UNIVERSITETET I AGDER

Assessing fish community dynamics in a Norwegian no-take marine reserve compared to a harvested area

BJØRG KARIN VARNES

SUPERVISOR

Prof. Esben Moland Olsen

University of Agder, 2022
Faculty of Engineering and Science
Department of Natural Sciences

The sea, the great unifier, is man's only hope. Now, as never before, the old phrase has a literal meaning: we are all in the same boat.

Jacques-Yves Cousteau

Universitetet i Agder
Fakultet for teknologi og realfag
Institutt for naturvitenskaplige fag
Gimlemoen 25
4604 Kristiansand
http://www.uia.no

Abstract

An ecosystem's ability to respond and maintain key functions during environmental change are largely determined by its biodiversity. As human activities continue to alter the composition of biological communities at all scales there is a need for up-to-date status of biodiversity, including how marine fisheries may affect diversity in coastal systems. In this study, I assessed the effect of protection from fishing on a coastal fish community in the Tvedestrand fjord on the Norwegian Skagerrak coast. I compared fish species richness, diversity, composition, catch per unit effort (CPUE), and fish size (body length) between a marine protected area (MPA) and a nearby fished area (i.e., the control). Sampling was conducted by beach seine at eight fixed stations, three in the MPA area and five in the control area, every year from 2011-2021. The MPA was established in 2012 and our sampling therefore included data from before protection (i.e., a before-after-control-impact (BACI) design). In total, more than 26 thousand fish representing 31 species was collected and measured for length. No effect of protection was detected on either species richness, diversity or evenness. Significant differences in species composition were, however, detected between the two areas after protection. In particular, goldsinny wrasse (*Ctenolabrus rupestris*) accounted for this variation (2012-2015: 27 %, 2016-2021: 14 %). All species combined, CPUE was significantly higher after protection, but this increase was seen in both the control area and the protected area, and therefore cannot be linked to protection. Species combined, mean fish length inside the MPA was significantly higher than in the control area, but this difference was also seen in the data collected before protection. The samples of cod (*Gadus morhua*), as well as three-spined stickleback (*Gasterosteus aculeatur*), black goby (*Gobius niger*) and goldsinny wrasse were analysed in further detail. There was a tendency for an increase in CPUE of black goby, cod and goldsinny wrasse after protection, but this increase could not be linked to protection as it was also seen in the control area. Body length of cod was significantly higher in the MPA area compared to the control area, but the analyses did not detect any change in this relationship in response to protection. For goldsinny wrasse, black goby and three-spined stickleback there was a greater tendency for a decline in mean body size towards the late period in the MPA area compared to the control area. The latter points toward a response to full protection, potentially involving biological control mechanisms and trophic interactions. Taken together, however, the major findings in this study suggest that MPAs may not necessarily have clear and predictable effects on diversity in the short- to mid-term. Even longer-term monitoring involving more refined data collection and diversity measures could be necessary to reveal community-level consequences of protection.

Table of contents

Preface

Without the advice and patience of many individuals, this project would not have been possible. I would like to express my gratitude to all those who helped me, who endured me talking about this thesis, and made it possible for me to manage it alongside my professional work and family life.

First of all, I would like to thank Esben Moland Olsen, my supervisor at University of Agder and Institute of Marine Research, who guided me throughout the entire process and allowed me to begin my work early enough to complete it alongside my family and work commitments. You have provided me with valuable assistance with statistical analysis, modelling, and academic writing due to your extensive knowledge and experience.

To my coworkers at Strand Videregående skole, thank you for putting up with the extra workload in my absence, and to my leaders, for making it possible to combine with work. I know it has been a puzzle. Additionally, to my fellow students, thank you for being an important source of support both during good and frustrating times.

Thanks also to my family, for putting up with all my mood swings accompanying the "ups and downs" during this study. Thank you Pål, for taking an extra load when I had to focus on other things. Thank you to my mom, for your unconditional love and for always being there for us, helping in any way you can. Especially thanks to my favorite people; Sondre, Sivert and Erle, for all the time I've spent on this, which was truly yours. Please forgive me, and hopefully I'll be able to make it up to you.

Last but not least, thank you to my dad for teaching me to love the ocean. You are with me forever and always, and this is dedicated to you.

Forsand, 20.05.2022

Bjørg Karin Varnes

1 Introduction

1.1 Biodiversity and human impacts

The planet is subject to human impacts, altering the biodiversity of communities and ecosystems in unpredictable ways (Pimm et al., 1995; Magurran, 2016). The concept of biodiversity represents the variety and degree of heterogeneity of organisms across all levels of the nature hierarchy, from molecules to ecosystems (Morris et al., 2014). Traditionally, the focus has been on species diversity, however other forms of diversity, such as phenotypic and genetic variation, are also significant and useful (Morris et al., 2014). Over the course of evolution, biodiversity has increased as species have adapted to their environments and evolved from one another (Allen and Gillooly, 2006). Over the past century, however, the trend has shifted, and biodiversity is declining throughout the world's ecosystems (Pimm et al., 1995; Zedler et al., 2001; Worm et al., 2006).

Ecosystems dominated by humans are experiencing an accelerating loss of populations and species, with little knowledge of the consequences (Worm et al., 2006). As global biodiversity losses accelerate, it may reduce ecosystems resilience and ability to resist change and decrease ecosystem function and services (Hooper et al., 2005). Understanding how ecological assemblages respond to novel conditions is essential in conserving biodiversity in a rapidly changing world (Pandolfi and Lovelock, 2014). Notably, all ecosystems change; with or without human impact there will always be a turnover in both presences of species and abundance (Magurran et al., 2015). For instance, fish populations worldwide are dynamic and subject to constant fluctuations over spatial and temporal scales (Cushing, 1994). These fluctuations are complex and rely on direct and indirect biological, environmental and anthropogenic effects (Fromentin et al., 1997). In protecting biodiversity, this baseline turnover should be considered (Magurran, 2016).

1.2 Biodiversity in the coastal zone

The coastal zone includes some of the world's most productive ecosystems (Waycott et al., 2009), containing habitats supporting a wide range of marine organisms with access to food, nursery grounds, and shelter from predation (Botsford et al., 1997; Jackson et al., 2001; Beck et al., 2003; Sheaves et al., 2006; Rönnbäck et al., 2007; Bergström et al., 2016). Several biotic and abiotic factors determine the distribution of fish species in these areas (Lekve et al., 1999; Pecuchet et al., 2016) and as different fish species consume different resources, the trophic levels and quantity of organisms will differ (Elliott and Dewailly, 1995; Agostini and Bakun, 2002; Beck et al., 2003; Bakun, 2013). For instance, predators may serve as agents of biological control (Symondson et al., 2002). A decline in the abundance of a dominant predator in an ecosystem can cause trophic cascades (Casini et al., 2008; Heithaus et al., 2008; Baum and Worm, 2009). These changes may be accompanied by a decline in intra-species variation and a loss of biodiversity, followed by a reduction in resilience and durability of the affected system (Hutchings, 2000; Frank et al., 2005; Worm et al., 2006; Hutchings et al., 2012; Hutchings, 2015).

As marine species are ultimately dependent on suitable habitats, their quality and quantity may serve as limiting factors (Carr, 1989; Vytenis and Joseph, 1993; Gibson, 1994). Some species live permanently in coastal habitats, while others may be present as juveniles, migrate seasonally or pass by (Pihl and Wennhage, 2002). This may result in altered species composition related to season, time of day and whether or not the habitat contains vegetation (Pihl and Wennhage, 2002)

Grazers, such as gastropods (Gastropoda) and amphipods (Amphipoda), provide food for mesopredators like wrasses (Labridae), sticklebacks (Gasterostediae), and gobies (Gobiidae) (Östman et al., 2016). Therefore mid-trophic mesopredatory fish are an essential part of the coastal ecosystems (Bergström et al., 2016). Traditionally these species have not been commercially exploited, but a fishery for wrasse has increased since the 1990s because of their role as cleaner-fish in the salmonid aquaculture industry (Darwall et al., 1992; Deady and Fives, 1995; Cowx et al., 2003). Even though gobies are not interesting commercially, they serve as an intermediate trophic level for connecting smaller benthic species and zooplankton with piscivores fish and other predators (Salvanes and Nordeide, 1993; Schückel et al., 2013). Changes in the abundance of mesopredators can therefore have consequences for other species in the coastal ecosystems (Bergström et al., 2016). Larger piscivorous fishes, like gadoids (Gadidae), occupies the higher trophic role as top-predators (Frank et al., 2005; Östman et al., 2016). They are attracted to the abundance of small mesopredators and influence these prey-populations through top-down control (Frank et al., 2005; Östman et al., 2016). Following intensive harvesting and the collapse of cod (*Gadus morhua*) populations in northern European coastal systems (Fernández-Chacón et al., 2017; Rogers et al., 2017), abundant mesopredators like wrasses are probably involved in trophic cascades, and could influence the state of seagrass beds and species occupying these habitats, by preying on algae-grazing amphipods and isopods (Östman et al., 2016).

1.3 Biodiversity and selective fisheries

Human exploitation strongly impacts fish dynamics and has been the main reason for the collapse of many fish populations (Garrod and Schumacher, 1994; Hutchings, 1996; Myers et al., 1996; Cook et al., 1997; Fromentin et al., 1997). Since the 1950's, fishing has been the driver with the greatest impact on marine biodiversity (IPBES, 2019). In order to maximize profits, fisheries are selective and usually target large individuals, as well as specific species, during certain times of the year (Zhou et al., 2010; Beardmore et al., 2015). Such fishing pressures may act on growth and behavioral traits and result in evolutionary changes to fish life histories as well as depletion of fish abundance (Hutchings, 2000; Jackson, 2001; Hutchings, 2005; Olsen et al., 2005; Fenberg and Roy, 2008; Olsen et al., 2009; Olsen and Moland, 2011; Olsen et al., 2012; Fernández-Chacón et al., 2017; Halvorsen et al., 2017b; Hollins et al., 2018). Additionally, fisheries management often aims to protect smaller fish by introducing minimum size limits, allowing them to reach maturity. The result may be fisheries induced selection against fast growth and early maturation, ultimately leading to a dominance of smaller, younger individuals (Berkeley et al., 2004; Olsen et al., 2004b; Fenberg and Roy, 2008; Zhou et al., 2010; Olsen and Moland, 2011). Over generations this may lead to altered life history traits associated with lower productivity (Olsen et al., 2005; Hollins et al., 2018). For territorial species that display high site-fidelity, Shepherd et al. (2010) found that size structure can act as an indicator of fishing pressure. Furthermore, by assuming that reproductive output is proportional to size, management risks ignoring the contribution of larger mothers to replenishment may compromise sustainability (Barneche et al., 2018). Fecundity of larger and older females is higher than that of younger and smaller ones, and they will probably devote more energy to each offspring and enhance their performance (Berkeley et al., 2004). Larger mothers could also indicate better quality larvae and timing of the spawning season (Meager et al., 2018). Notably, body size is not the only trait that could influence fishing gear selection (Hollins et al., 2018). Selection on bold, mobile, fast growing genotypes may lead to depletion of catch rates, and alter physiological traits within populations, affecting resource requirements, resilience, distributions, and responses to environmental changes (Hollins et al., 2018).

1.4 Biodiversity and fisheries management

Traditionally, fisheries management has focused on the commercially important species, while predators and prey of these species often has been ignored (Pikitch et al., 2004). As a consequence, the need for a more holistic management approach has grown (Pikitch et al., 2004). To shift away from the singular-species focus of traditional fisheries management, and toward an ecosystem-based approach, indicators of ecosystem health must be applied (Greenstreet and Rogers, 2006). This requires knowledge and identification of the area's fish communities (Costello and Chaudhary, 2017; Kraufvelin et al., 2017). In addition, to manage ecosystems effectively, ecological reference points must be identified, against which management objectives may be set (Greenstreet and Rogers, 2006). By identifying characteristics and traits of fishing communities, we may predict which species are key to ecosystem function (Wootton and Oemke, 1992). Identifying the relative frequency and distribution of species can, however, be challenging in topographic complex habitats (Harvey et al., 2007). With the new Marine resources Act in 2009, conservation and sustainable use was integrated in the management of Norwegian fisheries and conservation of biodiversity was stated as being an important part of sustainable management (Gullestad et al., 2017).

1.5 Biodiversity measures

Biodiversity is a comparative measure, and refers to the diversity of organisms in a community (Laamanen et al., 2017). It includes all aspects of the diversity of life, and can be approached from multiple angles (Loreau, 2010). 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 indexes used to describe biodiversity (Peet, 1974; Gallardo et al., 2011), and a fundamental component of many ecological models and conservation strategies (Gotelli and Colwell, 2001). Because species richness can positively impact many ecosystem functions (Hooper et al., 2005; Balvanera et al., 2006), it is widely regarded as a crucial indicator in quantitative assessments of community status (Dorazio 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 (Laamanen et al., 2017). Both Shannon's and Simpson's diversity indices combine richness and evenness. Shannon's focuses on rare species, whereas Simpson's focuses on the more common (Morris et al., 2014).

Lastly, the composition of species refers to the quantity of each species in a sample (Birks, 2012). Analyzing species composition can be done using analysis of similarity (ANOSIM) or permutational analysis of variance (ADONIS), which compare the species composition between different groups (areas, seasons, years) (Birks et al., 2012). A similarity of percentages (SIMPER) is often used with these parameters to determine which species are responsible for the variation between the groups, and identify "significant taxa" (Clarke, 1993). These are the species that contribute to the most variation between the groups (Clarke, 1993).

1.6 Marine protected areas

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 (Lubchenco et al., 2003; Fernandes et al., 2005; Lester et al., 2009; Gaines et al., 2010; Fenberg et al., 2012; Baskett and Barnett, 2015). A no-take MPA refers to a specific geographic area in the ocean where no harvesting is allowed. The primary expected response to a no-take MPA is increased abundance and biomass of harvested species (Lester et al., 2009). Indeed, MPAs have been found to positively affect abundance, biomass, body size and age of harvested fish populations (Moland et al., 2013; Baskett and Barnett, 2015; Halvorsen et al., 2017b; Fernández-Chacón et al., 2020). Also, there is growing evidence for MPAs to prevent fisheries-induced evolution and replenish populations and export of eggs, larvae and adults to adjacent fishing grounds (Stobart et al., 2009; Goñi et al., 2010; Harrison et al., 2012; Sørdalen et al., 2020).

Protection from fishing is expected to restore natural size structures of harvested fish, as more individuals survive to reach larger sizes (Baskett and Barnett, 2015; Fernández-Chacón et al., 2020), followed by increased reproductive output due to more mature individuals as well as increased fecundity as maternal age and size increase (Díaz et al., 2011; White et al., 2013; 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). In relation to this, no-take MPAs also provides unique opportunities for studies on fundamental ecological processes and vital rates, by eliminating harvest mortality as a driver of change in the ecosystems (Moland et al., 2013).

The effects of MPAs are related to their design. Individuals with small home ranges may experience higher survival, as they avoid fishing mortality by spending most of the time inside the MPA, and the effects of protection may be higher for these species (Moland et al., 2013; Villegas-Ríos et al., 2016). Consequently, the responses to MPAs are shaped by which species were harvested before the establishment, which species have characteristics that promote greater responses to protection, and cascading responses across protected and harvested areas that affects the whole community (Baskett and Barnett, 2015).

2 Study objective/aim of the study

In this project my aim is to assess the impact of protection from fishing on a coastal fish community in a region known for intense and size-selective fishing pressure. To this end, I compare the composition of fish species and sizes inside a no-take MPA to a control area outside the MPA, where fishing is allowed. I use a ten-year dataset collected with beach seine from three sites inside the MPA and five neighboring sites outside the MPA. I also compare with data collected the year before the establishment of the MPA.

Specifically, I analyze species richness, diversity, evenness, composition, catch per unit effort (CPUE), and length measures of fish caught inside and outside the MPA against the following hypotheses:

1. I hypothesize that the species richness, diversity, and evenness inside the MPA has increased during the years of protection, compared to the control area.
2. I hypothesize there is a difference in the composition of species between MPA and control area post-protection, and that harvested species contribute most to this difference.
3. I hypothesize that overall CPUE and mean length of fish inside the MPA has increased during the years of protection, relative to the control area.
4. I hypothesize that CPUE of harvested fish species has increased inside the MPA relative to the control area, and, if this is the case, that non-targeted fish species of mid trophic levels have decreased in abundance.
5. I hypothesize that harvested fish species, being protected from fisheries-induced selection, has increased in body size inside the MPA.
6. I hypothesize that non-targeted fish species of mid trophic levels may have decreased in mean length if abundance of predators or competition from other mid trophic level fish increase.

3 Materials and methods

3.1 Skagerrak coast study system

This study was conducted in coastal Skagerrak in southern Norway. Coastal Skagerrak waters are influenced by a mixture of brackish Baltic Sea water passing through the Kattegat, by North Sea coastal water, and by freshwater runoff from rivers (Albretsen et al., 2012). Streaming westward in the Skagerrak, the low salinity Norwegian Coastal Current continues northward along the Norwegian coast (Albretsen et al., 2012).

Several commercially important species of fish spawn and hatch in Norwegian coastal waters (Sætre et al., 2003). Historically, a variety of fisheries have been conducted in Skagerrak (Knutsen et al., 2022). Today, commercial fishing in this region is largely driven by bottom trawls that capture Northern shrimp (*Pandalus borealis*) (Knutsen et al., 2015). Due to decades of overfishing and pollution, water quality has been degraded, biodiversity has been lost, and traditional coastal fisheries have largely collapsed (Johannessen et al., 2012; Obst et al., 2018; Frigstad et al., 2020). Recent declines in both abundance and size of cod is particularly illustrative (Rogers et al., 2017). Cod fisheries in Skagerrak are size selective and unsustainable (Fernández-Chacón et al., 2017). The pressure on cod is enhanced by ocean warming which correlates with decreased cod growth rates (Rogers et al., 2011). More generally, fish communities in Skagerrak have now shifted towards smaller pelagic species, compared to what was seen during the colder period in the 1960s and the 1970s (Barceló et al., 2016; Fernández-Chacón et al., 2017).

Typical habitats in nearshore Skagerrak waters are eelgrass, kelp and sand (Rozas and Odum, 1988). Vegetated habitats, like kelp and seaweed, forms the basis for food webs with similar structure (Östman et al., 2016). Eelgrass and macroalgae beds are highly productive and provide a wide range of marine organisms with food, nursery grounds, and refuge from predators (Jackson, 2001). They contribute to coastal and benthic food webs by exporting organic material and biomass (Heck et al., 2008). As a result of the continual rearranging of the substrate due to wind and waves, sand habitats, containing either rock fragments or biological fragments, are dynamic feeding locations (Lasiak, 1984). A high concentration of nutrients yields an abundance of zooplankton, and bad visibility caused by turbidity offers good protection from predators (Lasiak, 1986).

3.2 Sampling design

The MPA included in this study was established in June 2012 with the aim of restoring a local cod population, and it is centered around an important cod spawning site in the Tvedestrand fjord (Ciannelli et al., 2010; Espeland et al., 2016) (Figure 1). The MPA covers 1.5 km^2 and is a strict no-take area where all harvesting of marine resources is forbidden. The Directorate of Fisheries, the Coast Guard and local police collaborate on policing the MPAs (Moland et al., 2013). In addition to cod spawning sites, the MPA holds important near-shore nursery and feeding habitats consisting of seagrass and seaweed, in addition to deeper, cooler basins (Freitas et al., 2015; Freitas et al., 2016).

Figure 1: Map of the study area in Tvedestrand. Red shaded area indicates no-take zone (referred to as MPA in this thesis), and green shaded areas partially protected areas. Blue dots represent beach seine sampling stations in the MPA, red dots in the control areas. Map created using Yggdrasil and maps.google.com.

The fish community was sampled with a beach seine and followed the standard approach maintained during a century-long monitoring program in Skagerrak (Lekve et al., 1999). Beach seines are used to estimate fish assemblage composition and length distribution (Tveite, 1971; Tveite, 1984). Since 1919, a beach seine survey has been conducted annually (except the period 1940-1944) along the Norwegian Skagerrak coast in September-October to monitor local fish populations, with a focus on recruitment of cod. The 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 14 mm and one haul covers up to 390 m^2 (Tveite, 1971). It is deployed from a boat and rowed in a semicircle from the shore. The depth at the sampling sites varies from about 3 to 15 m (Fromentin et al., 1997). The beach seine captures mainly the juvenile stages of larger species living in a wider range of habitats, such as cod, as well as older life stages of smaller species such as gobies and wrasses (Barceló et al., 2016).

For this study, I included all beach seine stations from the historic monitoring program that are located in Tvedestrand, representing five control sites (outside the MPA) and three impact sites (inside MPA) respectively (Figure 1, Table A-1). The control areas are in the Lyngørfjorden area approximately 3-9 kilometers east of the Tvedestrand fjord (Figure 1). Stations inside the MPA were only sampled since 2011, one year before the implementation of the MPA. Although longer time-series are available from the control sites we restricted our analyses to data collected during 2011-2021, for a direct comparison with the MPA sites. This study design corresponds to a before-after control-impact (BACI) contrast. The BACI method is regarded as the gold standard for assessing effect of MPAs (Russ, 2002; Osenberg et al., 2011; Moland et al., 2013). This design is effective due to the ability to detect the impacts from before to after, when compared to control areas where impacts persist (Moland et al., 2021).

3.2.1 Identification of species, CPUE and length

In the annual survey conducted by the Institute of Marine Research (IMR), fish length is measured for the first 100 cod per haul, and the first 50 individuals of other species (Tveite, 1971; Tveite, 1984). Length-measurements are rounded down to the nearest centimeter. Catch per unit effort (CPUE) in this study refers to the number of individuals caught per beach seine haul.

3.3 Analyses of species composition

The ANOSIM, ADONIS, and SIMPER approaches were used to compare species compositions (Oksanen et al., 2020).

ANOSIM is an analysis of similarity, measuring the difference between the mean ranks and determines whether the assemblage composition varies between and within groups (Birks et al., 2012). In this study, it was used to analyze similarities by comparing areas and periods by species composition. The number of permutations used was 999. In general, analysis of similarities uses distance or dissimilarity measures to examine statistically significant differences in species assemblages between different groups (Clarke, 1993; Clarke and Warwick, 1994; Clarke and Warwick, 2001; Birks et al., 2012; Legendre and Birks, 2012). Oksanen et al. (2020) suggest that ADONIS provides a more robust non-parametric analysis of variance with multivariate response data and should be preferred over ANOSIM (Birks et al., 2012). ADONIS partitions sums of squares by using semi-metric and metric distance matrices, and because it partitions the sums of squares of a multivariate data set, it is directly analogous to the multivariate analysis of variance (MANOVA) (Anderson, 2001; McArdle and Anderson, 2001). Anderson (2001) and McArdle and Anderson (2001) refers to the method as "permutational manova", and due to its inputs of linear predictors, and a response matrix of any number of columns (from two to millions), it is a robust alternative to parametric MANOVA and to ordination methods for explaining the relationships between experimental treatments and uncontrolled covariates. The function anosim() in R (R Core Team, 2021) can also confound within-group and between-group differences (Warton et al., 2012). For these reasons, adonis2() was the preferred analysis in R in this study, to compare species composition of the control and MPA areas over time (Oksanen et al., 2020).

The similarity percentage test SIMPER was used to identify which taxa accounted for the differences between the groups detected by ANOSIM and ADONIS (Clarke and Gorley, 2006; Sokal et al., 2008). The species was 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 (Clarke and Gorley, 2006).

3.4 Species richness, evenness and diversity

3.4.1 Species richness

Species richness was quantified inside the MPA and in the control area as the number of species present in a given beach seine haul.

3.4.2 Species evenness

Evenness was calculated using the Evenness index (E) using the following equation (Pielou, 1969):

$$E = \frac{H'}{Hmax}$$

where H is the Shannon diversity index (see below), and Hmax is number of species present in a given beach seine haul. The 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. (Mulder et al., 2004).

3.4.3 Species diversity (Shannon and Simpson)

Shannon-Wiener diversity index (H') is a measure of diversity, given by the equation (Shannon, 1948):

$$H' = -\sum_{i=1}^{n} p_i \, Inp_i$$

where n is the total number of species and p_i the fraction of each species i. The range is between 0 and 5, and the closer to 5, the more diverse the species in the sample are. A result of 0 means only one species is present. Consequently, if the index is low, it indicates some species dominate (Shannon, 1948; Morris et al., 2014). Shannon diversity assume all species in a specific community is represented and randomly sampled (Peet, 1974).

Simpson`s diversity index (D) also measures diversity, and is given by the equation (Simpson, 1949):

$$D = \frac{n-1}{lnN}$$

Where n is the number of species and N the number of individuals, and increases with species richness and ranges between 0 and 1 (Simpson, 1949). This index emphasizes evenness and common species to a greater extent than Shannon diversity index (Morris et al., 2014).

According to both indices, it is assumed that all species within a community are included and randomly sampled (Peet, 1974; Gamito, 2010). In this study, the diversity indexes were calculated for each beach seine haul. Community was defined as all species potentially captured by the beach seine. It was also assumed that the sampling was consistent, with a constant chance of catching the different species.

3.5 Selected species

Black goby (*Gobius niger*), goldsinny wrasse, Atlantic cod and three-spined stickleback (*Gasterosteus aculeatur*) were selected for in-depth analyses based on their perceived ecological role and the fact that they were captured in sufficient quantities. In the Skagerrak area, cod and goldsinny wrasse are harvested, while black goby and three-spined stickleback are not. Therefore, their reactions to protection are expected to differ.

3.5.1 Black goby

Black goby has little commercial value (Pethon, 2019), and is not subject of fisheries. The species is found in coastal areas from the shore down to a depth of about 70 m, from Cape Blanc in West-Africa to western Norway and the Baltic Sea. It is distributed in Eastern Atlantic and Mediterranean Sea and eastward to the Suez Canal (Vesey and Langford, 2006; Pethon, 2019). The black goby is a mesopredator and inhabits mud and sandy bottom, but also macroalgae and rocky bottoms. It is found in estuaries and tolerates brackish water (Vaas et al., 1975; Pethon, 2019). It's diet is variable and depending on habitat (Wennhage and Pihl, 2002). Mating occurs in May-August, and males make nests, court, and perform parental care on eggs. Younger males can adopt alternative mating tactics, sneaking into nests while spawning occurs (Immler et al., 2004). The black goby may reproduce repeatedly during several seasons, and may live for up to 5 years (Magnhagen, 1990). Larvae are pelagic and settle in benthic habitats when they reach 10-12 mm (Pethon, 2019).

3.5.2 Cod

Cod is a top predator and key species for coastal fisheries (Freitas et al., 2015; Villegas-Ríos et al., 2016; Moland et al., 2021). They feed on a wide variety of prey including mesopredators and have the capability to influence these prey-populations via top-down control (Frank et al., 2005; Östman et al., 2016).

In coastal Skagerrak, cod is harvested most commonly by hook and line, gillnet, fyke net and traps, and as by-catch by coastal shrimp trawlers (Moland et al., 2013). South of 62° the minimum legal size is 40 cm (Julliard et al., 2001; Moland et al., 2013). Skagerrak has experienced a marked decline in adult cod over the last decades (Svedäng, 2003; Olsen et al., 2009), with as much as 50 per cent of potentially mature cod may be removed by fishing each year (Olsen and Moland, 2011). The last 20 years, there has been exceptionally poor recruitment of cod along the Skagerrak coast, accompanied by a reduction in size-at-maturation and size-at-age (Olsen et al., 2004a; Olsen et al., 2005; Rogers et al., 2017).

Along the Norwegian Skagerrak coast, genetically different populations of cod can be found on a fjord-scale separated by 30 km or less (Jorde et al., 2007). Spawning in the coastal populations usually occurs in sheltered basins during February-April (Ciannelli et al., 2010), followed by metamorphosis of the pelagic larvae in May-June. At this stage the larvae have reached 3-5 cm and settle and feed on the bottom (Gotceitas et al., 1997). Together with most 1-group cod (fish in their second year of life) these 0-group cod stay in shallow waters (Fromentin et al., 2000).

They prefer vegetated areas that provide food and shelter for habitats. Most of the prey organisms are associated with this vegetation, but the youngest individuals also feed on planktonic crustaceans (Fjøsne and Gjøsæter, 1996). The 0-group cod will change diet in late autumn or winter and feed more on fish (Fjøsne and Gjøsæter, 1996; Bromley et al., 1997), such as the two-spotted goby (Fosså, 1991; Wennhage and Pihl, 2002).

Cod in Skagerrak matures relatively early compared to many other North Atlantic cod populations, and different cod populations inhabit different growth rates and age at maturation (Olsen et al., 2004a)

3.5.3 Goldsinny wrasse

Goldsinny wrasse is increasingly harvested in Skagerrak to be deployed as cleaner fish in salmonid aquaculture net pens (Darwall et al., 1992; Halvorsen et al., 2016). Such wrasse fisheries are size- and sex selective (Halvorsen et al., 2017b). The fishery is regulated with minimum size limits, gear modifications for the escapement of undersized fish and a spring fishing closure until 17 June to avoid fishing in the main spawning period (Skiftesvik et al., 2015).

Goldsinny wrasse is a mesopredator that connects smaller benthic species and zooplankton with piscivores fish and other predators (Salvanes and Nordeide, 1993; Schückel et al., 2013), and protection may therefore impose trophic cascades that influence CPUE and length through competitive or predatory interactions (Micheli et al., 2004). The species is found from the Black Ocean and the Mediterranean to Morocco in the south and Norway in the north (Pethon, 2019). Goldsinny wrasses prefer shallow, macroalgae covered, rocky habitats with access to refugee such as spaces between rocks (Costello, 1991; Darwall et al., 1992; Norderhaug et al., 2005; Pethon, 2019). Their diet consists of a wide range of invertebrates and crustaceans, and they constitute as prey for larger predatory fish and seabirds (Costello, 1991; Östman et al., 2016; Bourlat et al., 2021; Dehnhard et al., 2021).

Goldsinny wrasse has pelagic eggs and males defend territories for up to 2m^2 (Hilldén, 1981; Sayer, 1999; Olsen et al., 2019). Goldsinny may reach a maximum size of 30 cm, in Norway 28 cm (Darwall et al., 1992; Pethon, 2019). It can live for up to 20 years (Sayer et al., 1995). The goldsinny males can be divided in two categories, with territorial males that exhibit typical sexual characteristics, and sneaker males that appear to be identical to females and perform sneak fertilization (Hilldén, 1981; Uglem et al., 2000). Spawning occurs in spring and early summer along the Atlantic coasts (Darwall et al., 1992).

3.5.4 Three-spined stickleback

Three-spined stickleback have been fished since the 18th century and used for flour, fish oil, fertilizer, and with their spikes cut off as bait (Pethon, 2019), but there are no active fisheries for this species in the Skagerrak area at present. Three-spined sticklebacks also serve as an intermediate trophic level for connecting smaller benthic species and zooplankton with piscivores fish and other predators (Salvanes and Nordeide, 1993; Schückel et al., 2013).

The species is found in the northern hemisphere north of 40°N (Pethon, 2019). In Europe, the distribution extend south to the Black Sea, Italy and the Iberian Peninsula, in both fresh,- brackish and saltwater environments (Pethon, 2019). In the past, marine three-spiked sticklebacks have colonized different freshwater habitats repeatedly, resulting in morphological, behavioral, and physiological differences (McKinnon and Rundle, 2002).

Sticklebacks reach maturity at 1-2 years old (Pethon, 2019) and spawn from April to August (Sokołowska and Kulczykowska, 2006). When spawning season begins, males establish territories and build nests consisting of vegetation (Wootton, 1973; Jakobsson et al., 1999). Female sticklebacks spawn their eggs in the nests, and males guard the nests for the first 4-6 days after hatching (Wootton, 1973; Pethon, 2019). When they reaches 25 mm, they seek shallow water (Pethon, 2019). Gagnon et al. (2019) found sticklebacks were more abundant in habitats with high structural complexity (macroalgae beds and seagrass meadows), possibly trading off low predation success for a higher food supply and increased shelter against top predators. Their diet consists of isopods, amphipods, copepods, fish eggs, gastropods and mussels (Wennhage and Pihl, 2002; Bergström et al., 2016; Gagnon et al., 2019).

3.6 Data analysis and statistical methods

Data on fish species abundance, length composition and community composition were analyzed using the R and RStudio (R Core Team, 2021). The packages used include base R, Tidyverse, Vegan and ggplot2 (Wickham, 2016; Oksanen et al., 2020; Wickham et al., 2022). All graphics was created using the ggplot2 package (Wickham, 2016). The diversity measures and species composition analysis were calculated using the Vegan package (Oksanen et al., 2020).

Linear mixed effect models (Zuur et al., 2009) were fitted to analyze the effect of protection on diversity, overall body length and overall CPUE (all species combined). The analysis of overall mean body length was based on mean values per species and beach seine haul while overall CPUE represents the total CPUE for a given beach seine haul. Second, linear mixed effects models were also used for analyzing CPUE and length of selected species separately, namely black goby, cod, goldsinny wrasse and three-spined stickleback.

Linear regression is based on assumptions about normality and homogeneity (Zuur et al., 2009). Model validation was performed according to Zuur et al. (2009), and included plotting the residuals against each explanatory variable to determine independence; checking for homogeneity by plotting residuals vs fitted values and checking for normality by plotting QQ-plots and histograms of the residuals. Based on the results of this diagnostic (Figure C-1, Figure C-2, Figure C-3), distribution, length data were log-transformed (Zuur et al., 2010).

The model response variables include species richness, Shannon's and Simpson's diversity indexes, evenness, 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 material was not strong enough to run full-resolution models in years (all the models did not converge). To attain the complexity necessary to detect real differences, interaction effects also needed to be included.

For each of the response variables (analyses) I compared a set of five *a priory* defined models. The most complex model included an interaction between area (MPA vs. control) and period (before vs. early after vs. late after). This interaction was included to specifically evaluate an effect of protection on each of the diversity indexes as well as fish length and CPUE. Also, the beach seine stations will differ in, for instance, habitats, and station was therefore fitted as a random effect (Zuur and Ieno, 2016):

1. Response = Area x Period (1 | Station)
2. Response = Area + Period (1 | Station)
3. Response = Period (1 | Station)
4. Response = Area (1 | Station)
5. Response = 1 (1 | Station)

To determine which explanatory variables are important, the Aikake Information Criteria (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). Using AIC to compare models, I was able to evaluate each model relative to the best model, and when $\Delta AIC > 2$, the model is said to have substantial evidence of validity (Burnham and Anderson, 2002). All models were fitted using Maximum Likelihood (ML) estimation with the lme() function in R (Pinheiro et al., 2012).

4 Results

In the period 2011-2021, a total of 26522 individual fish was collected and measured for length in the three stations inside the MPA (n = 9159) and five stations in the control area (n = 17454).

4.1 Overall CPUE and body length

In the MPA, mean overall CPUE (all species combined) was 295.5 individuals (range: 29 – 2505) compared to 317.4 in the control area (range: 8 – 4444; figure 2).

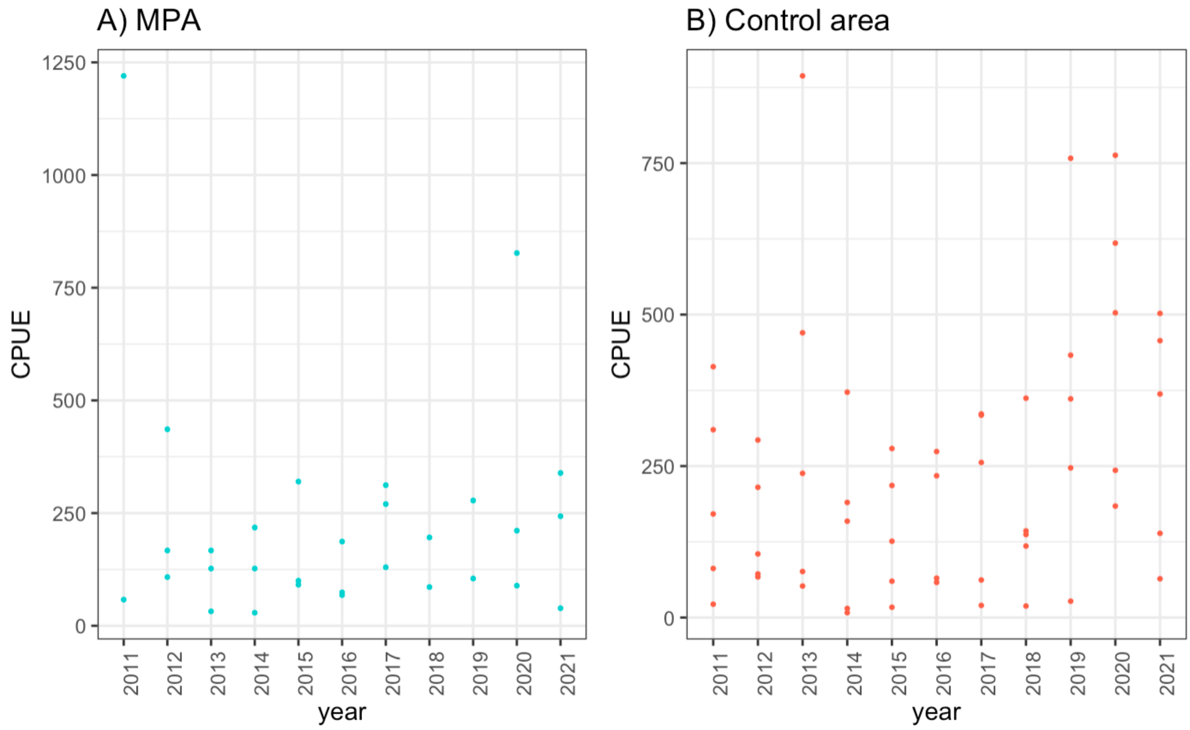

Figure 2: CPUE (number of individuals caught at each station) for alle species caught in A) MPA (3) and B) control area (5) during the survey from 2011-2021. To outliers not shown, A) 2505 fish caught in one station inside the MPA in 2019 (2500 sprat) and B) 4444 fish caught in one station inside the control area in 2016 (4220 sprat).

For all species combined, model selection supported an effect of period on CPUE, while models containing an effect of area produced higher AIC-values and thus received lower support (Table 1).

Table 1: Model selection. Linear mixed effect modelling of CPUE) combining all fish species caught in the beach seine survey during 2011-2021. 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, the AIC score and the distance in AIC score from the model selected for statistical inference (in bold).

Response	Model structure	Parameters	AIC	ΔAIC
CPUE	Period * Area (1 | station)	6	393.80	4.74
	Period + Area (1 | station)	4	391.00	1.94
	Period (1 | station)	**3**	**389.06**	**0**
	Area (1 | station)	2	401.85	12.79
	1 (1 | station)	1	399.85	10.79

Parameter estimates based on the most parsimonious model, with an additive effect of period on overall CPUE, indicates that CPUE was significantly higher in the early and late periods, compared to the before-period (Table 2). Overall predicted CPUE increased from approximately 332 individuals per seine in the before period to 2310 individuals per seine in the late period.

Table 2: Summary of the most parsimonious linear mixed effect model predicting CPUE of all species combined, showing the response variable and model coefficients with associated parameter estimates, standard error and P value. Significant terms are illustrated with a p-value in bold. Reference level is 2011 survey.

Response	Coefficients	Estimate	Std. Error	P value
CPUE	(Intercept)	332.66	375.28	0.39
	Period Early	398.47	472.93	0.41
	Period Late	1978.47	472.93	**0.001**

All species combined, mean body length in the MPA was 9.9 cm (range: 3 – 61; figure 3). In the control area, overall mean body length was 8.5 cm (range: 3 – 65, figure 3).

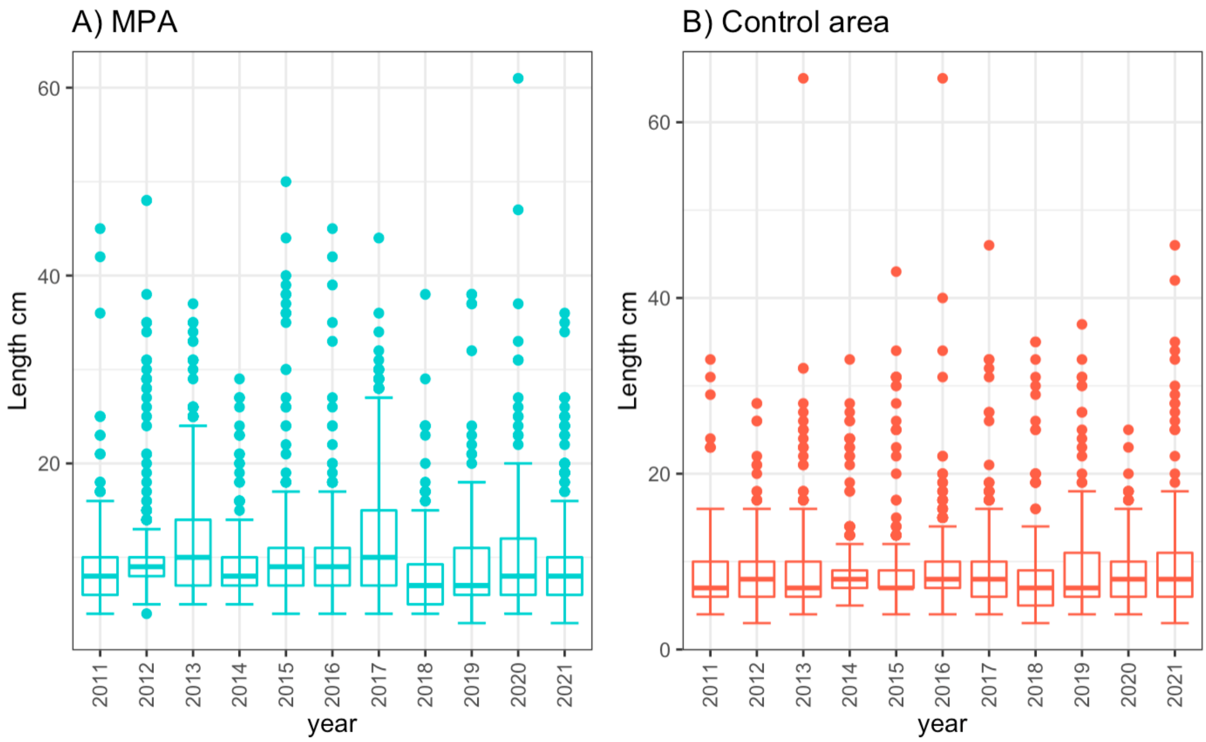

Figure 3: Boxplots showing (from bottom to top) the minimum, first quartile (25 %), median (solid horizontal lines), third quartile (75 %) and maximum body length (cm) of all fish caught at each station inside the A) MPA and in the B) control area during the survey from 2011-2021. Filled dots are outliers.

All species combined, model selection based on mean length of each species supported an effect of area on overall mean body length, while models containing an effect of period produced higher AIC-values and thus received lower support (Table 3).

Table 3: Model selection. Linear mixed effect modelling of overall mean body length (log-transformed response variables) combining all fish species caught in the beach seine survey during 2011-2021. 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, the AIC score and the distance in AIC score from the model selected for statistical inference (in bold).

Response	Model structure	Parameters	AIC	ΔAIC
Length	Period * Area (1 | station)	6	1276.10	5.03
	Period + Area (1 | station)	4	1274.11	3.04
	Period (1 | station)	3	1279.58	8.51
	Area (1 | station)	**2**	**1271.07**	**0**
	1 (1 | station)	1	1276.73	5.66

Parameter estimates based on the most parsimonious model, with an additive effect of area on mean length, indicates that mean length was significantly higher in the MPA, compared to the control area (Table 4). All species combined, mean predicted length in the MPA area was 10.4 cm compared to 8.8 cm in the control area.

Table 4: Summary of the most parsimonious linear mixed effect model predicting overall mean body length of all species, showing the response variable and model coefficients with associated parameter estimates, standard error and P value. Significant terms are illustrated with a p-value in bold. Reference level is control area.

Response	Coefficients	Estimate	Std. Error	P value
Length	(Intercept)	2.15	0.02	**<0.0001**
	Area MPA	0.15	0.04	**0.01**

4.2 Species composition

The total catch in this survey was comprised of 31 different species of fish from 14 families (Table 5).

Table 5: List of species caught in control area and MPA, with number of individuals, proportion of total catch in control and MPA (%), mean length and minimum/maximum (range). All length measurements in centimeters (cm).

Area	Species	Latin name	Number of individuals	Proportion of total catch (%)	Length Mean	Min	Max
Control	Eel	*Anguilla anguilla*	3	0.02	45.7	7	65
	Eelpout	*Zoarces viviparus*	2	0.01	18.5	12	25
	Ballan wrasse	*Labrus bergylta*	28	0.16	19.1	4	37
	Goldsinny wrasse	*Ctenolabrus rupestris*	2170	12.47	7.4	3	18
	Cuckoo wrasse	*Labrus mixtus*	11	0,06	9.3	5	30
	Sprat	*Sprattus sprattus*	4343	24.96	7.9	6	10
	Longspined bullhead	*Taurulus bubalis*	8	0.05	12.4	10	14
	Rock cook	*Centrolabrus exoletus*	48	0.28	5.2	4	9
	Corkwing wrasse	*Symphodus melops*	554	3.18	6.6	3	20
	Whiting	*Merlangius merlangus*	633	3.64	12.0	7	18
	Greater pipefish	*Syngnathus acus*	9	0.05	38.1	31	46
	Pollack	*Pollachius pollachius*	241	1.39	14.6	9	32
	Mackerel	*Scomber scombrus*	2	0.01	26.5	26	27
	Sea trout	*Salmo trutta*	15	0.09	27.3	7	42
	European plaice	*Pleuronectes platessa*	4	0.02	18.5	18	19

	Sand goby	*Pomatoschistus minutus*	470	2.70	6.7	4	9
	Saithe	*Pollachius virens*	252	1.45	13.2	10	25
	Herring	*Clupea harengus*	4	0.02	7.0	6	8
	European flounder	*Platichthys flesus*	21	0.12	26.1	7	35
	Black goby	*Gobius niger*	4019	23.10	8.2	3	15
	Broadnosed pipefish	*Syngnathus typhle*	68	0.39	20.9	13	28
	Sea stickleback	*Spinachia spinachia*	16	0.09	11.1	8	13
	Cod	*Gadus morhua*	536	3.08	9.2	6	31
	Three-spined stickleback	*Gasterosteus aculeatus*	3919	22.53	5.2	3	8
	Shorthorn sculpin	*Myoxocephalus scorpius*	21	0.12	16.7	12	27
MPA	Ballan wrasse	*Labrus bergylta*	72	0.79	20.7	6	38
	Goldsinny wrasse	*Ctenolabrus rupestris*	1834	20.10	8.4	4	15
	Sprat	*Sprattus sprattus*	2565	28.11	6.3	6	7
	Rock cook	*Centrolabrus exoletus*	57	0.62	6.1	4	13
	Corkwing wrasse	*Symphodus melops*	449	4.92	8.0	3	21
	Whiting	*Merlangius merlangus*	54	0.59	12.7	7	18
	Lesser pipefish	*Syngnathus rostellatus*	3	0.03	26.0	24	27
	Greater pipefish	*Syngnathus acus*	16	0.18	40.9	33	50
	Pollack	*Pollachius pollachius*	434	4.76	17.5	4	42
	Mackerel	*Scomber scombrus*	2	0.02	29.5	24	35
	Sea trout	*Salmo trutta*	2	0.02	35.0	25	45
	Cuckoo wrasse	*Labrus mixtus*	20	0.22	10.3	6	26
	Sand goby	*Pomatoschistus minutus*	12	0.13	6.7	6	8
	Saithe	*Pollachius virens*	53	0.58	22.2	11	35
	Herring	*Clupea harengus*	10	0.11	6.0	5	7
	Brill	*Scophthalmus rhombus*	2	0.02	34.0	31	36
	European flounder	*Platichtys flesus*	1	0.01	33.5	34	34
	Black goby	*Gobius niger*	962	10.54	8.4	4	14
	Poor-cod	*Trisopterus minutus*	2	0.02	7.5	7	8
	Horse mackerel	*Trachurus trachurus*	330	3.62	9.3	5	11
	Broadnosed pipefish	*Syngnathus typhle*	66	0.72	21.4	11	31
	Sea stickleback	*Spinachia spinachia*	32	0.35	11.8	10	14
	Cod	*Gadus morhua*	205	2.25	11.2	7	61
	Three-spined stickleback	*Gasterosteus aculeatus*	1927	21.12	5.2	3	8
	Shorthorn sculpin	*Myoxocephalus scorpius*	15	0.16	16.7	6	23

The species contributing the most to the catch in the MPA were: sprat (28.11 %), three-spined stickleback (21.12 %), goldsinny wrasse (20.10 %), and black goby (10.54 %). In the control area, sprat contributed the most (24.96 %), followed by black goby (23.10 %), three-spined stickleback (22.53 %), and goldsinny wrasse (12.47 %).

The ANOSIM analysis did not detect significant differences in species composition between the areas in any of the periods. In contrast, the ADONIS analysis detected significant differences between the areas in both the early and late period after protection, but not before protection (Table 6).

Table 6: Differences in catch composition between control area and MPA using both ANOSIM and ADONIS analyses. Significant terms are illustrated with a p-value in bold. R^2 values provided in Table B-1.

Period	P-values, MPA vs. control area	
	ADONIS	ANOSIM
Before (2011)	0.477	0.34
Early (2013-2014)	**0.011**	0.19
Late (2015-2021)	**0.004**	0.379

According to the SIMPER analyses, four species accounted for the first 70 % of the variation between the two areas (Figure 4). In the early period, the species were goldsinny wrasse, black goby, three-spined stickleback and sand goby, with goldsinny wrasse contributing most to the variance (27 %) (Figure 4). In the MPA, goldsinny made up higher proportion of the total catch (40.3 %) than in the control area (19.8 %). Black goby, stickleback, and sand goby accounted for the higher part of the total in the control area (19.8 %, 29.8 %, 6.6 %) than in the MPA (17.2 %, 3.54 %, 0.05 %).

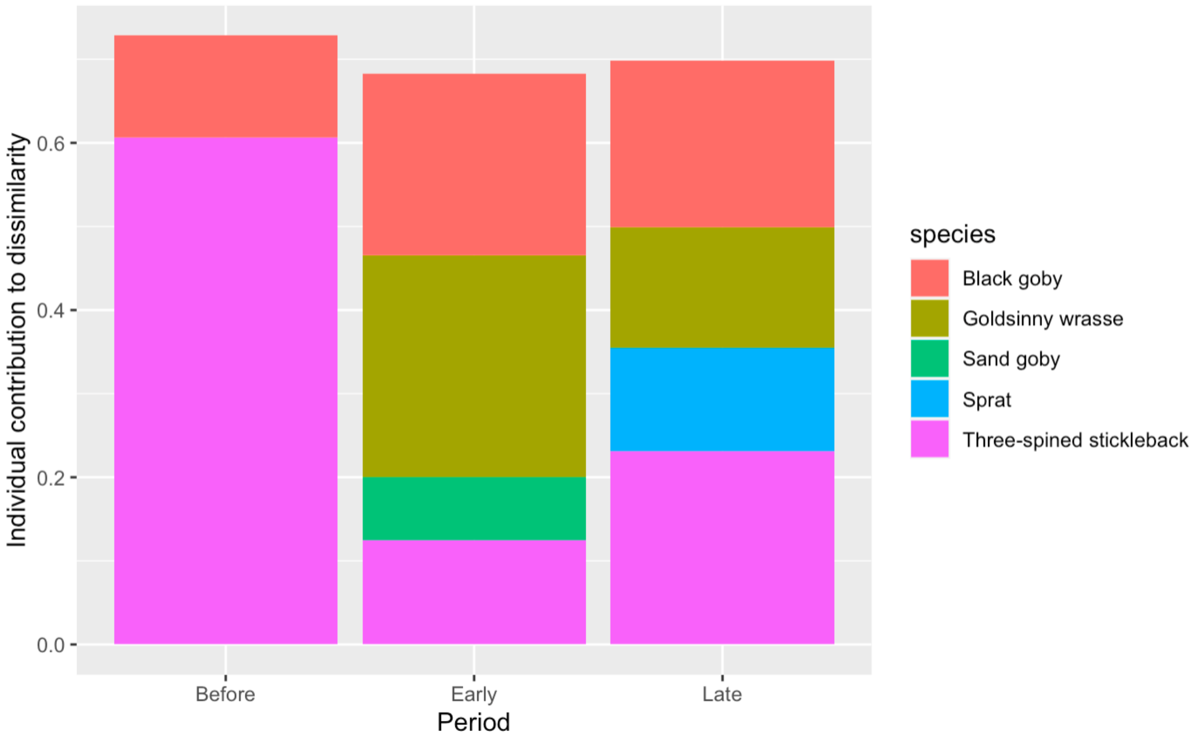

Figure 4: Species' contribution to dissimilarities in sampled fish community (~70%) between the MPA and control area in the before-protection period (2011), early period after protection (2012-2015) and late period after protection (2016-2021), as revealed by the SIMPER analysis.

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 (23 %) (Figure 4). In the MPA, goldsinny and sprat made up a higher proportion of the total catch (14.6 %, 43.0 %) than in the control area (9.1 %, 34.7 %). Stickleback and black goby accounted for a higher proportion of the total catch in the control area (20.7 %, 21.2 %) than in the MPA (15.1 %, 10.0 %).

4.3 Species diversity, evenness and richness

In the MPA, the mean value of Shannon's diversity 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; figure 5). For Simpson's diversity index of species diversity, the mean value in the MPA was 0.64 (range: 0.0 – 0.82) compared to 0.60 in the control area (range: 0.10 – 0.83; figure 5). The mean species evenness in the MPA was 0.63 (range: 0.01 – 0.90) compared to 0.62 in the control area (range: 0.12 – 0.97; figure 5). Mean species richness (number of species) in the MPA was 10.61 (range: 4 – 16), compared to 9.62 in the control area (range: 4 -16; figure 5).

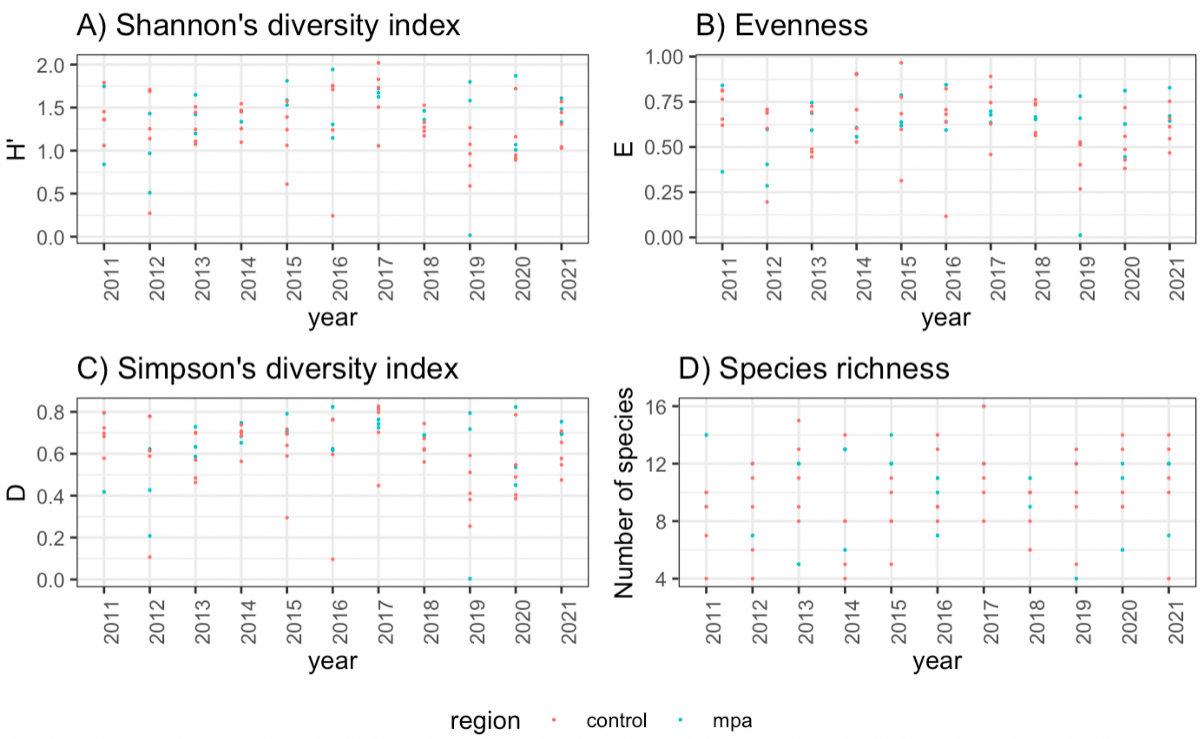

Figure 5: A) Shannon's diversity index, B) evenness, C) Simpson's diversity index and D) species richness describing the fish community at stations inside the MPA (blue dots) and control area (red dots) during the survey from 2011-2021.

Model selection did not support effects of area (that is, protection level) on either Shannon's diversity, Simpson's diversity or evenness (Table 7). Model selection did support an effect of period on species richness, while models containing an effect of area produced higher AIC-values and thus received lower support (Table 7). Parameter estimates based on the most parsimonious model, with an additive effect of period on species richness, indicates an incline in the number of species in the late period, compared to the before-period (Table 8). 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.

Table 7: Model selection. Linear mixed effect modelling of Shannon's diversity, Simpson'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, the AIC score and the distance in AIC score from the model selected for statistical inference (in bold).

Response	Model structure	Parameters	AIC	ΔAIC
Shannon	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**
Simpson	Period * Area (1 | station)	6	-51.62	6.94
	Period + Area (1 | station)	4	-53.71	4.85
	Period (1 | station)	3	-55.31	3.25
	Area (1 | station)	2	-56.93	1.63
	1 (1 | station)	**1**	**-58.56**	**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

Table 8: Summary of the most parsimonious linear mixed effect models predicting species diversity, evenness and richness, showing the response variable and model coefficients with associated parameter estimates, standard error and P value. Significant terms are illustrated with a p-value in bold. Reference level is the before-period.

Response	Coefficients	Estimate	Std. Error	P value
Shannon	(Intercept)	1.31	0.07	**<0.0001**
Evenness	(Intercept)	0.62	0.03	**<0.0001**
Simpson	(Intercept)	0.61	0.03	**<0.0001**
Species richness	(Intercept)	8.66	1.10	**<0.0001**
	Period early	1.00	0.90	0.27
	Period late	1.63	0.87	0.06

4.4 Analyses of selected species

A total of 4981 black goby, 741 cod, 4004 goldsinny wrasse and 5846 three-spined sticklebacks was captured and measured for length between 2011-2021 (Table 5).

4.4.1 CPUE

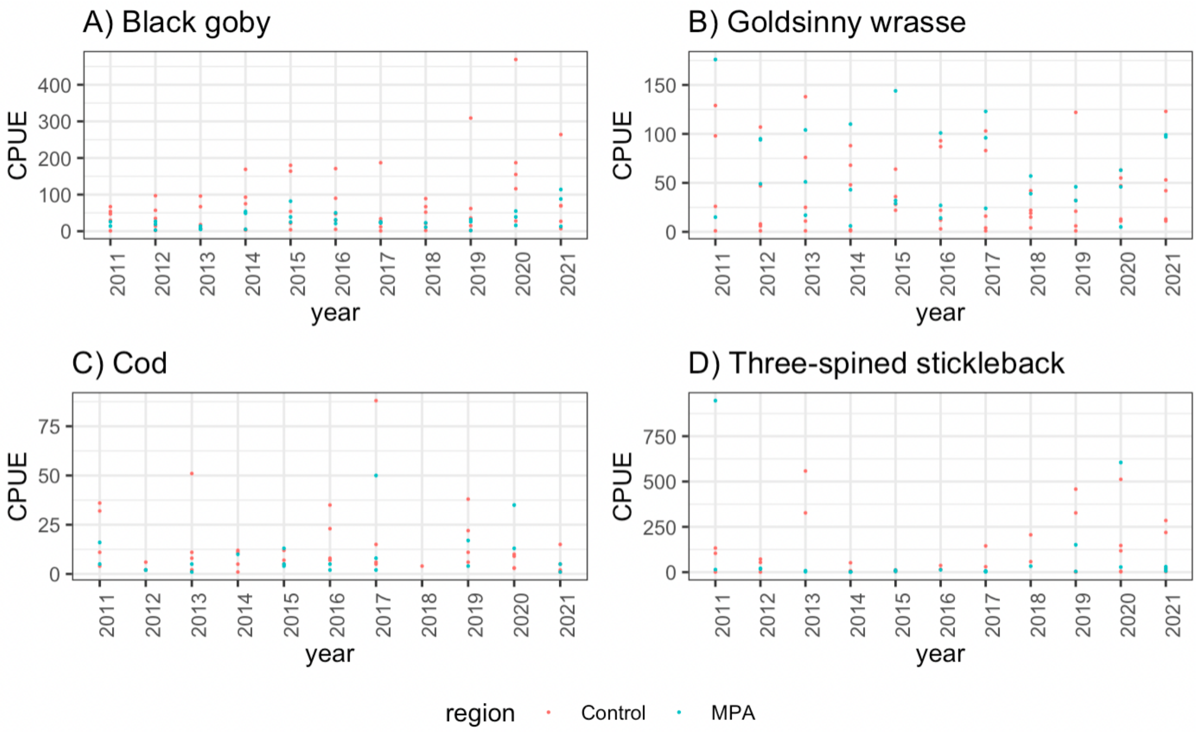

Figure 6: CPUE (number of individuals caught at each station) of A) black goby, B) goldsinny wrasse, C) cod and D) three-spined stickleback caught at each station inside the MPA (blue dots) and control area (red dots) during the survey from 2011-2021.

For black goby, mean CPUE in the MPA was 31.0 individuals (range: 2 – 114) compared to 73.1 in the control area (range: 1 – 469; figure 6). For goldsinny wrasse, mean CPUE in the MPA was 63.2 individuals (range: 5 – 176) compared to 49.9 in the control area (range: 1 – 138, figure 6). Mean number of cod caught at each station in the MPA were 9.8 (range: 1 – 50). In the control area an average of 13.4 cod was caught at each station (range: 1 – 88; figure 6). For three-spined stickleback, mean CPU in the MPA was 83.8 (range: 1 – 946) compared to 126.4 in the control area (range: 1 – 558; figure 6).

For black goby, model selection supported an effect of period and area on CPUE (Table 9). For cod and goldsinny wrasse, model selection supported an effect of period on CPUE, while models containing an effect of area produced higher AIC-values and thus received lower support (Table 9). For three-spined stickleback the model selection supported no effect of neither period nor MPA (Table 9).

Table 9: 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, the AIC score and the distance in AIC score from the model selected for statistical inference (in bold).

Response	Species	Model structure	Parameters	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**

Table 10: Summary of the most parsimonious linear mixed effect models predicting CPUE of black goby, cod, goldsinny wrasse and corkwing wrasse, showing the response variable and model coefficients with associated parameter estimates, standard error and P value. Significant terms are illustrated with a p-value in bold. Reference level is the before-period and the control area.

Response	Species	Coefficients	Estimate	Std. Error	P value
CPUE	Black goby	(Intercept)	82.94	91.64	0.38
		Period Early	168.36	119.43	0.18
		Period Late	386.60	119.43	**0.01**
		Area MPA	-170.81	101.11	0.14
	Cod	(Intercept)	9.34	15.55	0.56
		Period Early	13.04	15.56	0.42
		Period Late	47.91	15.56	**0.01**
	Goldsinny wrasse	(Intercept)	33.14	58.53	0.58
		Period Early	160.73	41.93	**0.002**
		Period Late	217.86	41.93	**0.0002**
	Three-spined stickleback	(Intercept)	309.58	115.42	**0.02**

For black goby, parameter estimates based on the most parsimonious model, with an additive effect of period and area on CPUE, indicates that mean predicted CPUE was significantly higher in the late period, compared to the before period in both the MPA and control area (Table 10, Figure 7).

For goldsinny wrasse, parameter estimates based on the most parsimonious model, with an additive effect of period on CPUE, indicates that CPUE was significantly higher in the early and late period, compared to the before period. However, this pattern was seen in both the MPA and control area (Table 10, Figure 7).

For cod, parameter estimates based on the most parsimonious model, with an additive effect of period on CPUE, indicates that mean predicted CPUE was significantly higher in the late period compared to the before. This was the case for both the MPA and control area (Table 10, Figure 7).

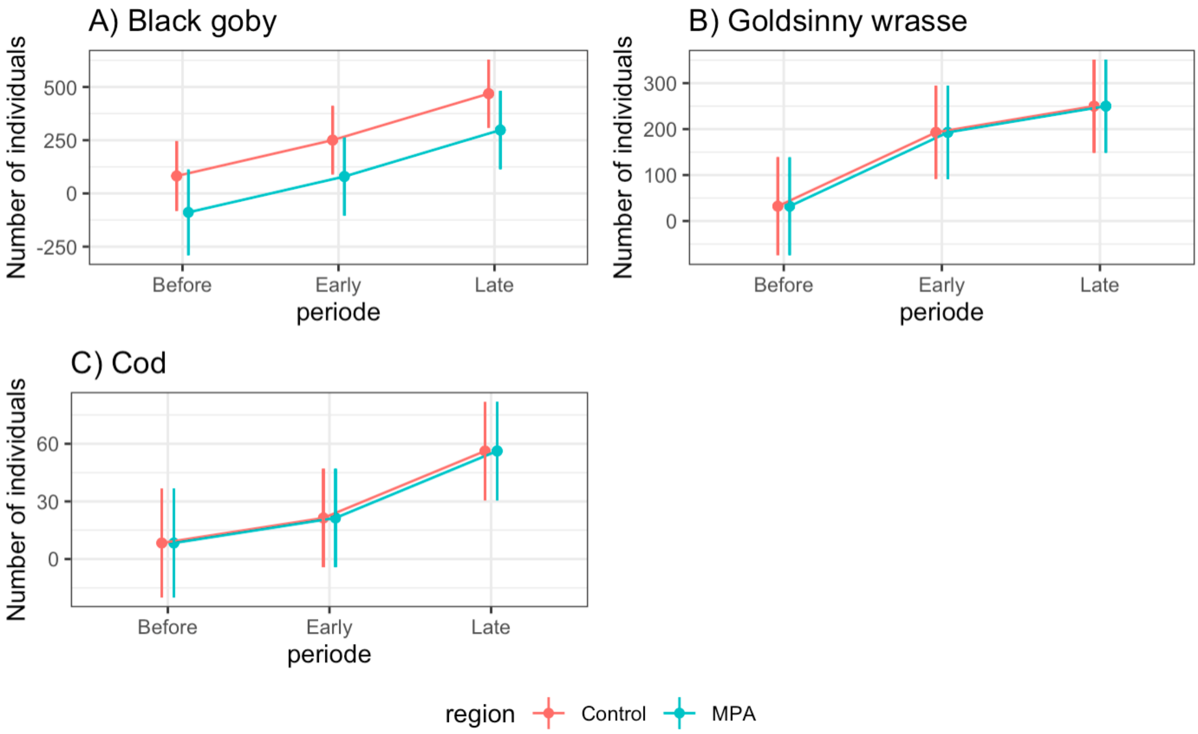

Figure 7: Predicted CPUE (show ±1 standard error) of A) black goby, B) goldsinny wrasse and C) cod in the MPA area (blue) and control area (red) before protection (2011), in the early period after protection (2012-2015) and late period (2016-2021).

4.4.2 Body size

For black goby, mean body length of fish sampled inside the MPA was 8.4 cm (range: 4 -14 cm, figure 8). For cod, mean body length of fish sampled inside the MPA was 11.2 cm (range: 7 – 61, figure 8). For goldsinny wrasse, mean body length of fish sampled inside the MPA was 8.4 cm (range: 4 – 15, figure 8). For three-spined sticklebacks, mean body length of fish sampled inside the MPA was 5.2 cm (range: 3 – 8; figure 8). There was great variation in counts of three-spined sticklebacks (Figure 4), but a small variation in length measurements (Figure 8).

For black goby, mean body length of fish caught in the control area was 8.2 cm (range: 3 – 15 cm, figure 9). For cod, mean body length of fish caught in the control area was 9.2 cm (range: 6 – 31 cm, figure 9). For goldsinny wrasse, mean body length of fish caught in the control area was 7.4 cm (range: 3 – 18 cm, figure 9). For three-spined stickleback, mean body length of fish caught in the control area was the same as in the MPA (Figure 8, Figure 9).

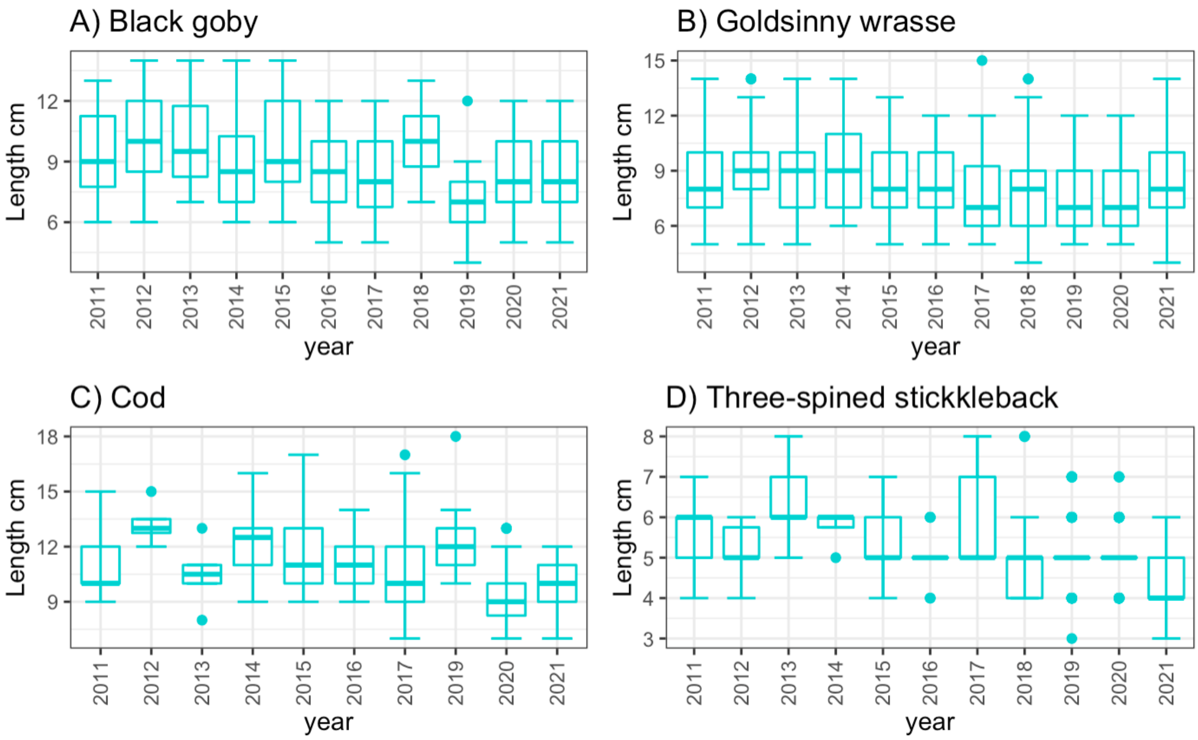

Figure 8: Boxplots showing the minimum, first quartile (25 %), median (solid horizontal lines), third quartile (75 %) and maximum body length (cm) of A) black goby, B) goldsinny wrasse, C) cod and D) three- spined stickleback caught at each station inside the MPA) during the survey from 2011-2021. Filled dots are outliers. One outlier not shown (a 61 cm cod caught in 2020).

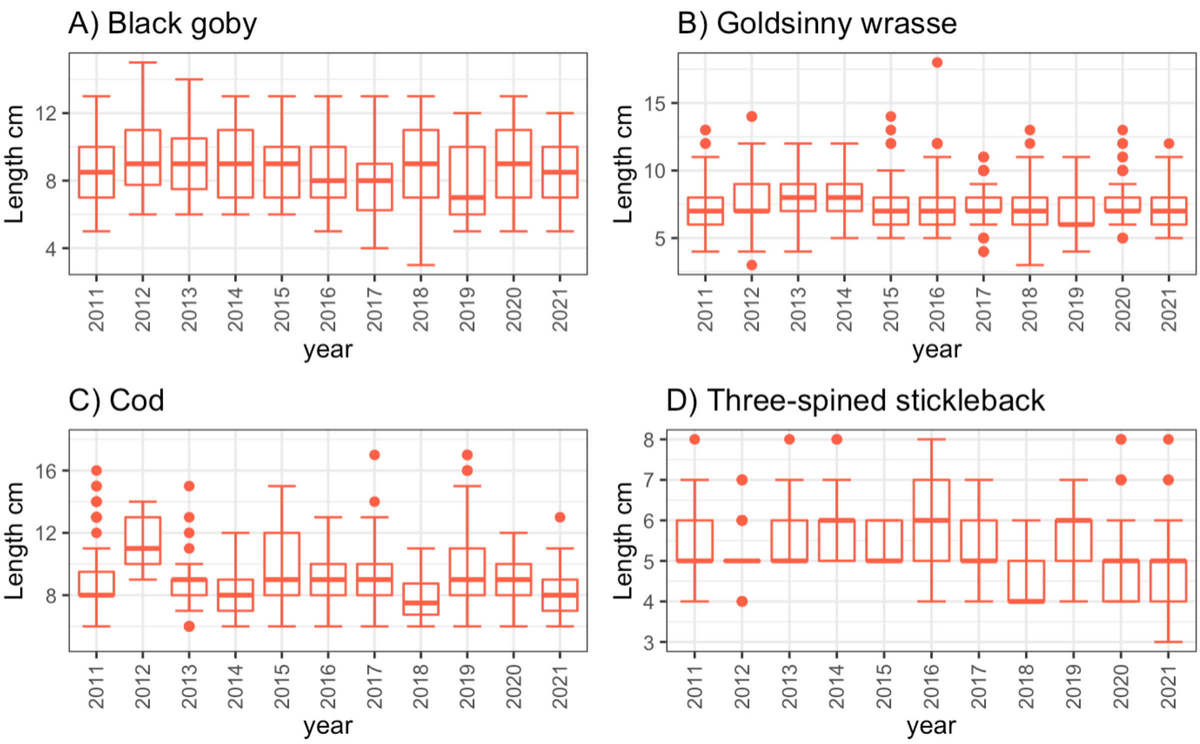

Figure 9: Boxplots showing the minimum, first quartile (25 %), median (solid horizontal lines), third quartile (75 %) and maximum body length (cm) of A) black goby, B) goldsinny wrasse, C) cod and D) three-spined stickleback caught at each station in the control area during the survey from 2011-2021. Filled dots are outliers. Three outliers not shown: one 26 cm cod caught in 2012, one 31 cm cod caught in 2015 and one 31 cm cod caught in 2017.

Model selection supported an interaction effect between period and area on body length for black goby, goldsinny wrasse, and three-spined stickleback. For cod, model selection supported an effect of area on body length, while models containing an effect of period produced higher AIC-values and thus received lower support (Table 11).

Table 11: Model selection. Linear mixed effect modelling of body length of black goby, cod, goldsinny wrasse and corkwing wrasse (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, the AIC score and the distance in AIC score from the model selected for statistical inference (in bold).

Response	Species	Model structure	Parameters	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

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 goldsinny wrasse, black goby and three-spined stickleback (Table 12, Figure 10).

The mean predicted body length of cod was significantly higher in the MPA compared to the control area, however this was the case in all periods (Table 12, Figure 10).

Table 12: Summary of the most parsimonious linear mixed effect models predicting body length of black goby, cod, goldsinny wrasse and corkwing wrasse, showing the response variable and model coefficients with associated parameter estimates, standard error and P value. Significant terms are illustrated with a p-value in bold. Reference level is the before-period and the control area.

Response	Species	Coefficients	Estimate	Std. Error	P value
Length	Black goby	(Intercept)	2.04	0.02	**<0.0001**
		Period Early	0.05	0.02	**0.002**
		Period Late	0.04	0.02	**0.01**
		Area MPA	0.13	0.05	**0.04**
		Period Early : Area MPA	-0.07	0.04	0.09
		Period Late : Area MPA	-0.14	0.04	**0.0002**
	Cod	(Intercept)	2.19	0.02	**<0.0001**
		Area MPA	0.20	0.03	**<0.0001**
	Goldsinny wrasse	(Intercept)	1.94	0.03	**<0.0001**
		Period Early	0.08	0.02	**0.0002**
		Period Late	0.01	0.02	0.62
		Area MPA	0.13	0.04	**0.02**
		Period Early : Area MPA	-0.004	0.03	0.87
		Period Late : Area MPA	-0.06	0.03	**0.03**
	Three-spined stickleback	(Intercept)	1.59	0.03	**<0.0001**
		Period Early	0.05	0.02	**0.004**
		Period Late	-0.03	0.02	0.11
		Area MPA	0.10	0.04	0.06
		Period Early : Area MPA	-0.05	0.03	0.11
		Period Late : Area MPA	-0.09	0.03	**0.001**

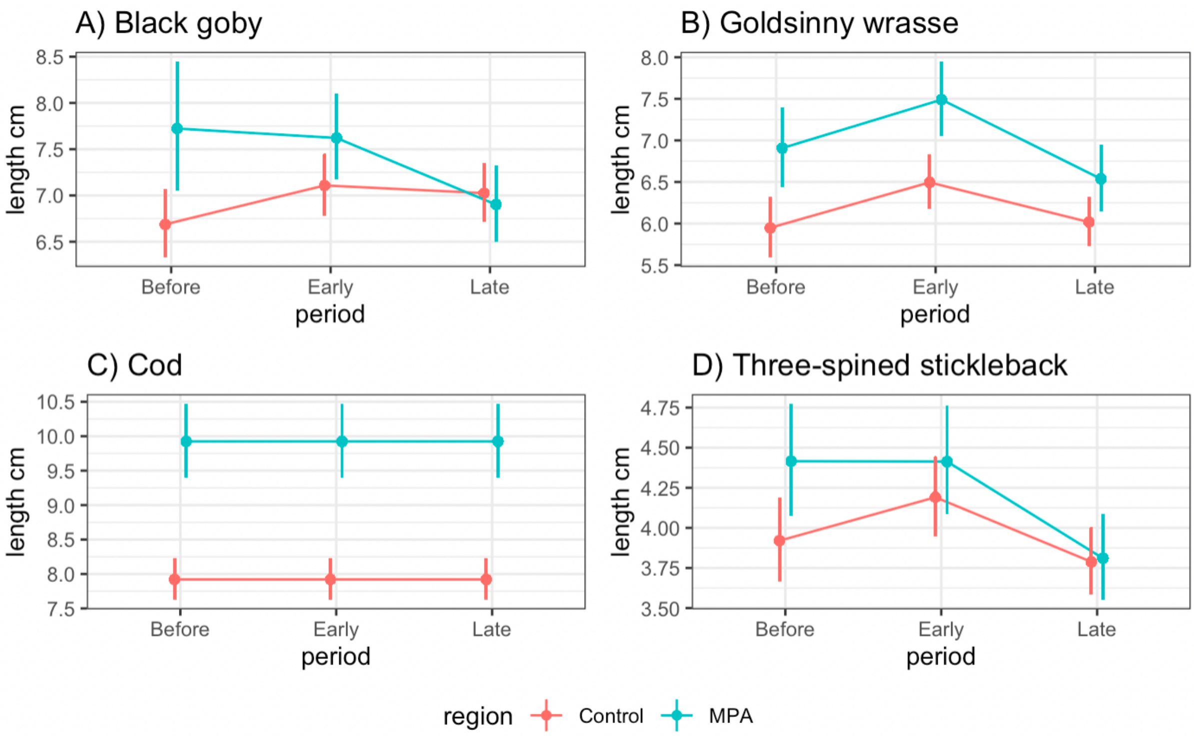

Figure 10: Interaction plots showing the mean predicted body length (show ±1 standard error) of A) black goby, B) goldsinny wrasse, C) cod and D) three-spined stickleback in the MPA area (blue) and control area (red) before protection (2011), in the early period after protection (2012-2015) and late period (2016-2021).

5 Discussion

This study assessed the impact of protection on a coastal fish community by comparing the composition of species and sizes inside a no-take MPA to control sites outside the MPA, where fishing is allowed, and also to data collected at the same locations prior to MPA establishment. With such a BACI design, no effect of protection was detected on overall CPUE and body length (all species combined), species richness, species diversity or species evenness. Significant differences in species composition were, however, detected between the areas in both the early and late periods following MPA establishment. Detailed analyses of selected species showed that there was tendency for an increase in CPUE for black goby, cod and goldsinny wrasse towards the late period after protection, but this increase could not be linked to protection as it was also seen in the control area. In contrast, analyses of sizes of selected species point towards a more pronounced decrease in body length of goldsinny wrasse, black goby and three-spined stickleback in the MPA compared to the control area. The latter suggests that biological control mechanisms and trophic interactions linked to protection may be involved. In the following sections, I further discuss these findings and how they relate to the proposed hypotheses. I argue that MPAs may not necessarily have clear and predictable effects on diversity within fish communities in the (relatively) short term, and that even longer-term monitoring is necessary to fully resolve such dynamics.

5.1 MPA-effects on species richness, evenness, diversity and composition

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 the initial hypothesis of increased diversity in protected areas, but is consistent with that of Soykan and Lewison (2015), who found no consistent differences between MPAs and control sites with respect to species richness or Shannon 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. For example, Stobart et al. (2009) found lower species diversity inside an MPA. They reported this could be explained by the fact that common bycatch fish species have increased inside the MPA, while other species that are occasionally caught have not increased, which could lower richness and diversity measures. They also conclude that conflicting results suggest that further research is needed on the responses of these indices to fishing. This is consistent with the finding of Lester et al. (2009), who concluded that increases in species richness and other diversity metrics typically do not occur as consistently as increased body size, abundance and biomass. They report there could be several reasons for this, including the fact that not all species increase, and some decline after MPAs are established, suggesting an indirect effect of protection through competitive or predatory interactions (Micheli et al., 2004; Lester et al., 2009; Baskett and Barnett, 2015). Complex trophic interactions frequently mediate community level responses to MPA establishment (Graham et al., 2003; Willis and Anderson, 2003; Takashina et al., 2012), causing unexpected changes to species richness. Overall, species richness may be an easy metric to interpret, but it appears to have limited ability to detect changes in community composition (Pillans et al., 2007; Lyashevska and Farnsworth, 2012). Also, species richness describes only one aspect of an ecological community, whereas alternate metrics describe other aspects of community structure, for instance species composition through abundance distribution between species (Pillans et al., 2007).

My study detected significant differences in catch composition between the protected and unprotected areas after protection, but not before. This result is similar to those of Stobart et al. (2009) and Claudet et al. (2006), who also found that species composition changed between protected areas and control areas. The results of Stobart et al. (2009) clearly indicated that the fish community in the protected area changed continuously during a period of 8 to 16 years after MPA establishment. Greater abundance and biomass inside MPAs may lead to shifts in the relative abundance of different species and the possibility of greater diversity (Baskett and Barnett, 2015). That said, community-level responses to protection will expectedly depend on which species are harvested before the MPA is established, their life-history characteristics and trophic interactions with non-harvested species (Baskett and Barnett, 2015).

In my study, four species accounted for 70 % of the variation in species composition between the protected and the unprotected area. Both before and after protection, three-spined stickleback and black goby accounted for a large fraction of the variation. Goldsinny wrasse only accounted for a large fraction of the variation after protection. These results support the initial hypothesis that there would be a difference in catch composition between the areas after protection. Goldsinny wrasse comprised a greater proportion of the total catch inside the protected area than in the unprotected area and accounted for a larger fraction of the difference after protection establishment. This is in support of the hypothesis that harvested species would contribute most to the variance in species composition between the areas. However, the findings of the current study were not able to find support of protection effect on the increased abundance (CPUE) of goldsinny wrasse. This outcome is contrary to that of Claudet et al. (2006) who found goldsinny wrasse, among other commercial species, increased in abundance after protection. The non-harvested species contributing most to the variance in the current study, that is, three-spined stickleback and black goby, did so in the before period as well as the early and late periods, and they also accounted for a larger proportion of the total catch in the unprotected area than in the protected area. These results corroborate the findings of Claudet et al. (2006), who detected significant differences in abundance between the protected and unprotected areas for all species except unfished species. They further discovered that the difference in abundance between protected and unprotected areas was more significant for large fish than for smaller fish and concluded that changes in the composition of the whole fish assemblage should be assessed across MPAs boundaries. The CPUE analysis in the current study may be less sensitive due to a small number of data points and large variation. This may explain why I did not detect an effect of protection on CPUE of goldsinny wrasse. At the same time, the large number of sprats caught in one haul in 2011 (before) could make it difficult to detect any other patterns in the data, thus contributing to goldsinny wrasse not comprising more variance this year.

5.2 MPA effects on overall CPUE and length

All species combined, mean fish length inside the MPA was significantly higher than in the control area, but no effect of protection was detected since this difference was also seen in the data collected before protection. Similarly, an increase in overall CPUE throughout the study could not be linked to protection as it was also seen in the control area. These results, therefore, do not support the initial hypothesis that overall CPUE and size of fishes inside the MPA should increase during the years of protection. This could be explained by the fact that when all species are pooled in the same model, some species will increase and some will decrease, both in length and abundance, which could cancel out any clear change and mask trends for particular species (Baskett and Barnett, 2015).

5.3 MPA effects on selected species

CPUE of goldsinny wrasse and black goby increased in both areas during the last period of the study, but no effect of protection within the MPA was detected. For the other non-targeted mesopredator, three-spined stickleback, CPUE was variable but with no clear change over time or between areas. These results do not support the initial hypothesis that CPUE of harvested fish species has increased inside the MPA relative to the control area, and, if this is the case, that non-targeted fish species of mid trophic levels have decreased in abundance. The outcome is contrary to that of Halvorsen et al. (2017a), which reported a 33-36 % increase in CPUE of goldsinny wrasse within MPAs. Halvorsen et al. (2017a) sampled four partially protected MPAs and neighboring control areas in Skagerrak, in contrast to one fully protected area in our study. While our data was collected using beach seine, Halvorsen et al. (2017a) used fyke nets and unbated wrasse pots, and deployed on rocky, kelp covered substrate. These differences in study design and sampling could explain why the two studies reached different results (Halvorsen et al., 2021).

No effect from protection was detected for CPUE or body length of cod. These results do not support the initial hypothesis, that cod, as a harvested top predator, should increase in both size and abundance being protected from fisheries-induced selection. There could be a number of explanations for this discrepancy. The initial effects of protection on abundance can include oscillations within a generation, especially for species with a long lifespan, a late age at maturity, and high levels of harvest intensity and duration (White et al., 2013). During this transition period, White et al. (2013) reported that the abundance of a species may remain unchanged or decline relative to conditions before protection, even when the long-term equilibrium outcome is an increasing abundance. Over time, though, species of high trophic levels are expected to increase more in MPAs, as they more often are subject of harvesting (Jennings, 2000; Baskett and Barnett, 2015). Cod along the Skagerrak coast have experienced overfishing followed by declines in stock size and changes in life-history traits (Olsen et al., 2008; Olsen et al., 2012; Fernández-Chacón et al., 2017). Interestingly, Hutchings (2000) reported that overfished cod have experienced little, if any, population recovery as much as 15 years after 45-99% reductions in reproductive biomass. He suggests Allee effects may affect population growth at low densities (Hutchings, 2005; 2015) and this could be the reason why I could not detect an increase in CPUE of cod. Basically, a recovery could take a very long time (Hutchings, 2000). Also, in our study, cod were primarily sampled as a juveniles in nursery areas or feeding grounds (Perry et al., 2018), and sampling by beach seine will not reveal the full protection effect on older life stages. In contrast, Moland et al. (2013) found an increase in population density and body size of older life-stages of cod in partially protected MPAs in Skagerrak, sampled with fyke nets.

There was 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 size towards the late period in the MPA compared to the control area for all these fish species. This finding supports the initial hypothesis that the response of mid-trophic species to protection could be a decrease in length. Goldsinny wrasse is also a harvested species, and the hypothesis states I expect an increase in size for harvested species inside the MPA. The effect of protection on these species, indicates that the initial size-response to protection from harvest could be countered by effects from trophic cascades (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). It could also be persistent with the results for goldsinny wrasse, black goby and stickleback in this study, that changes in size precedes changes in abundance. 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).

Interpreting the goldsinny wrasse's response to protection, both as a harvested species and as prey of harvested predator species, is challenging. The wrasse is also probably a competitor to the unharvested mesopredators black goby and three-spined stickleback. 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 harvested species to MPA establishment. According to Baskett and Barnett (2015), these interactions may be hard to interpret and could prevent trophic levels from providing a specific indication on community-level responses to MPAs.

5.4 Limitations and future recommendations

Major limitations in this study include the absence of additional MPAs and control areas and only one year of data before protection. Even though there are several stations within each area, it remains possible, in principle, that a change within the MPA is not the result of the protection as such. Instead, a change may result from biological processes specific to this area. The 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, 1992; Underwood, 1994). Additional years of data before protection establishment could make it more robust. Also, since the CPUE and diversity models in this study are based on a simple count or index for each station and year, additional stations would provide a better foundation for the models and evaluation of hypotheses. It should be noted that studies based on a replicated BACI design in relation to MPAs are still rare, likely because there are considerable challenges involved in sampling with such a design (Russ, 2002; Willis and Anderson, 2003; Tetreault and Ambrose, 2007; Osenberg et al., 2011). Because of the increasing use of MPAs to conserve and manage fisheries and target species, the need for more replicated BACI design studies assessing the effect of them is urgent, as monitoring single MPAs may give variable conclusions (Underwood, 1992; Underwood, 1994).

The beach seine used for sampling in this study is considered adequate for obtaining abundance indices of fish inhabiting coastal shallow water areas (Tveite, 1971; Tveite, 1984). Even so, it will not sample all components of the fish community, and the sampling efficiency is likely to vary with abiotic conditions such as light and temperature. Low temperatures can affect the presence of wrasses, as they prefer warmer water, and occupies shallow water when temperatures are high (Gjøsaeter, 2002; Freitas et al., 2021). Gadoids may be affected by high temperatures, as it makes them seek deeper water, and vice-a-versa shallower water when temperatures drop (Espeland et al., 2010; Freitas et al., 2015; Freitas et al., 2016; Freitas et al., 2021). Cod also has a marked diurnal vertical migration and larger individuals are typically absent from the shallow water habitats during daytime (Espeland et al., 2010).

The mesh size of the seine makes it possible for some fishes, like small-sized gobies, to slip through the meshes. As a result, the samples are not representative of fish of this size. Beach seines are among the least selective fishing methods available (Faltas and Akel, 2003). Even so, it is to some extent selective, since it selects fish that inhabit shallow water habitats during the day. The results of Halvorsen et al. (2017a) and Moland et al. (2013) demonstrates that data collected by different methods could yield different results. Therefore, I would recommend including different sampling methods to detect the effects of protection, since it is more appropriate to compare the same life stages of different species.

Regarding the ADONIS and ANOSIM analyses, the low R^2 values (Table B-1) indicates that a lot of variation between the groups is unexplained. This is not unexpected, as marine fish are known for their large variation in year-class strength (Hjort, 1914), even in cases where spawning biomass and reproductive output does not change substantially (Morgan et al., 2011). Year class size of marine fish is determined primarily by the survival rates of larvae and early juvenile individuals (Cushing, 1990). Thus, it is expected that our data will be subject to variations that cannot be explained. But the significant differences in the early and late periods detected by ADONIS, the preferred analysis to compare species composition in this study

(Warton et al., 2012), means that despite this, the observed differences can be accounted to area (Birks et al., 2012).

Exactly how the populations respond to protection depends on many factors, connectivity between protected and harvested areas being one of them (Moland et al., 2013; Baskett and Barnett, 2015; Villegas-Ríos et al., 2016). Villegas-Ríos et al. (2016) suggests that spillover may have a demographic benefit to fisheries, however in an evolutionary context, these same fisheries might erode the spillover capacity by constantly removing individuals as they exit the MPA. Therefore, there is a need for connected patches of juvenile and adult habitats in protected areas if a species, like cod, migrates ontogenically (Baskett and Barnett, 2015). A seascape mosaic of MPAs can help to preserve behavioral variation in populations, and improve the population's ability to resist change (Moland et al., 2021). This is consistent with the conclusions of Halvorsen et al. (2021),that a network of small strategically located MPAs may be effective to protect wrasses from selective fishing.

6 Conclusions

Norway's only no-take MPA set the stage for this study where the main objective was to assess the impact of protection from fishing on a coastal fish community. Even though the data spanned one decade and included a control area open to fishing as well as before-protection data, no clear effect of protection could be detected on either species richness, species diversity or species evenness. Significant differences in species composition were, however, detected between the protected and unprotected area in the periods after MPA establishment. In particular, goldsinny wrasse contributed to this difference after protection was introduced. Also, this study revealed that the mean body size of three mesopredators – the goldsinny wrasse, black goby and three-spined stickleback – declined within the MPA after protection, relative to the control area. This suggests that biological control mechanisms and trophic interactions may be involved. We were not, however, able to detect any effects from protection on cod. Together, these findings suggest that fish communities may be influenced by small-scale MPAs, but that trophic effects and diversity may be hard to measure adequately and may also take considerable time to develop.

References

Agostini, V. N., and Bakun, A. 2002. ‘Ocean triads' in the Mediterranean Sea: physical mechanisms potentially structuring reproductive habitat suitability (with example application to European anchovy, Engraulis encrasicolus). Fisheries Oceanography, 11: 129-142.

Albretsen, J., Aure, J., Sætre, R., and Danielssen, D. S. 2012. Climatic variability in the Skagerrak and coastal waters of Norway. ICES journal of marine science, 69: 758-763.

Allen, A. P., and Gillooly, J. F. 2006. Assessing latitudinal gradients in speciation rates and biodiversity at the global scale. Ecology Letters, 9: 947-954.

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology, 26: 32-46.

Babcock, R. C., Shears, N. T., Alcala, A. C., Barrett, N. S., Edgar, G. J., Lafferty, K. D., McClanahan, T. R., et al. 2010. Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. Proceedings of the National Academy of Sciences, 107: 18256-18261.

Bakun, A. 2013. Ocean eddies, predator pits and bluefin tuna: implications of an inferred ‘low risk–limited payoff’ reproductive scheme of a (former) archetypical top predator. Fish and Fisheries, 14: 424-438.

Balvanera, P., Pfisterer, A., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D., and Schmid, B. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecology Letters, 9: 1146-1156.

Barceló, C., Ciannelli, L., Olsen, E. M., Johannessen, T., and Knutsen, H. 2016. Eight decades of sampling reveal a contemporary novel fish assemblage in coastal nursery habitats. Global Change Biology, 22: 1155-1167.

Barneche, D. R., Robertson, D. R., White, C. R., and Marshall, D. J. 2018. Fish reproductive-energy output increases disproportionately with body size. Science, 360: 642.

Baskett, M., Micheli, F., and Levin, S. 2006. Designing marine reserves for interacting species: Insights from theory. Biological Conservation, 137: 163-179.

Baskett, M. L., and Barnett, L. A. K. 2015. The Ecological and Evolutionary Consequences of Marine Reserves. Annual Review of Ecology, Evolution, and Systematics, 46: 49-73.

Baum, J. K., and Worm, B. 2009. Cascading top-down effects of changing oceanic predator abundances. Journal of Animal Ecology, 78: 699-714.

Beardmore, B., Hunt, L. M., Haider, W., Dorow, M., and Arlinghaus, R. 2015. Effectively managing angler satisfaction in recreational fisheries requires understanding the fish species and the anglers. Canadian Journal of Fisheries and Aquatic Sciences, 72: 500-513.

Beck, J. G., Heck, K., Able, K., Childers, D., Eggleston, D., Gilanders, B., Halpern, B., et al. 2003. The Role of Nearshore Ecosystems as Fish and Shellfish Nurseries. Issues in Ecology, 11: 1-12.

Bergström, L., Karlsson, M., Bergström, U., Pihl, L., and Kraufvelin, P. 2016. Distribution of mesopredatory fish determined by habitat variables in a predator-depleted coastal system. Marine Biology, 163: 201.

Berkeley, S. A., Hixon, M. A., Larson, R. J., and Love, M. S. 2004. Fisheries Sustainability via Protection of Age Structure and Spatial Distribution of Fish Populations. Fisheries (Bethesda), 29: 23-32.

Birks, H., Lotter, A., Juggins, S., and Smol, J. 2012. Tracking Environmental Change Using Lake Sediments: Data Handling and Numerical Techniques.

Birks, H. J. B. 2012. Ecological palaeoecology and conservation biology: controversies, challenges, and compromises. International Journal of Biodiversity Science, Ecosystem Services & Management, 8: 292-304.

Botsford, L. W., Castilla, J. C., and Peterson, C. H. 1997. The Management of Fisheries and Marine Ecosystems. Science, 277: 509-515.

Bourlat, S. J., Faust, E., Wennhage, H., Wikström, A., Rigby, K., Vigo, M., Kraly, P., et al. 2021. Wrasse fishery on the Swedish West Coast: towards ecosystem-based management. ICES Journal of Marine Science 78: 1386-1397.

Bromley, P. J., Watson, T. G., and Hislop, J. R. 1997. Diel feeding patterns and the development of food webs in pelagic 0-group cod (Gadus morhua L.), haddock (Melanogrammus aeglefinus L.), whiting (Merlangiusmerlangus L.), saithe (Pollachius virens L.), and Norway pout (Trisopterus esmarkii Nilsson) in the northern North Sea. Journal of Materials Science, 54: 846-853.

Burnham, K., and Anderson, D. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, Springer.

Carr, M. H. 1989. Effects of macroalgal assemblages on the recruitment of temperate zone reef fishes. Journal of Experimental Marine Biology and Ecology 126: 59-76.

Casini, M., Lövgren, J., Hjelm, J., Cardinale, M., Molinero, J.-C., and Kornilovs, G. 2008. Multi-level trophic cascades in a heavily exploited open marine ecosystem. Proceedings of the Royal Society, Series B: Biological Sciences, 275: 1793-1801.

Ciannelli, L., Knutsen, H., Olsen, E. M., Espeland, S. H., Asplin, L., Jelmert, A., Knutsen, J. A., et al. 2010. Small-scale genetic structure in a marine population in relation to water circulation and egg characteristics. Ecology, 91: 2918-2930.

Clarke, K., and Gorley, R. N. 2006. Primer v6: user manual/tutorial. pp. 1060-1065, Plymouth, UK.

Clarke, K., and Warwick, R. 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. Plymouth, UK.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology, 18: 117-143.

Clarke, K. R., and Warwick, R. M. 1994. Similarity-based testing for community pattern: the two-way layout with no replication. Marine Biology, 118: 167-176.

Claudet, J., Pelletier, D., Jouvenel, J. Y., Bachet, F., and Galzin, R. 2006. Assessing the effects of marine protected area (MPA) on a reef fish assemblage in a northwestern Mediterranean marine reserve: Identifying community-based indicators. Biological Conservation, 130: 349-369.

Cook, R. M., Sinclair, A., and Stefánsson, G. 1997. Potential collapse of North Sea cod stocks. Nature, 385: 521-522.

Costello, M. J. 1991. Review of the biology of wrasse (Labridae: Pisces) in Northern Europe. Progress in Underwater Science, 16: 29-51.

Costello, M. J., and Chaudhary, C. 2017. Marine Biodiversity, Biogeography, Deep-Sea Gradients, and Conservation. Current Biology, 27: R511-R527.

Cowx, I., O'Grady, K., Sundt, R., and Jørstad, K. 2003. Genetic population structure of goldsinny wrasse, Ctenolabrus rupestris (L.), in Norway: Implications for future management of parasite cleaners in the salmon farming industry. Fisheries Management and Ecology, 5: 291-302.

Cushing, D. H. 1990. Plankton Production and Year-class Strength in Fish Populations: an Update of the Match/Mismatch Hypothesis. *In* Advances in Marine Biology, pp. 249-293. Ed. by J. H. S. Blaxter, and A. J. Southward. Academic Press.

Cushing, D. H. 1994. Marine climate, weather and fisheries: The effects of weather and climatic changes on fisheries and ocean resources. Reviews in Fish Biology and Fisheries, 4: 138-139.

Darwall, W. R. T., Costello, M. J., Donnelly, R., and Lysaght, S. 1992. Implications of life-history strategies for a new wrasse fishery. Journal of fish biology, 41: 111-123.

Deady, S., and Fives, J. M. 1995. The diet of corkwing wrasse, Crenilabrus melops, in Galway Bay, Ireland, and in Dinard, France. Journal of the Marine Biological Association of the United Kingdom, 75: 635-649.

Dehnhard, N., Langset, M., Aglen, A., Lorentsen, S.-H., and Anker-Nilssen, T. 2021. Fish consumption by great cormorants in Norwegian coastal waters - a human wildlife conflict for wrasses, but not gadids. ICES Journal of Marine Science 78: 1074-1089.

Díaz, D., Mallol Martínez, S., Parma, A., and Goñi, R. 2011. Decadal trend in lobster reproductive output from a temperate marine protected area. Marine Ecology Progress Series, 433: 149-157.

Dorazio, R., Royle, J. a., Söderström, B., and Glimskär, A. 2006. Estimating species richness and accumulation by modeling species occurrence and detectability. Ecology, 87: 842-854.

Elliott, M., and Dewailly, F. 1995. The structure and components of European estuarine fish assemblages. Netherland Journal of Aquatic Ecology, 29: 397-417.

Espeland, S., Kleiven, A., Moland, E., Nillos-Kleiven, P., Halvorsen, K., Bodvin, T., Olsen, E., et al. 2016. Aktiv forvaltning av marine ressurser - lokalt tilpasset forvaltning.

Espeland, S. H., Thoresen, A. G., Olsen, E. M., Stige, L. C., Knutsen, H., Gjøsæter, J., and Stenseth, N. C. 2010. Diel vertical migration patterns in juvenile cod from the Skagerrak coast. Marine Ecology Progress Series, 405: 29-37.

Faltas, S., and Akel, E. 2003. Investigation of Beach Seine Catch of Abu Qir Bay (Egypt). Bulletin of the Institute of Oceanography and Fisheries, 29: 117-135.

Fenberg, P., Caselle, J., Claudet, J., Clemence, M., Gaines, S., García-Charton, J., Gonçalves, E., et al. 2012. The science of European marine reserves: Status, efficacy, and future needs. Marine Policy, 36: 1012-1021.

Fenberg, P. B., and Roy, K. 2008. Ecological and evolutionary consequences of size-selective harvesting: how much do we know? Molecular Ecology 17: 209-220.

Fernandes, L., Day, J., Lewis, A., Kerrigan, B., Breen, D., Cameron, D., Jago, B., et al. 2005. Establishing Representative No-Take Areas in the Great Barrier Reef: Large-Scale Implementation of Theory on Marine Protected Areas. Conservation Biology, 19: 1733-1744.

Fernández-Chacón, A., Moland, E., Espeland, S. H., Kleiven, A. R., and Olsen, E. M. 2017. Causes of mortality in depleted populations of Atlantic cod estimated from multi-event modelling of mark–recapture and recovery data. Canadian Journal of Fisheries and Aquatic Sciences, 74: 116-126.

Fernández-Chacón, A., Villegas-Ríos, D., Moland, E., Baskett, M. L., Olsen, E. M., and Carlson, S. M. 2020. Protected areas buffer against harvest selection and rebuild phenotypic complexity. Ecological Applications, 30: e02108.

Fjøsne, K., and Gjøsæter, J. 1996. Dietary composition and the potential of food competition between 0-group cod (Gadus morhua L.) and some other fish species in the littoral zone. ICES Journal of Marine Science 53: 757-770.

Fosså, J. H. 1991. The ecology of the two-spot goby (Gobiusculus flavescens Fabricius): the potential for cod enhancement. ICES Marine Science Symposia, 192: 147-155.

Frank, K. T., Petrie, B., Choi, J. S., and Leggett, W. C. 2005. Trophic Cascades in a Formerly Cod-Dominated Ecosystem. Science, 308: 1621-1623.

Freitas, C., Olsen, E. M., Knutsen, H., Albretsen, J., and Moland, E. 2016. Temperature-associated habitat selection in a cold-water marine fish. Journal of Animal Ecology, 85: 628-637.

Freitas, C., Olsen, E. M., Moland, E., Ciannelli, L., and Knutsen, H. 2015. Behavioral responses of Atlantic cod to sea temperature changes. Ecology and Evolution, 5: 2070-2083.

Freitas, C., Villegas-Ríos, D., Moland, E., and Olsen, E. M. 2021. Sea temperature effects on depth use and habitat selection in a marine fish community. Journal of Animal Ecology, 90: 1787-1800.

Frigstad, H., Kaste, Ø., Deininger, A., Kvalsund, K., Christensen, G., Bellerby, R. G. J., Sørensen, K., et al. 2020. Influence of Riverine Input on Norwegian Coastal Systems. Frontiers in Marine Science, 7: 1-14.

Fromentin, J. M., Gjøsæter, J., Bjørnstad, O. N., and Stenseth, N. C. 2000. Biological processes and environmental factors regulating the dynamics of the Norwegian Skagerrak cod populations since 1919. ICES Journal of Marine Science 57: 330-338.

Fromentin, J. M., Stenseth, N. C., Gjøsæter, J., Bjørnstad, O. N., Falck, W., and Johannessen, T. 1997. Spatial patterns of the temporal dynamics of three gadoid species along the Norwegian Skagerrak coast. Marine Ecology Progress Series, 155: 209-222.

Gagnon, K., Gräfnings, M., and Boström, C. 2019. Trophic role of the mesopredatory three-spined stickleback in habitats of varying complexity. Journal of Experimental Marine Biology and Ecology 510: 46-53.

Gaines, S. D., White, C., Carr, M. H., and Palumbi, S. R. 2010. Designing marine reserve networks for both conservation and fisheries management. Proceedings of the National Academy of Sciences, 107: 18286-18293.

Gallardo, B., Gascón, S., Quintana, X., and Comín, F. 2011. How to choose a biodiversity indicator-Redundancy and complementarity of biodiversity metrics in a freshwater ecosystem. Ecological Indicators, 11: 1177-1184.

Gamito, S. 2010. Caution is needed when applying Margalef diversity index. Ecological Indicators, 10: 550-551.

Garrod, D. J., and Schumacher, A. 1994. North Atlantic cod: The broad canvas. Marine Ecology Progress Series, 198: 59-76.

Gibson, R. N. 1994. Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. Netherlands Journal of Sea Research, 32: 191-206.

Gjøsaeter, J. 2002. Distribution and density of goldsinny wrasse (Ctenolabrus rupestris) (Labridae) in the Risør and Arendal areas along the Norwegian Skagerrak coast. Sarsia: North Atlantic Marine Science, 87: 75-82.

Goñi, R., Hilborn, R., Díaz, D., Mallol, S., and Adlerstein, S. 2010. Net contribution of spillover from a marine reserve to fishery catches. Marine Ecology Progress Series, 400: 233-243.

Gotceitas, V., Fraser, S., and Brown, J. A. 1997. Use of eelgrass beds (Zostera marina) by juvenile Atlantic cod (Gadus morhua). Canadian Journal of Fisheries and Aquatic Sciences, 54: 1306-1319.

Gotelli, N. J., and Colwell, R. K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters, 4: 379-391.

Graham, N. A. J., Evans, R. D., and Russ, G. R. 2003. The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. Environmental Conservation, 30: 200-208.

Greenstreet, S., and Rogers, S. 2006. Indicators of the health of the North Sea fish community: identifying reference levels for an ecosystem approach to management. ICES Journal of Marine Science 63: 573-593.

Gullestad, P., Abotnes, A. M., Bakke, G., Skern-Mauritzen, M., Nedreaas, K., and Søvik, G. 2017. Towards ecosystem-based fisheries management in Norway – Practical tools for keeping track of relevant issues and prioritising management efforts. Marine Policy, 77: 104-110.

Halvorsen, K., Larsen, T., Sørdalen, T., Vøllestad, L., Knutsen, H., and Olsen, E. 2017a. Impact of harvesting cleaner fish for salmonid aquaculture assessed from replicated coastal marine protected areas. Marine Biology Research, 13: 359-369.

Halvorsen, K. T., Larsen, T., Browman, H. I., Durif, C., Aasen, N., Vøllestad, L. A., Cresci, A., et al. 2021. Movement patterns of temperate wrasses (Labridae) within a small marine protected area. Journal of fish biology, 99: 1513-1518.

Halvorsen, K. T., Sørdalen, T. K., Durif, C., Knutsen, H., Olsen, E. M., Skiftesvik, A. B., Rustand, T. E., et al. 2016. Male-biased sexual size dimorphism in the nest building corkwing wrasse (Symphodus melops): implications for a size regulated fishery. ICES Journal of Marine Science 73: 2586-2594.

Halvorsen, K. T., Sørdalen, T. K., Vøllestad, L. A., Skiftesvik, A. B., Espeland, S. H., and Olsen, E. M. 2017b. Sex- and size-selective harvesting of corkwing wrasse (Symphodus melops)—a cleaner fish used in salmonid aquaculture. ICES Journal of Marine Science 74: 660-669.

Harrison, Hugo B., Williamson, David H., Evans, Richard D., Almany, Glenn R., Thorrold, Simon R., Russ, Garry R., Feldheim, Kevin A., et al. 2012. Larval Export from Marine

Reserves and the Recruitment Benefit for Fish and Fisheries. Current Biology, 22: 1023-1028.

Harvey, E. S., Cappo, M., Butler, J. J., Hall, N., and Kendrick, G. A. 2007. Bait attraction affects the performance of remote underwater video stations in assessment of demersal fish community structure. Marine Ecology Progress Series, 350: 245-254.

Heck, K. L., Carruthers, T. J. B., Duarte, C. M., Hughes, A. R., Kendrick, G., Orth, R. J., and Williams, S. W. 2008. Trophic Transfers from Seagrass Meadows Subsidize Diverse Marine and Terrestrial Consumers. Ecosystems, 11: 1198-1210.

Heithaus, M. R., Frid, A., Wirsing, A. J., and Worm, B. 2008. Predicting ecological consequences of marine top predator declines. Trends in Ecology & Evolution, 23: 202-210.

Hilldén, N.-O. 1981. Territoriality and reproductive behaviour in the goldsinny, Ctenolabrus rupestris L. Behavioural Processes, 6: 207-221.

Hjort, J. 1914. Fluctations in the great fisheries of northern Europe viewed in the light of biological research. Rapports et Procès-Verbaux Des Réunions Du Conseil International Pour l'Exploration de la Mer 19: 1-228.

Hollins, J., Thambithurai, D., Koeck, B., Crespel, A., Bailey, D. M., Cooke, S. J., Lindström, J., et al. 2018. A physiological perspective on fisheries-induced evolution. Evolutionary Applications, 11: 561-576.

Hooper, D. U., Chapin Iii, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs, 75: 3-35.

Hutchings, J. 1996. Spatial and Temporal Variation in the Density of Northern Cod and a Review of Hypotheses of the Stock's Collapse. Canadian Journal of Fisheries and Aquatic Sciences 53: 943-962.

Hutchings, J. A. 2000. Collapse and recovery of marine fishes. Nature, 406: 882-885.

Hutchings, J. A. 2005. Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (Gadus morhua). Canadian Journal of Fisheries and Aquatic Sciences, 62: 824-832.

Hutchings, J. A. 2015. Thresholds for impaired species recovery. Proceedings of the Royal Society B: Biological Sciences, 282: 20150654.

Hutchings, J. A., Côté, I. M., Dodson, J. J., FlemingIan, A., Jennings, S., Mantua, N. J., Peterman, R. M., et al. 2012. Climate change, fisheries, and aquaculture: trends and consequences for Canadian marine biodiversity. Environmental Reviews 20: 220-311.

Immler, S., Mazzoldi, C., and Rasotto, M. B. 2004. From sneaker to parental male: change of reproductive traits in the black goby, Gobius niger (Teleostei, Gobiidae). Journal of Experimental Zoology, Part A: Ecological Genetics and Physiology 301: 177-185.

IPBES. 2019. Summary for Policymakers of the Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. 56.

Jackson, E., Rowden, A., Attrill, M., S.J, B., and B, J. 2001. The importance of seagrass beds as a habitat for fishery species Oceanography and marine biology, 39: 269-304.

Jackson, J. B. C. 2001. Historical Overfishing and the Recent Collapse of Coastal Ecosystems. Science, 293: 629-637.

Jakobsson, S., Borg, B., Haux, C., and Hyllner, S. J. 1999. An 11-ketotestosterone induced kidney-secreted protein: the nest building glue from male three-spined stickleback, Gasterosteus aculeatus. Fish Physiology and Biochemistry, 20: 79-85.

Jennings, S. 2000. Patterns and prediction of population recovery in marine reserves. Reviews in Fish Biology and Fisheries, 10: 209-231.

Johannessen, T., Dahl, E., Falkenhaug, T., and Naustvoll, L. J. 2012. Concurrent recruitment failure in gadoids and changes in the plankton community along the Norwegian Skagerrak coast after 2002. ICES Journal of Marine Science 69: 795-801.

Jorde, P., Knutsen, H., Espeland, S., and Stenseth, N. C. 2007. Spatial scale of genetic structuring in coastal cod Gadus morhua and geographic extent of local populations. Marine Ecology-progress Series 343: 229-237.

Julliard, R., Nils Chr, S., Gjøsæter, J., Lekve, K., Fromentin, J.-M., and Danielssen, D. S. 2001. Natural Mortality and Fishing Mortality in a Coastal Cod Population: A Release-Recapture Experiment. Ecological Applications, 11: 540-558.

Knutsen, H., Jorde, P. E., Blanco Gonzalez, E., Eigaard, O. R., Pereyra, R. T., Sannæs, H., Dahl, M., et al. 2015. Does population genetic structure support present management regulations of the northern shrimp (Pandalus borealis) in Skagerrak and the North Sea? ICES Journal of Marine Science 72: 863-871.

Knutsen, J., Kleiven, A., Olsen, E., Knutsen, H., Espeland, S., Sørdalen, T., Thorbjørnsen, S., et al. 2022. Lobster reserves as a management tool in coastal waters: Two decades of experience in Norway. Marine Policy, 136: 104908.

Kraufvelin, P., Svensson, F., Fredriksson, R., Bergström, L., Karlsson, M., Wennhage, H., Wikström, A., et al. 2017. Inventering och modellering av fisk- och kräftdjurssamhällen i Kosterhavets nationalpark.

Lasiak, T. A. 1984. Structural aspects of the surf-zone fish assemblage at King's Beach, Algoa Bay, South Africa: Long-term fluctuations. Estuarine, Coastal and Shelf Science, 18: 459-483.

Lasiak, T. A. 1986. Juveniles, food and the surf zone habitat: implications for teleost nursery areas. South African Journal of Zoology, 21: 51-56.

Legendre, P., and Birks, H. 2012. From Classical to Canonical Ordination. *In* Tracking Environmental Change Using Lake Sediments, pp. 201-248. Springer, The Netherlands.

Lekve, K., Stenseth, N. C., Gjøsæter, J., Fromentin, J.-M., and Gray, J. S. 1999. Spatio-temporal patterns in diversity of a fish assemblage along the Norwegian Skagerrak coast. Marine Ecology-progress Series, 178: 17-27.

Lester, S., Halpern, B., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B., Gaines, S., Airame, S., et al. 2009. Biological Effects Within No-Take Marine Reserves: A Global Synthesis. Marine Ecology-progress Series, 384: 33-46.

Loreau, M. 2010. Biodiversity and Ecosystem Functioning. *In* Populations to Ecosystems: Theoretical Foundations for a New Ecological Synthesis (MPB-46), pp. 56-78. Princeton University Press.

Lubchenco, J., Palumbi, S. R., Gaines, S. D., and Andelman, S. 2003. Plugging a hole in the ocean: The emerging science of marine reserves. Ecological Applications, 13: 3-7.

Lyashevska, O., and Farnsworth, K. D. 2012. How many dimensions of biodiversity do we need? Ecological Indicators, 18: 485-492.

Laamanen, M., Korpinen, S., Zweifel, U. L., and Andersen, J. H. 2017. Ecosystem health. *In* Biological Oceanography of the Baltic Sea, pp. 589-608. Ed. by P. Snoeijs-Leijonmalm, H. Schubert, and T. Radziejewska. Springer Netherlands, Dordrecht.

Magnhagen, C. 1990. Reproduction under predation risk in the sand goby, Pomatoschistus minutes, and the black goby, Gobius niger: the effect of age and longevity. Behavioral Ecology and Sociobiology, 26: 331-335.

Magurran, A. E. 2016. How ecosystems change. Science, 351: 448-449.

Magurran, A. E., Dornelas, M., Moyes, F., Gotelli, N. J., and McGill, B. 2015. Rapid biotic homogenization of marine fish assemblages. Nature Communications, 6: 8405.

McArdle, B. H., and Anderson, M. J. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology, 82: 290-297.

McKinnon, J., and Rundle, H. 2002. Speciation in nature: The threespine stickleback model systems. Trends in Ecology & Evolution, 17: 480-488.

Meager, J., Fernö, A., and Skjæraasen, J. 2018. The behavioural diversity of Atlantic cod: insights into variability within and between individuals. Reviews in Fish Biology and Fisheries, 28: 1-24.

Micheli, F., Halpern, B., Botsford, L., and Warner, R. 2004. Trajectories and Correlates of Community Change in No-Take Marine Reserves. Ecological Applications 14: 1709-1723.

Moland, E., Fernández-Chacón, A., Sørdalen, T. K., Villegas-Ríos, D., Thorbjørnsen, S. H., Halvorsen, K. T., Huserbråten, M., et al. 2021. Restoration of Abundance and Dynamics of Coastal Fish and Lobster Within Northern Marine Protected Areas Across Two Decades. Frontiers in Marine Science, 8.

Moland, E., Olsen, E. M., Knutsen, H., Garrigou, P., Espeland, S. H., Kleiven, A. R., André, C., et al. 2013. Lobster and cod benefit from small-scale northern marine protected areas: inference from an empirical before–after control-impact study. Proceedings of the Royal Society B: Biological Sciences, 280: 20122679.

Molloy, P., McLean, I., and Côté, I. 2009. Effects of marine reserve age on fish populations: A global meta-analysis. Journal of Applied Ecology, 46: 743-751.

Morgan, M., Pérez-Rodríguez, A., and Saborido-Rey, F. 2011. Does increased information about reproductive potential result in better prediction of recruitment? Canadian Journal of Fisheries and Aquatic Sciences, 68: 1361-1368.

Morris, E. K., Caruso, T., Buscot, F., Fischer, M., Hancock, C., Maier, T. S., Meiners, T., et al. 2014. Choosing and using diversity indices: insights for ecological applications from the German Biodiversity Exploratories. Ecology and Evolution, 4: 3514-3524.

Mulder, C. P. H., Bazeley-White, E., Dimitrakopoulos, P. G., Hector, A., Scherer-Lorenzen, M., and Schmid, B. 2004. Species evenness and productivity in experimental plant communities. Oikos, 107: 50-63.

Myers, R. A., Hutchings, J. A., and Barrowman, N. J. 1996. Hypotheses for the decline of cod in the North Atlantic. Marine Ecology Progress Series, 138: 293-308.

Norderhaug, K., Christie, H., Fosså , J. H., and Fredriksen, S. 2005. Norderhaug KM, Christie H, Fosså JH, Fredriksen S.. Fish-macrofauna interactions in a kelp (Laminaria hyperborea) forest. Journal of the Marine Biological Association of the United Kingdom, 85: 1279-1286.

Obst, M., Vicario, S., Lundin, K., Berggren, M., Karlsson, A., Haines, R., Williams, A., et al. 2018. Marine long-term biodiversity assessment suggests loss of rare species in the Skagerrak and Kattegat region. Marine Biodiversity, 48: 2165-2176.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P., et al. 2020. Vegan community ecology package version 2.5-7 November 2020.

Olsen, E., Carlson, S., Gjøsaeter, J., and Stenseth, N. C. 2009. Nine decades of decreasing phenotypic variability in Atlantic cod. Ecology Letters, 12: 622-631.

Olsen, E., Heupel, M., Simpfendorfer, C., and Moland, E. 2012. Harvest selection on Atlantic cod behavioral traits: Implications for spatial management. Ecology and Evolution, 2: 1549-1562.

Olsen, E., Knutsen, H., Gjøsæter, J., Jorde, P., Knutsen, J., and Stenseth, N. C. 2004a. Life-history variation among local populations of Atlantic cod from the Norwegian Skagerrak coast. Journal of Fish Biology 64: 1725-1730.

Olsen, E. M., Halvorsen, K. T., Larsen, T., and Kuparinen, A. 2019. Potential for managing life history diversity in a commercially exploited intermediate predator, the goldsinny wrasse (Ctenolabrus rupestris). ICES Journal of Marine Science 76: 410-417.

Olsen, E. M., Heino, M., Lilly, G. R., Morgan, M. J., Brattey, J., Ernande, B., and Dieckmann, U. 2004b. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. Nature, 428: 932-935.

Olsen, E. M., Knutsen, H., Gjøsæter, J., Jorde, P. E., Knutsen, J. A., and Stenseth, N. C. 2008. Small-scale biocomplexity in coastal Atlantic cod supporting a Darwinian perspective on fisheries management. Evolutionary Applications, 1: 524-533.

Olsen, E. M., Lilly, G. R., Heino, M., Morgan, M. J., Brattey, J., and Dieckmann, U. 2005. Assessing changes in age and size at maturation in collapsing populations of Atlantic cod (Gadus morhua). Canadian Journal of Fisheries and Aquatic Sciences, 62: 811-823.

Olsen, E. M., and Moland, E. 2011. Fitness landscape of Atlantic cod shaped by harvest selection and natural selection. Evolutionary Ecology, 25: 695-710.

Osenberg, C. W., Shima, J. S., Miller, S. L., and Stier, A. C. 2011. Ecology – Assessing effects of marine protected areas: confounding in space and possible solutions. pp. 143-167. Cambridge University Press.

Pandolfi, J. M., and Lovelock, C. E. 2014. Novelty Trumps Loss in Global Biodiversity. Science, 344: 266.

Pecuchet, L., Törnroos, A., and Lindegren, M. 2016. Patterns and drivers of fish community assembly in a large marine ecosystem. Marine Ecology Progress Series, 546: 239–248.

Peet, R. K. 1974. The Measurement of Species Diversity. Annual review of ecology and systematics, 5: 285-307.

Perry, D., Staveley, T. A. B., and Gullström, M. 2018. Habitat Connectivity of Fish in Temperate Shallow-Water Seascapes. Frontiers in Marine Science, 4: 5-20.

Pethon, P. 2019. Aschehougs store fiskebok, H. Aschehoug & Co, Oslo. 484 pp.

Pielou, E. C. 1969. An introduction to mathematical ecology, New York, USA, Wiley-Interscience. 286 pp.

Pihl, L., and Wennhage, H. 2002. Structure and diversity of fish assemblages on rocky and soft bottom shores on the Swedish west coast. Journal of fish biology, 61: 148-166.

Pikitch, E. K., Santora, C., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., Dayton, P., et al. 2004. Ecosystem-Based Fishery Management. Science, 305: 346.

Pillans, S., Pillans, R. D., and Possingham, H. P. 2007. The impact of marine reserves on nekton diversity and community composition in subtropical eastern Australia. Biological Conservation, 136: 455-469.

Pimm, S. L., Russell, G. J., Gittleman, J. L., and Brooks, T. M. 1995. The Future of Biodiversity. Science, 269: 347.

Pinheiro, J. C., Bates, D. J., DebRoy, S., and Sakar, D. 2012. The Nlme Package: Linear and Nonlinear Mixed Effects Models, R Version 3.

R Core Team 2021. R: A language and enviroment for statistical computing. R foundation for Statistical Computing, Vienna, Austria.

Rogers, L., A., Stige, L., C., Olsen, E., M., Knutsen, H., Chan, K.-S., and Stenseth, N. C. 2011. Climate and population density drive changes in cod body size throughout a century on the Norwegian coast. Proceedings of the National Academy of Sciences, 108: 1961-1966.

Rogers, L. A., Storvik, G. O., Knutsen, H., Olsen, E. M., and Stenseth, N. C. 2017. Fine-scale population dynamics in a marine fish species inferred from dynamic state-space models. Journal of Animal Ecology, 86: 888-898.

Rozas, L. P., and Odum, W. E. 1988. Occupation of submerged aquatic vegetation by fishes: testing the roles of food and refuge. Oecologia, 77: 101-106.

Russ, G. 2002. Yet Another Review of Marine Reserves as Reef Fishery Management Tools. *In* Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem, pp. 421-443. Ed. by P. Sale. Academic Press, San Diego.

Rönnbäck, P., Kautsky, N., Pihl, L., Troell, M., Söderqvist, T., and Wennhage, H. 2007. Ecosystem Goods and Services from Swedish Coastal Habitats: Identification, Valuation, and Implications of Ecosystem Shifts. Ambio, 36: 534-544.

Salvanes, A. G. V., and Nordeide, J. T. 1993. Dominating sublittoral fish species in a west Norwegian fjord and their trophic links to cod (Gadus morhua L.). Sarsia, 78: 221-234.

Sayer, M. D. J. 1999. Duration of refuge residence by goldsinny, Ctenolabrus rupestris. Journal of the Marine Biological Association of the United Kingdom, 79: 571-572.

Sayer, M. D. J., Gibson, R. N., and Atkinson, R. J. A. 1995. Growth, diet and condition of goldsinny on the west coast of Scotland. Journal of Fish Biology 46: 317-340.

Schückel, S., Sell, A. F., Kihara, T. C., Koeppen, A., Kröncke, I., and Reiss, H. 2013. Meiofauna as food source for small-sized demersal fish in the southern North Sea. Helgoland Marine Research, 67: 203-218.

Shannon, C. E. 1948. A mathematical theory of communication. The Bell System Technical Journal, 27: 379-423.

Sheaves, M., Baker, R., and Johnston, R. 2006. Marine nurseries and effective juvenile habitats: An alternative view. Marine Ecology-progress Series 318: 303-306.

Shepherd, S. A., Brook, J. B., and Xiao, Y. 2010. Environmental and fishing effects on the abundance, size and sex ratio of the blue-throated wrasse, Notolabrus tetricus, on South Australian coastal reefs. Fisheries Management and Ecology, 17: 209-220.

Simpson, E. H. 1949. Measurement of Diversity. Nature, 163: 688-688.

Skiftesvik, A. B., Durif, C. M. F., Bjelland, R. M., and Browman, H. I. 2015. Distribution and habitat preferences of five species of wrasse (Family Labridae) in a Norwegian fjord. ICES journal of marine science, 72: 890-899.

Sokal, M. A., Hall, R. I., and Wolfe, B. B. 2008. Relationships between hydrological and limnological conditions in lakes of the Slave River Delta (NWT, Canada) and quantification of their roles on sedimentary diatom assemblages. Journal of Paleolimnology, 39: 533-550.

Sokołowska, E., and Kulczykowska, E. 2006. Annual reproductive cycle in two free living populations of three-spined stickleback (Gasterosteus aculeatus L.): Patterns of ovarian and testicular development. Oceanologia, 48: 103-124.

Soykan, C. U., and Lewison, R. L. 2015. Using community-level metrics to monitor the effects of marine protected areas on biodiversity. Conservation Biology, 29: 775-783.

Stobart, B., Warwick, R., González, C., Mallol, S., Díaz, D., Reñones, O., and Goñi, R. 2009. Long-term and spillover effects of a marine protected area on an exploited fish community. Marine Ecology Progress Series, 384: 47-60.

Svedäng, H. 2003. The inshore demersal fish community on the Swedish Skagerrak coast: Regulation by recruitment from offshore sources. ICES Journal of Marine Science 60: 23-31.

Symondson, W. O. C., Sunderland, K. D., and Greenstone, M. H. 2002. Can Generalist Predators be Effective Biocontrol Agents? Annual Review of Entomology, 47: 561-594.

Sætre, R., Aure, J., and Danielssen, D. S. 2003. Long-term hydrographic variability patterns off the Norwegian coast and in the Skagerrak. ICES Marine Science Symposia 219: 150-159.

Sørdalen, T. K., Halvorsen, K. T., Vøllestad, L. A., Moland, E., and Olsen, E. M. 2020. Marine protected areas rescue a sexually selected trait in European lobster. Evolutionary Applications, 13: 2222-2233.

Takashina, N., Mougi, A., and Iwasa, Y. 2012. Paradox of marine protected areas: suppression of fishing may cause species loss. Population Ecology, 54: 475-485.

Taylor, B., and McIlwain, J. 2010. Beyond abundance and biomass: Effects of marine protected areas on the demography of a highly exploited reef fish. Marine Ecology Progress Series, 411: 243-258.

Tetreault, I., and Ambrose, R. F. 2007. Temperatre marine reserves enhance targeted but not untargeted fishes in multiple no- take MPAs. Ecological Applications, 17: 2251-2267.

Tveite, S. 1971. Fluctuations in year-class strength of cod and pollack in southeastern Norwegian coastal waters during 1920-1969. Fiskeridirektoratets havforskningsinstitutt.

Tveite, S. 1984. 0-group cod investigations on the Norwegian Skagerrak coast. In: The propagation of cod Gadus morhua L.: an international symposium, Arendal, 14 - 17 June 1983. Havforskningsinstituttet.

Uglem, I., Rosenqvist, G., and Wasslavik, H. S. 2000. Phenotypic variation between dimorphic males in corkwing wrasse. Journal of Fish Biology 57: 1-14.

Underwood, A. J. 1992. Beyond BACI: the detection of environmental impacts on populations in the real, but variable, world. Journal of Experimental Marine Biology and Ecology 161: 145-178.

Underwood, A. J. 1994. On Beyond BACI: Sampling Designs that Might Reliably Detect Environmental Disturbances. Ecological Applications, 4: 3-15.

Vesey, G., and Langford, T. 2006. The biology of the black goby, Gobius niger L. in an English south-coast bay. Journal of Fish Biology 27: 417-429.

Villegas-Ríos, D., Moland, E., and Olsen, E. 2016. Potential of contemporary evolution to erode fishery benefits from marine reserves. Fish and Fisheries 18: 571-577.

Vytenis, G., and Joseph, A. B. 1993. Substrate Selection by Juvenile Atlantic Cod (Gadus morhua): Effects of Predation Risk. Oecologia, 93: 31-37.

Vaas, K. F., Vlasblom, A. G., and De Koeijer, P. 1975. Studies on the black Goby (Gobius Niger, Gobiidae, pisces) in the veerse meer, SW Netherlands. Netherlands Journal of Sea Research, 9: 56-68.

Warton, D. I., Wright, S. T., and Wang, Y. 2012. Distance-based multivariate analyses confound location and dispersion effects. Methods in Ecology and Evolution, 3: 89-101.

Wennhage, H., and Pihl, L. 2002. Fish feeding guilds in shallow rocky and soft bottom areas on the Swedish west coast. Journal of Fish Biology 61: 207-228.

White, J. W., Botsford, L., Hastings, A., Baskett, M., Kaplan, D., Barnett, L., and White, C. 2013. Transient responses of fished populations to marine reserve establishment. Conservation Letters 6: 180-191.

Wickham, H. 2016. ggplot2: Elegant Graphics for Data Analysis, Springer, New York.

Wickham, H., François, R., Henry, L., and Müller, K. 2022. dplyr: A Grammar of Data Manipulation.

Willis, T., and Anderson, M. 2003. Structure of cryptic reef fish assemblages: Relationships with habitat characteristics and predator density. Marine Ecology Progress Series, 257: 209-221.

Wootton, J. T., and Oemke, M. P. 1992. Latitudinal differences in fish community trophic structure, and the role of fish herbivory in a Costa Rican stream. Environmental Biology of Fishes 35: 311-319.

Wootton, R. J. 1973. Fecundity of the three-spined stickleback, Gasterosteus aculeatus (L.). Journal of Fish Biology 5: 683-688.

Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., Jackson, J. B. C., et al. 2006. Impacts of Biodiversity Loss on Ocean Ecosystem Services. Science, 314: 787.

Zedler, J. B., Callaway, J. C., and Sullivan, G. 2001. Declining Biodiversity: Why Species Matter and How Their Functions Might Be Restored in Californian Tidal Marshes. BioScience, 51: 1005-1017.

Zhou, S., Smith, A. D. M., Punt, A. E., Richardson, A. J., Gibbs, M., Fulton, E. A., Pascoe, S., et al. 2010. Ecosystem-based fisheries management requires a change to the selective fishing philosophy. Proceedings of the National Academy of Sciences, 107: 9485.

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A., and Smith, G. M. 2009. Mixed Effects Models and Extensions in Ecology With R.

Zuur, A. F., and Ieno, E. N. 2016. A protocol for conducting and presenting results of regression-type analyses. Methods in Ecology and Evolution, 7: 636-645.

Zuur, A. F., Ieno, E. N., and Elphick, C. S. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution, 1: 3-14.

Östman, Ö., Eklöf, J., Eriksson, B. K., Olsson, J., Moksnes, P.-O., and Bergström, U. 2016. Top-down control as important as nutrient enrichment for eutrophication effects in North Atlantic coastal ecosystems. Journal of Applied Ecology, 53: 1138-1147.

Appendices

Appendix A

Table A-1: Stations sampled each year in the study period (2011-2021). Table contains station name, area (MPA/control), coordinates, vegetation type and visibility (1: very bad, 2: bad, 3: moderate, 4: good, 5: very good, 9: not observed).

Year	Area	Station	Latitude N	Longitude E	Vegetation	Visibility
2011	MPA	Furøyholmen	58.600239	8.950063	Eelgrass	Very bad
2011	MPA	Fjerdingskjær	58.605806	8.950062	Eelgrass	Very good
2011	Control	81	58.614314	9.023106	Kelp	Very bad
2011	Control	82	58.614283	9.029033	Eelgrass	Very bad
2011	Control	83	58.620285	9.056222	Kelp	Very bad
2011	Control	85	58.623033	9.058217	Eelgrass	Very bad
2011	Control	86	58.625355	9.107110	Kelp	Bad
2012	MPA	Furøyholmen	58.600239	8.950063	Eelgrass	Moderate
2012	MPA	Fjerdingskjær	58.605806	8.950062	Eelgrass	Good
2012	MPA	Langesand	58.595644	8.944010	Kelp	Moderate
2012	Control	81	58.614314	9.023106	Kelp	Moderate
2012	Control	82	58.614283	9.029033	Eelgrass	Good
2012	Control	83	58.620285	9.056222	Kelp	Moderate
2012	Control	85	58.623033	9.058217	Eelgrass	Moderate
2012	Control	86	58.625355	9.107110	Kelp	Moderate
2013	MPA	Furøyholmen	58.600239	8.950063	Eelgrass	Good
2013	MPA	Fjerdingskjær	58.605806	8.950062	Eelgrass	Moderate
2013	MPA	Langesand	58.595644	8.944010	Kelp	Moderate
2013	Control	81	58.614314	9.023106	Kelp	Moderate
2013	Control	82	58.614283	9.029033	Eelgrass	-
2013	Control	83	58.620285	9.056222	Kelp	Good
2013	Control	85	58.623033	9.058217	Eelgrass	Good
2013	Control	86	58.625355	9.107110	Kelp	-
2014	MPA	Furøyholmen	58.600239	8.950063	Eelgrass	Moderate
2014	MPA	Fjerdingskjær	58.605806	8.950062	Eelgrass	Moderate
2014	MPA	Langesand	58.595644	8.944010	Kelp	Moderate
2014	Control	81	58.614314	9.023106	Kelp	Bad
2014	Control	82	58.614283	9.029033	Eelgrass	Good
2014	Control	83	58.620285	9.056222	Kelp	Moderate
2014	Control	85	58.623033	9.058217	Eelgrass	Good
2014	Control	86	58.625355	9.107110	Kelp	Good
2015	MPA	Furøyholmen	58.600239	8.950063	Eelgrass	Very bad
2015	MPA	Fjerdingskjær	58.605806	8.950062	Eelgrass	Very bad
2015	MPA	Langesand	58.595644	8.944010	Kelp	Very bad
2015	Control	81	58.614314	9.023106	Kelp	Very bad
2015	Control	82	58.614283	9.029033	Eelgrass	Very bad
2015	Control	83	58.620285	9.056222	Kelp	Moderate
2015	Control	85	58.623033	9.058217	Eelgrass	Moderate
2015	Control	86	58.625355	9.107110	Kelp	Bad
2016	MPA	Furøyholmen	58.600239	8.950063	Eelgrass	Good
2016	MPA	Fjerdingskjær	58.605806	8.950062	Eelgrass	Good
2016	MPA	Langesand	58.595644	8.944010	Kelp	Good
2016	Control	81	58.614314	9.023106	Kelp	Moderate
2016	Control	82	58.614283	9.029033	Eelgrass	Good
2016	Control	83	58.620285	9.056222	Kelp	Good
2016	Control	85	58.623033	9.058217	Eelgrass	Good
2016	Control	86	58.625355	9.107110	Kelp	Good
2017	MPA	Furøyholmen	58.600239	8.950063	Eelgrass	Moderate

2017	MPA	Fjerdingskjær	58.605806	8.950062	Eelgrass	Bad
2017	MPA	Langesand	58.595644	8.944010	Kelp	Bad
2017	Control	81	58.614314	9.023106	Kelp	Moderate
2017	Control	82	58.614283	9.029033	Eelgrass	Moderate
2017	Control	83	58.620285	9.056222	Kelp	Bad
2017	Control	85	58.623033	9.058217	Eelgrass	Good
2017	Control	86	58.625355	9.107110	Kelp	Moderate
2018	MPA	Furøyholmen	58.600239	8.950063	Eelgrass	Good
2018	MPA	Fjerdingskjær	58.605806	8.950062	Eelgrass	Moderate
2018	Control	81	58.614314	9.023106	Kelp	Moderate
2018	Control	82	58.614283	9.029033	Eelgrass	Moderate
2018	Control	83	58.620285	9.056222	Kelp	Moderate
2018	Control	85	58.623033	9.058217	Eelgrass	Moderate
2018	Control	86	58.625355	9.107110	Kelp	Moderate
2019	MPA	Furøyholmen	58.600239	8.950063	Eelgrass	Good
2019	MPA	Fjerdingskjær	58.605806	8.950062	Eelgrass	Moderate
2019	MPA	Langesand	58.595644	8.944010	Kelp	Moderate
2019	Control	81	58.614314	9.023106	Kelp	Bad
2019	Control	82	58.614283	9.029033	Eelgrass	Good
2019	Control	83	58.620285	9.056222	Kelp	Moderate
2019	Control	85	58.623033	9.058217	Eelgrass	Good
2019	Control	86	58.625355	9.107110	Kelp	Moderate
2020	MPA	Furøyholmen	58.600239	8.950063	Eelgrass	Moderate
2020	MPA	Fjerdingskjær	58.605806	8.950062	Eelgrass	Moderate
2020	MPA	Langesand	58.595644	8.944010	Kelp	Good
2020	Control	81	58.614314	9.023106	Kelp	Good
2020	Control	82	58.614283	9.029033	Eelgrass	Good
2020	Control	83	58.620285	9.056222	Kelp	Good
2020	Control	85	58.623033	9.058217	Eelgrass	Good
2020	Control	86	58.625355	9.107110	Kelp	Good
2021	MPA	Furøyholmen	58.600239	8.950063	Eelgrass	Good
2021	MPA	Fjerdingskjær	58.605806	8.950062	Eelgrass	Good
2021	MPA	Langesand	58.595644	8.944010	Kelp	Moderate
2021	Control	81	58.614314	9.023106	Kelp	Moderate
2021	Control	82	58.614283	9.029033	Eelgrass	Good
2021	Control	83	58.620285	9.056222	Kelp	Moderate
2021	Control	85	58.623033	9.058217	Eelgrass	Good
2021	Control	86	58.625355	9.107110	Kelp	Moderate

Appendix B

Table B-1: R^2-values comparing catch composition between stations in control area and MPA using both ANOSIM and ADONIS. R^2 indicates proportion of variance explained by variables in model/independent variable.

Period	**R^2 values for ANOSIM/ADONIS comparing mpa with control area**	
	ADONIS	**ANOSIM**
Before (2011)	0.147	0.036
Early (2013-2014)	0.107	0.061
Late (2015-2021)	0.052	0.008

Appendix C

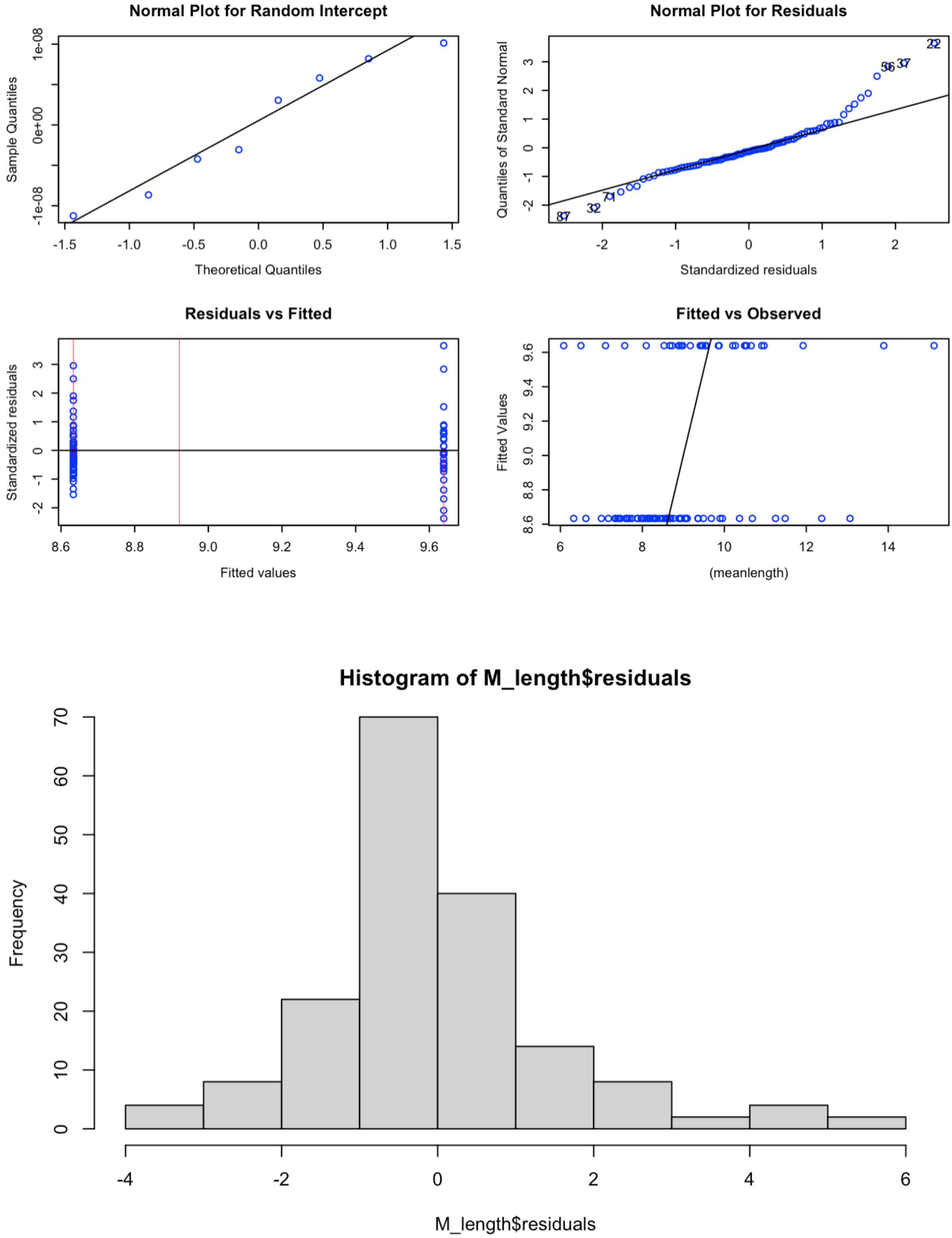

Figure C-1: Diagnostic plots for linear mixed model on total length of all species before log transformation of body length (cm).

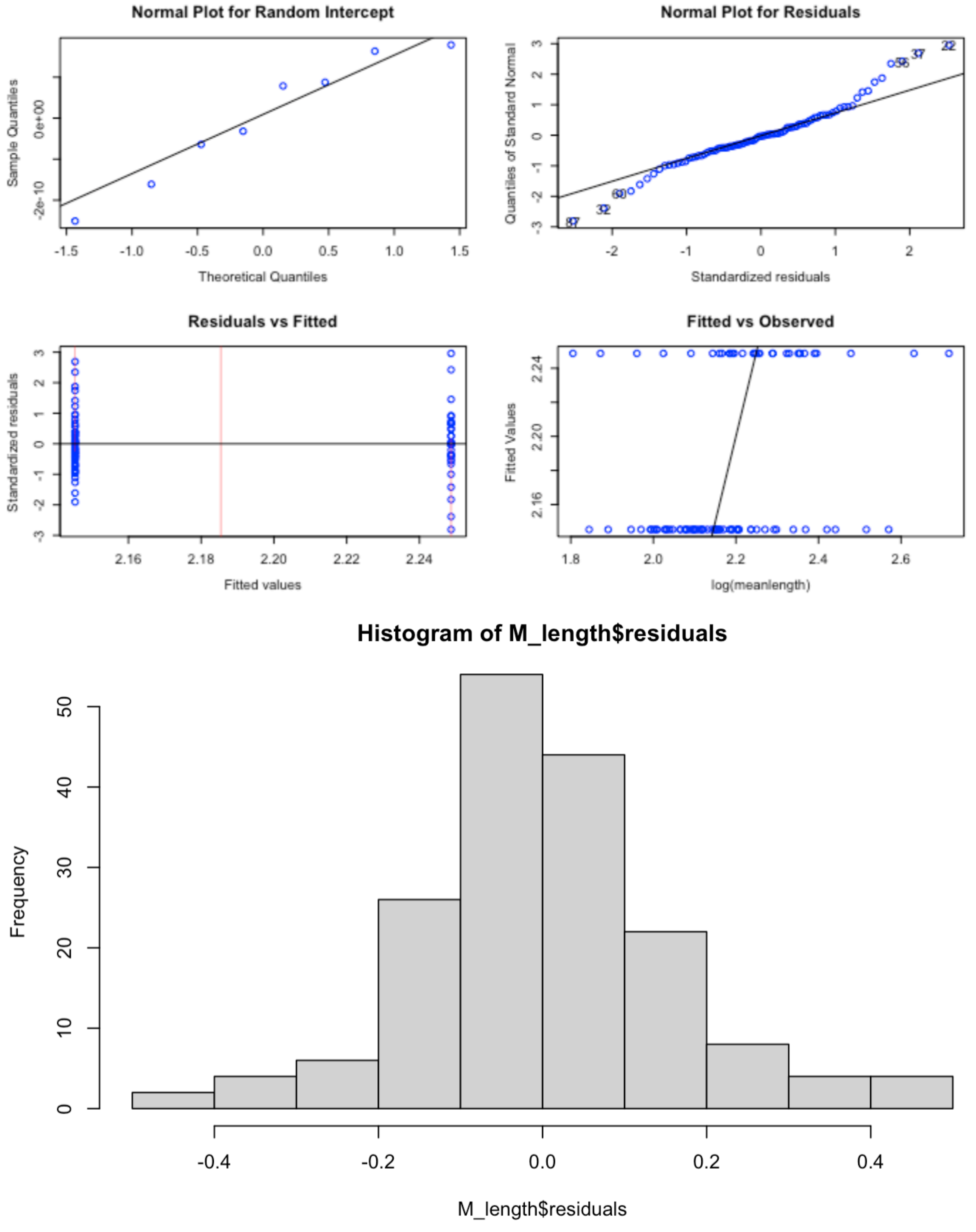

Figure C-2: Diagnostic plots for linear mixed model on total length of all species after log transformation of body length (cm).

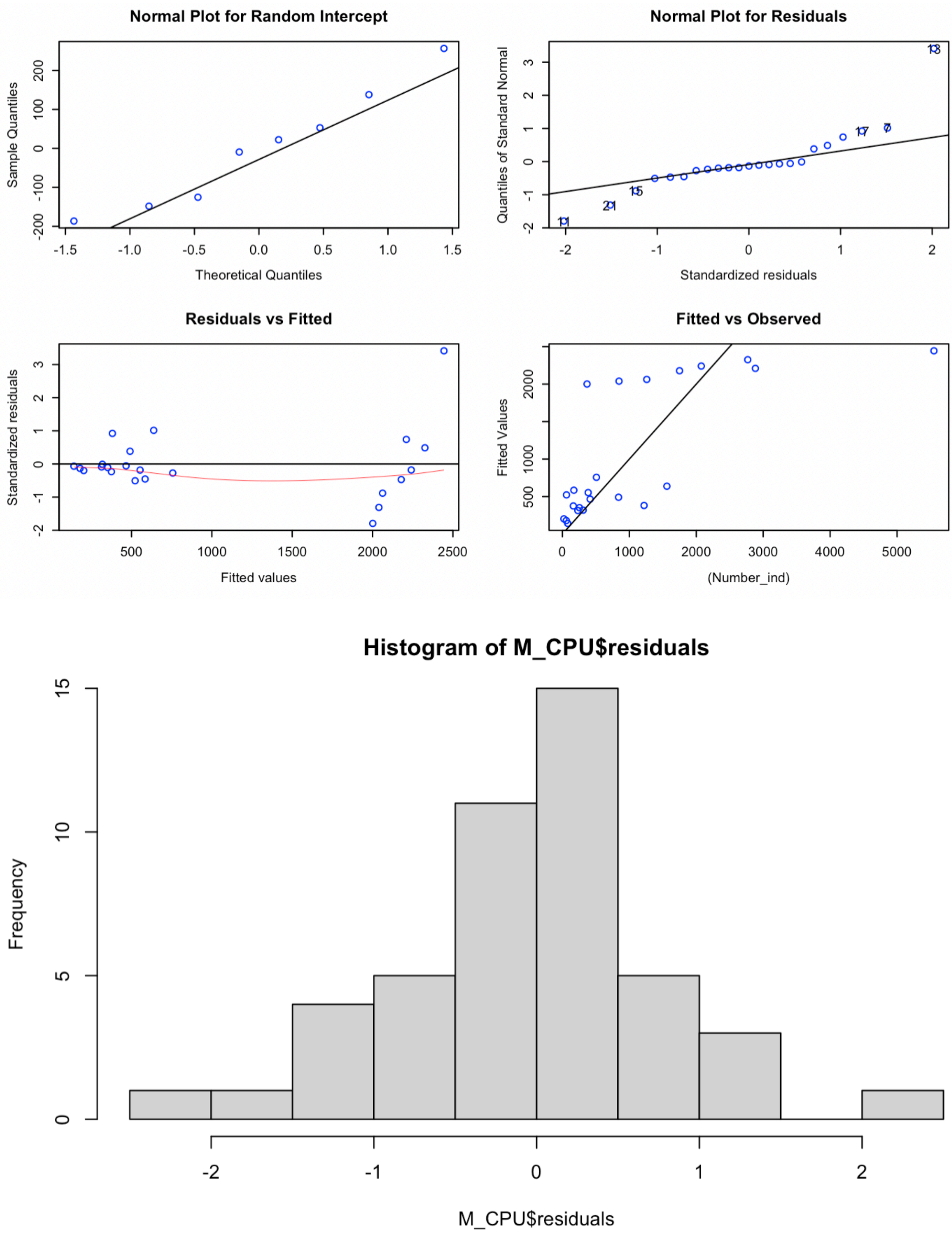

Figure C-3: Diagnostic plots for linear mixed models on CPUE data of all species before log transformation.