).

Our working hypotheses were that: (1) fish species diversity has increased inside the no-take MPA relative to the fished area, (2) the abundance and body size of harvested fish species have increased inside the no-take MPA relative to the fished area (i.e. a direct effect of protection), and (3) species representing mid-trophic levels may have decreased in abundance and body size as a result of trophic interactions with top predators (i.e. an indirect effect of protection).

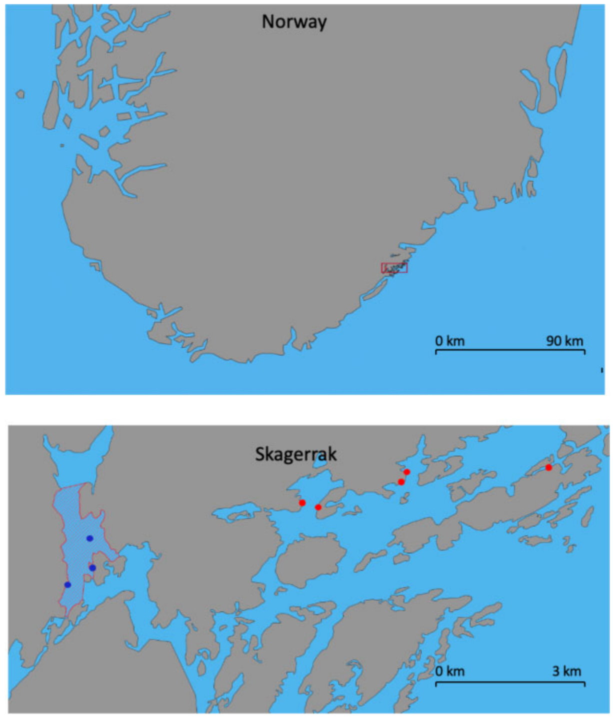

Figure 1. Study area (red rectangle, upper panel) showing the location of the no-take MPA (red lined area, lower panel), beach seine sampling stations in the MPA (blue dots, lower panel), and in the control area (red dots, lower panel).

Material and methods

Study system

This study was conducted in the coastal Skagerrak in southern Norway, a dynamic system with variable influence from freshwater runoff and more saline Atlantic waters, where surface temperatures may drop below 0°C in winter and rise above 20°C in summer (Albretsen *et al.*, 2012). In addition to the impact of fisheries described above, long-term changes in the fish community in coastal Skagerrak also correlates with climate change. Specifically, there has been a shift towards smaller pelagic species while the abundance and growth of demersal fish, notably the Atlantic cod, have declined (Rogers *et al.*, 2011; Barceló *et al.*, 2016). The no-take MPA included in this study was established in June 2012 in the inner part of the Tvedestrand fjord (Figure 1). Enforcement of the no-take regulation is conducted by local police and the coast guard.

Sampling of fish community

The fish community was sampled with a beach seine and followed a standardised approach maintained during a century-long monitoring program (Lekve *et al.*, 1999). For this study, we used data from all beach seine monitoring stations located within the Tvedestrand municipality. This includes five control stations located outside the MPA and three impact stations located inside the MPA (Figure 1, Supplementary Table S1). The stations inside the MPA were established in 2011, one year before the MPA was implemented. Thus, our study is based partly on historically defined sampling stations (the control sites) and partly on more recently defined sampling stations (the MPA sites). Although longer time series are available from the control stations outside the MPA, we restricted our analyses to data collected during 2011–2021 for a direct comparison with the MPA stations. This study design corresponds to a before-after control-impact (BACI) contrast, a widely recommended approach for assessing biodiversity responses to environmental impacts, including MPAs (Moland *et al*., 2021). All stations were sampled with one beach seine haul in September each year.

The beach seine is 38 m long, 3.8 m deep, and has a 20 m long rope in each end. The mesh size can be stretched to 15 mm and one haul covers up to about 700 m^2. The seine is deployed from a boat and rowed in a semicircle from the shore, sampling depths down to about 10 m. It captures mainly the juvenile stages of larger species, such as cod, as well as older life stages of smaller species, such as gobies and wrasses (Barceló *et al*., 2016). For each haul, the catch is identified, measured, and thereafter released at the capture location. Individuals are identified to species and measured for length, rounded down to the nearest cm. For cod, the first 100 fish are measured while the rest are counted. For other species the first 50 individuals are measured. Sprat (*Sprattus sprattus*) and juvenile herring (*Clupea harengus*) are sometimes captured in larger schools and in such cases individuals in a sub-sample of one litre are counted and measured, from which the total catch is estimated. A few very small species, notably the two-spotted goby (*Gobiusculus flavescens*) and transparent goby (*Aphia minuta*), will often escape through the meshes and are therefore not counted and measured.

Components of biodiversity

Biodiversity is a comparative measure and refers to the diversity of organisms in a community. It includes all aspects of the diversity of life and can be approached from multiple angles. Therefore, quantifying biodiversity remains a challenge even after deciding on the type of diversity to measure, because there is no one index to summarize the concept (Morris *et al*., 2014). Species richness, defined as the number of species in a community, is one of the main indices used to describe biodiversity, and a fundamental component of many ecological models and conservation strategies (Gotelli and Colwell, 2001). Because species richness can positively impact many ecosystem functions, it is regarded as a crucial indicator in quantitative assessments of community status (Balvanera *et al*., 2006). Species evenness can be defined as the probability that two individuals selected at random belong to the same species and can also be used to describe the distribution of individuals among different taxa (Morris *et al*., 2014). We quantified species evenness index (E) using the following equation (Pielou, 1969):

$$E = \frac{H'}{H'\,max}, \tag{1}$$

where H' is the Shannon–Wiener diversity index and H'_{max} is the maximal value of the index (log number of species present in a given beach seine haul). The evenness index ranges between 0 and 1. If the result is 0, it indicates that all biomass is accounted for by one species (low diversity). As the number approaches 1, it indicates that all species are equally abundant. The Shannon–Wiener diversity index (H') is a measure of diversity given by the equation (Shannon, 1948):

$$H' = -\sum_{i=1}^{n} p_i \, ln p_i, \tag{2}$$

where n is the total number of species and p_i is the fraction of each species i. Consequently, if the index is low, it indicates a few species dominate. The Shannon–Wiener diversity index assumes all species in a specific community are represented and randomly sampled. Lastly, species composition refers to the quantity of each species in a sample (Birks *et al*., 2012). In our study, the aforementioned components of biodiversity were calculated for each beach seine haul.

Four species were selected for more detailed analyses: Atlantic cod, goldsinny wrasse, black goby (*Gobius niger*), and three-spined stickleback (*Gasterosteus aculeatus*). These species were chosen because they represent contrasting trophic levels and histories of harvesting (Salvanes and Nordeide, 1993; Vesey and Langford, 2006; Gagnon *et al*., 2019), and also because they were captured in sufficient quantities in the beach seine. In Skagerrak, cod and goldsinny wrasse are harvested, while black goby and three-spined stickleback are not (Fernández-Chacón *et al*., 2017; Halvorsen *et al*., 2017). Therefore, their responses to protection are expected to differ. For each of these selected species, abundance was estimated as catch per unit effort (CPUE), that is, the number of individuals caught per beach seine haul.

Statistical analyses

Data on fish species abundance, length composition, and community composition were analysed using the R software (R Core Team, 2021). The diversity measures and species composition analysis were calculated using the vegan package (Oksanen *et al*., 2020). We used the ADONIS approach (Birks *et al*., 2012) to compare the species composition of the control and MPA areas over time. The number of permutations used was 999. Also, the similarity percentage test SIMPER was used to identify which taxa accounted for the differences between the groups detected by ADONIS (Clarke, 1993). The species were arranged in decreasing order of their importance in determining dissimilarity between the areas in the different periods based on their overall percentage contribution to average dissimilarity.

Linear mixed effect models (Zuur *et al*., 2009) were fitted to analyse the effect of protection within the MPA on species diversity, as well as CPUE and mean length of selected species representing different ecosystem components (as described above). The beach seine stations will differ in, for instance, habitat composition, and station was therefore fitted as a random effect. Fish length data was log-transformed for normalization (Zuur *et al*., 2010). The model response variables included species richness, Shannon–Wiener's diversity index, evenness, fish length (cm) and CPUE. For the analyses, it was necessary to combine the annual data into three periods: before protection (2011), early after-protection (2012–2015) and late (2016–2021). Preliminary analysis showed that the data was not strong enough to run full-resolution models on annual data, as none of the models converged. For each of the response variables, we compared a set of five *a priori* defined models. The most complex model included an interaction between area (MPA vs. control) and period (before vs. early after vs. late after). Following the approach previously used by Pardini *et al*. (2018) and Christensen-Dalsgaard *et al*. (2020) such a mixed model BACI interaction term was included to specif-

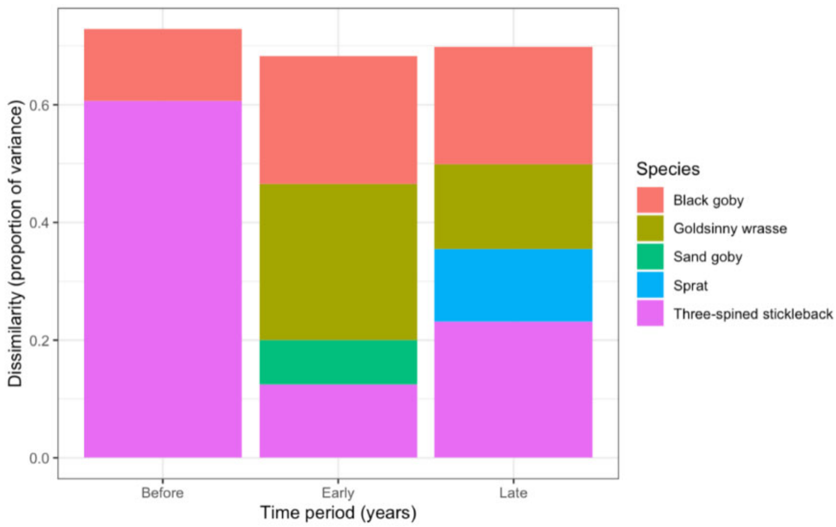

Figure 2. Species' contribution to dissimilarities in the sampled fish community, comparing the MPA and control area in the before-protection period (2011), early period after protection (2012–2015), and late period after protection (2016–2021).

ically evaluate an effect of protection on each of the diversity indices as well as on body size and CPUE of selected species. Simpler models included additive effects of either area, period, or both, compared to a null model. The Akaike Information Criterion (AIC) was used for model selection. AIC considers both model complexity (number of parameters included) and goodness of fit, and the model with the lowest AIC is, according to this method, the most parsimonious one (Zuur *et al.*, 2009). All models were fitted using maximum likelihood estimation with the lme function in R (Pinheiro *et al.*, 2012).

Results

In the period 2011–2021, a total of 9 159 individual fish were collected at the three stations inside the MPA, while 17 454 fish were collected at the five stations in the control area.

Species composition

The total catch was comprised of 31 different species of fish from 14 families (Supplementary Table S2). The species contributing the most to the catch in the MPA were: sprat (28.1%), three-spined stickleback (21.1%), goldsinny wrasse (20.1%), and black goby (10.5%). In the control area, sprat contributed the most (25.0%), followed by black goby (23.1%), three-spined stickleback (22.5%), and goldsinny wrasse (12.5%). The ADONIS analysis detected significant differences between the MPA and control areas in both the early ($p = 0.011$, $R^2 = 0.107$) and late period ($p = 0.004$, $R^2 = 0.052$) after MPA implementation, but not before impementation ($p = 0.477$, $R^2 = 0.147$). According to the SIMPER analysis, four species accounted for the first 70% of the variation between the two areas. In the early period, these species were goldsinny wrasse, black goby, three-spined stickleback, and sand goby, with goldsinny wrasse contributing most to the variance (Figure 2). In the MPA, goldsinny wrasse made up a higher proportion of the total catch (40.3%) than in the control area (19.8%). Black goby, stickleback, and sand goby accounted for the largest contribution to the community composition in the control area (19.8%, 29.8%, and 6.6%, respectively) compared to in the MPA (17.2%, 3.5%, and 0.05% respectively). In the late period, the species contributing most to the variance in catch composition between the protected and unprotected areas were three-spined stickleback, black goby, goldsinny wrasse, and sprat, with three-spined stickleback being the species contributing most to the variance (Figure 2). In the MPA, goldsinny and sprat made up a higher proportion of the total catch (14.6% and 43.0%, respectively) than in the control area (9.1% and 34.7%, respectively). Stickleback and black goby accounted for a higher proportion of the total catch in the control area (20.7% and 21.2%, respectively) than in the MPA (15.1% and 10.0%, respectively).

Species diversity, evenness, and richness

In the MPA, the mean value of Shannon–Wiener's index of species diversity was 1.28 (range: 0.02–1.94), compared to 1.39 in the control area (range: 0.24–2.02, Supplementary Figure S1). The mean species evenness in the MPA was 0.63 (range: 0.01–0.90), which was nearly equal to that in the control area, 0.62 (range: 0.1–0.97, Supplementary Figure S1). The mean species richness (number of species) in the MPA was 10.6 (range: 4–16), compared to 9.6 in the control area (range: 4–16, Supplementary Figure S1). Model selection did not support effects of area (that is, the protection level) on either Shannon–Wiener's diversity or evenness (Table 1). Model selection did support an effect of time period on species richness, while models containing an effect of area produced higher AIC-values and thus received lower support (Table 1). Parameter estimates based on the most parsimonious model, with an additive effect of period on species richness, indicate an increase in the number of species in the late period, compared to the before-period (Supplementary Table S3). Predicted species richness increased from 8.7 species in the before period to 9.7 species in the early period and 10.3 species in the late period in both areas.

CPUE and body length of selected species

A total of 4981 black goby, 741 cod, 4004 goldsinny wrasse, and 5846 three-spined stickleback were captured and measured for length between 2011 and 2021 (Supplementary Table S2, Supplementary Figure S2). Model selection did not sup-

Table 1. Model selection. Linear mixed effect modelling of Shannon–Wiener's diversity, evenness, and species richness (response variables). Explanatory variables include area (MPA and control) and period (before protection, early years after protection and late years after protection). Beach seine station is included as a random effect. The table also shows the number of estimated parameters for each model (Par), the AIC score, and the distance in AIC score from the model selected for statistical inference (in bold).

Response	Model structure	Par	AIC	ΔAIC
Shannon–Wiener	Period ∗ Area (1 | station)	6	82.44	8.09
	Period + Area (1 | station)	4	79.75	5.40
	Period (1 | station)	3	78.18	3.83
	Area (1 | station)	2	75.94	1.59
	1 (1 | station)	**1**	**74.35**	**0**
Evenness	Period ∗ Area (1 | station)	6	− 44.98	6.36
	Period + Area (1 | station)	4	− 47.02	4.32
	Period (1 | station)	3	− 48.98	2.36
	Area (1 | station)	2	− 49.36	1.98
	1 (1 | station)	**1**	**− 51.34**	**0**
Species richness	Period ∗ Area (1 | station)	6	401.54	0.84
	Period + Area (1 | station)	4	402.54	1.74
	Period (1 | station)	**3**	**400.80**	**0**
	Area (1 | station)	2	402.87	2.07
	1 (1 | station)	1	401.15	0.35

port the inclusion of a BACI interaction term between area (level of protection) and time period on CPUE for any of the four species (Table 2). For black goby, the most parsimonious model, supported by model selection (Table 2), predicted that CPUE was higher in the late period compared to the before period, and higher in the control area than in the MPA (Figure 3, Supplementary Table S4). For goldsinny wrasse, the most parsimonious model (Table 2, Supplementary Table S4) predicted that CPUE was higher in the early and late period, compared to the before period (Figure 3). For cod, the most parsimonious model predicted that CPUE was higher in the late period compared to the before period (Figure 3, Supplementary Table S4). For the three-spined stickleback, none of the fixed effects were retained in the most parsimonious model (Table 2).

The analyses of mean body length of selected species supported a BACI interaction term between area (level of protection) and time period for black goby, goldsinny wrasse, and three-spined stickleback (Table 3). Interaction plots of model predictions revealed that there was a greater tendency for a decline in mean body size towards the late period in the MPA compared to the control area for these three species (Figure 4, Supplementary Table S5, Supplementary Figures S3 and S4). For cod, model selection did not support a BACI interaction term, but an additive effect of area was retained in the most parsimonious model (Table 3). The mean predicted body length of cod was higher in the MPA compared to the control area for the duration of the study (Figure 4, Supplementary Table S5).

Discussion

This study assessed the impact of an inshore no-take MPA—where all fishing is forbidden—on the local fish community. Specifically, we compared the composition of demersal fish species and sizes inside the MPA to control sites where fishing is allowed, and also compared these data to data collected at the same locations prior to MPA establishment. With such BACI data spanning one decade, no effect of the MPA was detected on either species richness, species diversity, or species evenness. Significant differences in species composition were, however, detected between the areas following MPA establishment when using a multivariate approach. Further, univariate analyses of commonly observed species showed that there was a tendency for an increase in CPUE of some mesopredators towards the late period after protection, but this increase could not be linked to the MPA as it was also seen in the control area. In contrast, there was statistical support for a more pronounced decrease in mesopredator body length in the MPA compared to the control area (i.e., a BACI interaction effect), suggesting that trophic interactions linked to protection may be involved. In the following sections these findings are discussed.

First, we point out that the available sampling gear will inevitably leave footprints in the data. The beach seine used in this study is probably among the least selective fishing methods available for nearshore systems (Fromentin *et al.*, 1997). Even so, it will not sample all components of the fish community, and the sampling efficiency is likely to vary with abiotic conditions as well as life stages (Gjøsaeter, 2002; Freitas *et al.*, 2021). For example, larger cod typically do not exploit shallow nearshore habitats during daylight hours; instead they are often found in deeper water out of range from the seine (Freitas *et al.*, 2021).

The BACI analyses revealed no clear effects of protection from fishing on either species richness, species diversity, or species evenness. These findings do not support our hypothesis of increased diversity in protected areas, but they are consistent with the conclusions of Soykan and Lewison (2015), who reviewed 36 abundance and 14 biomass data sets on fish assemblages in order to compare MPAs with nearby control sites for differences in community structure. They found no consistent differences between MPAs and control sites with respect to species richness or Shannon–Wiener diversity, and suggested that these measures are not very useful for MPA assessments, and that community-based responses to protection may be difficult to predict and detect.

Our study detected significant differences in catch composition between the protected and unprotected areas after protection status was established in the MPA. Four species accounted for 70% of the variation in species composition between the protected and the unprotected area. In particular, goldsinny wrasse comprised a greater proportion of the total catch inside the protected area than in the unprotected

Table 2. Model selection. Linear mixed effect modelling of CPUE of black goby, cod, goldsinny wrasse and corkwing wrasse. Explanatory variables include area (MPA and Control) and period (Before protection, Early years after protection and Late years after protection). Beach seine station is included as a random effect. The table also shows the number of estimated parameters for each model (Par), the AIC score and the distance in AIC score from the model selected for statistical inference (in bold).

Response	Species	Model structure	Par	AIC	ΔAIC
CPUE	Black goby	Period ∗ Area (1 | station)	6	325.00	1.95
		Period + Area (1 | station)	**4**	**323.05**	**0**
		Period (1 | station)	3	324.14	1.09
		Area (1 | station)	2	329.27	6.22
		1 (1 | station)	1	328.88	5.83
	Cod	Period ∗ Area (1 | station)	6	232.13	5.57
		Period + Area (1 | station)	4	228.15	1.59
		Period (1 | station)	**3**	**226.56**	**0**
		Area (1 | station)	2	232.53	5.97
		1 (1 | station)	1	230.92	3.36
	Goldsinny wrasse	Period ∗ Area (1 | station)	6	280.59	2.72
		Period + Area (1 | station)	4	279.55	1.68
		Period (1 | station)	**3**	**277.87**	**0**
		Area (1 | station)	2	290.84	12.97
		1 (1 | station)	1	289.43	11.56
	Three-spined stickleback	Period ∗ Area (1 | station)	6	276.91	1.26
		Period + Area (1 | station)	4	279.61	3.96
		Period (1 | station)	3	277.68	2.03
		Area (1 | station)	2	277.27	1.62
		1 (1 | station)	**1**	**275.65**	**0**

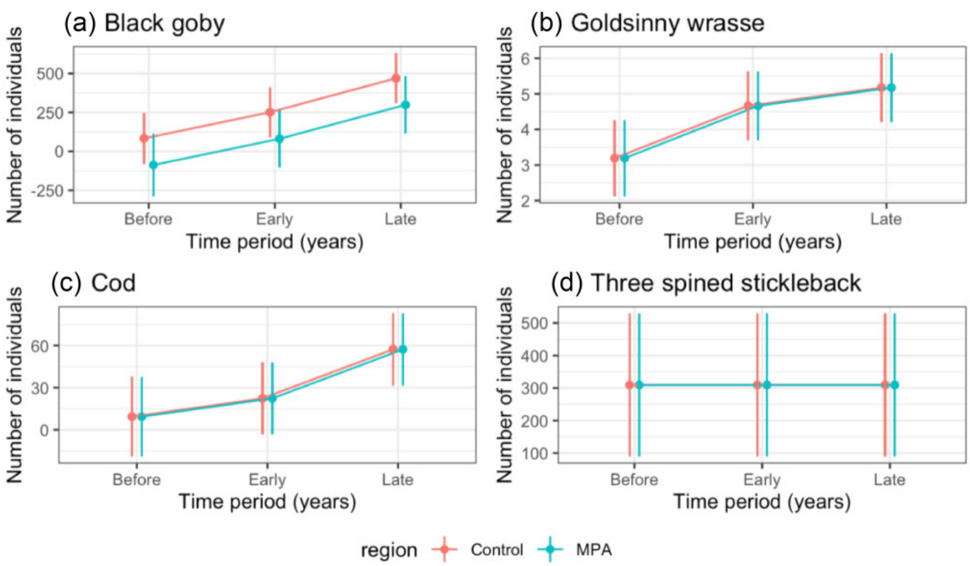

Figure 3. Predicted CPUE (mean ± 1 standard error) of (a) black goby, (b) goldsinny wrasse, (c) cod, and (d) three-spined stickleback in the MPA area (blue) and control area (red) before protection (2011), in the early period after protection (2012–2015), and late period (2016–2021).

area and accounted for a larger fraction of the difference after protection establishment. However, when considering the abundance (CPUE) of this species, we found no clear effect of protection. This outcome is contrary to that of Claudet *et al.* (2006) who found goldsinny wrasse, among other commercial species, increased in abundance after protection. Also, our finding is contrary to that of Halvorsen *et al.* (2017), which reported a 33%–36% increase in the CPUE of goldsinny wrasse within partially protected MPAs, where hook and line fishing is allowed.

We saw no significant effect of protection on either the abundance (CPUE) or body length of cod. Importantly, cod was mostly captured at the juvenile stage so our data therefore primarily reflects variation in recruitment. In a previous study, Moland *et al.* (2013) sampled older life stages of cod and detected an increase in body size within partially protected MPAs in Skagerrak. Cod along the Skagerrak coast have experienced very high fishing mortality associated with strong declines in population size and correlated changes in life-history traits (Olsen *et al.*, 2008; Olsen *et al.*, 2012; Fernández-Chacón *et al.*, 2017). Clearly, such depleted populations of Atlantic cod can take decades to recover even under a moratorium on fishing, where Allee-effects may negatively affect recruitment at low densities (Hutchings, 2015). In addition, the inshore systems in south Norway are affected by eutrophication (Johannessen *et al.*, 2012), and in some cases also industrial pollution, which can have a negative impact on cod recruitment (Ono *et al.*, 2019).

Table 3. Model selection. Linear mixed effect modelling of body length of black goby, cod, goldsinny wrasse, and three-spined stickleback (log-transformed response variables). Explanatory variables include area (MPA and control) and period (before protection, early years after protection, and late years after protection). Beach seine station is included as a random effect. The table also shows the number of estimated parameters for each model (Par), the AIC score and the distance in AIC score from the model selected for statistical inference (in bold).

Response	Species	Model structure	Par	AIC	ΔAIC
Length	Black goby	**Period ∗ Area (1 | station)**	**6**	**– 969.32**	**0**
		Period + Area (1 | station)	4	– 946.01	23.31
		Period (1 | station)	3	– 947.64	21.68
		Area (1 | station)	2	– 929.25	40.07
		1 (1 | station)	1	– 930.73	38.59
	Cod	Period ∗ Area (1 | station)	6	– 100.05	1.38
		Period + Area (1 | station)	4	– 99.76	1.67
		Period (1 | station)	3	– 88.71	12.72
		Area (1 | station)	**2**	**– 101.43**	**0**
		1 (1 | station)	1	– 89.73	11.70
	Goldsinny wrasse	**Period ∗ Area (1 | station)**	**6**	**– 608.11**	**0**
		Period + Area (1 | station)	4	– 601.10	7.01
		Period (1 | station)	3	– 597.21	10.90
		Area (1 | station)	2	– 496.64	111.47
		1 (1 | station)	1	– 490.30	117.81
	Three-spined stickleback	**Period ∗ Area (1 | station)**	**6**	**– 1076.06**	**0**
		Period + Area (1 | station)	4	– 1068.50	7.56
		Period (1 | station)	3	– 1070.02	6.04
		Area (1 | station)	2	– 996.71	79.35
		1 (1 | station)	1	– 997.55	78.51

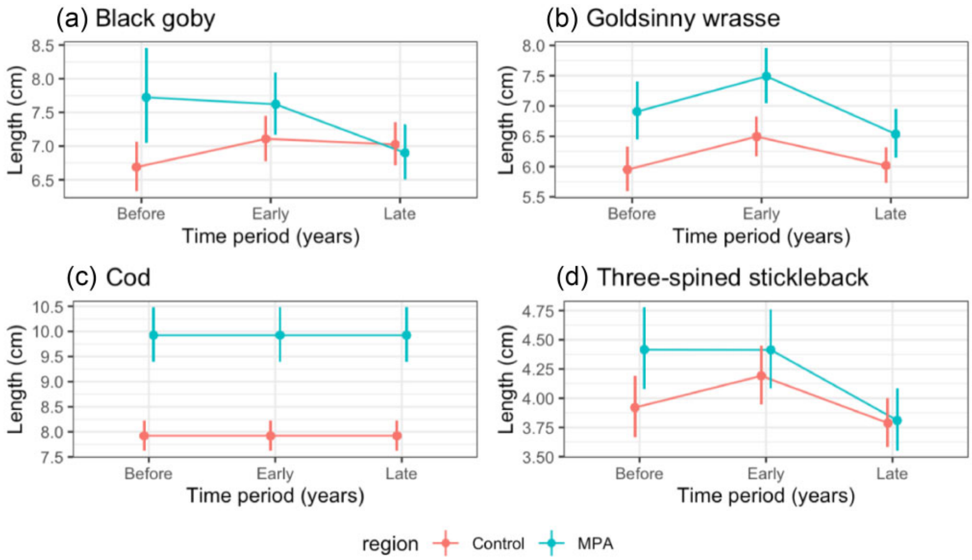

Figure 4. Interaction plots showing the mean predicted body length (±1 standard error) of (a) black goby, (b) goldsinny wrasse, (c) cod, and (d) three-spined stickleback in the MPA area (blue) and control area (red) before protection (2011), in the early period after protection (2012–2015), and late period (2016–2021).

This study did reveal an effect of protection on the body length of goldsinny wrasse, black goby, and three-spined stickleback, seen as a significant interaction effect between time period and area in the statistical models. Specifically, there was a greater tendency for a decline in mean body size of these species towards the late period in the MPA compared to the control area. Goldsinny wrasse is a harvested species, and as such, we expected to see an increase in body size inside the MPA. It may be that indirect effects linked to trophic interactions are countering or masking the more direct and expected effects from protection (Babcock *et al*., 2010). In general, trophic cascades involve a secondary response of prey to the initial response of predators, and therefore typically occur over longer time scales than direct responses of harvested species (Baskett and Barnett, 2015). Changes in biomass due to an increased or decreased body size can occur within a generation, whereas increases in abundance caused by higher reproductive output takes place over several generations (Molloy *et al*., 2009). Baskett *et al*. (2006) stated that cascading effects can occur due to the protection of previously harvested competitors and prey of non-target species, and the complex interactions between these species can change the response of the fish community to MPA establishment. Therefore, it may be challenging to develop generalized predictions about community-level responses to MPAs (Baskett and Barnett, 2015).

A recommended study design is to have replication on the contrast between MPAs and control areas to account for spatial heterogeneity and temporal variation independent of biological processes and disturbances other than harvest (Underwood, 1994). Our study therefore suffers from the limitation of a single no-take MPA. However, note that this is currently the only no-take MPA that exists in Norway. Linked to the increasing use of MPAs to conserve and manage fisheries and target species, there is an urgent need for more replicated BACI studies, where, in contrast, monitoring single MPAs will likely produce variable conclusions. For example, the magnitude and timing of lobster population responses to protection were highly variable among three pairs of partially protected areas and fished areas in Norway (Knutsen *et al.*, 2022).

How populations respond to protection will be tied to MPA-design and the level of connectivity between protected and harvested areas. In our study system, individual tracking of cod and sympatric higher-level predators has shown that their home ranges will often extend beyond the borders of the Tvedestrand no-take MPA and into areas open to regular fishing activities (Freitas *et al.*, 2021; Thorbjørnsen *et al.*, 2021; Villegas-Ríos *et al.*, 2021). Also, cod recruitment processes, including the dispersal of pelagic eggs and larvae, will typically happen at larger spatial scales even in inshore coastal habitats (Espeland *et al.*, 2015).

In conclusion, this study revealed that fish species composition, as well as the body size of mesopredators, changed inside a no-take MPA relative to an unprotected are following MPA implementation. This suggests that trophic interactions may be linked to the MPA. We were not able to detect any effects from protection on the abundance of Atlantic cod juveniles. Effective protection of larger and mobile species such as the cod likely require an upscaling of MPAs compared to our case study.

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Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Author contributions

B.K.V. analysed the data and wrote the manuscript. E.M.O. contributed to the data collection, assisted with the data analyses, and edited the text.

Conflict of interest

The authors have no conflicts of interest to declare.

Data availability

The beach seine raw data used in this article is available from the Institute of Marine Research via the Norwegian Marine Data Centre.

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