Can small-scale northern marine protected areas work as management tools for a mobile temperate fish species? A before-after control-impact study of coastal Atlantic cod (Gadus morhua)

University College of Southeast Norway
Faculty of Arts and Sciences
Institute of Environmental and Health studies
PO Box 235
NO-3603 Kongsberg, Norway
http://www.usn.no
© 2016 Kristine Olaussen

This thesis is worth 60 study points

## Summary

The recruitment and spawning stock biomass of Atlantic cod (Gadus morhua) along the Skagerrak coast have been extremely low the last years and overfishing seems to be one of the main factors for this decrease. Marine protected areas may promote recovery of exploited populations within their boundaries and have received increasingly attention as fisheries and conservation tools. However, few studies are conducted in temperate areas and there is a lack of information form before MPA establishment in many studies, which will limit the interpretation of the results. In this study, we investigated MPA effects on cod using a before-after control-impact (BACI) approach. When protecting a portion of an exploited stock, it is expected that density of targeted species within protected areas will increase. Significantly higher mean size/age, and significantly higher production of propagules of target species are also major expectations. Therefore, body size and cod density was measured in three partly protected areas and one no-take reserve implemented in the municipality of Tvedestrand in 2012. We also collected data from control areas with varying distances from the MPAs. By 2015, cod inside the no-take reserve and two of the partly protected areas was on average 10 cm longer than in any of the control areas. An increase in cod density (measured in catch per unit effort (CPUE)) inside the MPAs compared to controls, was only significant in one of the partly protected areas. Potential causes for these differences are discussed in the thesis. For Marine protected areas to work as a management tool they should in the long term compensate for the loss of fishing area. If they not fully compensates for this loss, they will still act as a reserve of spawning stock from which to start a recovery. After three years of protection, the effects of protection on cod populations are not clear and it is highly recommended to continue this research as the signs of recovery may take years to observe.

## Contents

Summary ..... 3
Preface ..... 5

1. Introduction ..... 6
2. Methods ..... 10
2.1 Study species ..... 10
2.2 Study area ..... 11
2.3 Data collection ..... 13
2.4 Data analysis ..... 15
3. Results ..... 18
3.1 Fyke nets ..... 18
3.2 Large cod traps ..... 25
4. Discussion ..... 28
5. Conclusion ..... 32

## Preface

This thesis is part of my Master education at the Department of Environmental and Health studies (INHM) at the University College of Southeast Norway (HSN) in Bø, Telemark. The thesis is a collaboration between HSN and the Institute of Marine Research (IMR) in Flødevigen, Arendal. The fieldwork started in April 2015 and was conducted in the municipality of Arendal and Tvedestrand.

I am grateful for getting the opportunity to collaborate with IMR and to learn more about marine research and fieldwork methods. I would like to thank Sebastian Bosgraaf, Hanne Sannæs and the rest of the staff in Flødevigen for making me welcome and helping me with my fieldwork. A special thank goes to my supervisor Sigurd Heiberg Espeland for sharing his knowledge, and making this thesis possible. I would also thank my supervisor at HSN, Stefanie Reinhardt for reading through the thesis, correcting mistakes and for valuable comments.

Thanks to Patricia Graf for help with the statistical program R.

Bø, Telemark, 13.05.16

Kristine Olaussen

## 1. Introduction

Marine ecosystems around the world face an increasing number of threats, including overexploitation of living marine resources, habitat degradation and destruction, climate changes, and pollution (Halpern et al. 2008; Game et al. 2009; Maxwell et al. 2013). According to the living planet index there has been a $39 \%$ decline for marine vertebrates in the last 40 years (McRae et al. 2014). Marine species that are important food for humans are often intensively harvested (Cook et al. 1997). Throughout history, the Atlantic cod (Gadus morhua) has been the most important fish species on the Skagerrak coast. The cod stock in Skagerrak includes both cod from Denmark and fjords systems along the Swedish and Norwegian coast and is managed as a separate unit of the North Sea cod (ICES 2014a). The recruitment and spawning stock biomass have been extremely low the last years and overfishing, availability of food, predation and cannibalism has been reported as the most important factors (ICES 2014b). The Institute of Marine Research (IMR) has reported a heavy decrease in the coastal cod stock in the Skagerrak region. From 1999 to 2010 there has been a 43\% decline for age 0 juveniles and 85\% for age 1 juveniles compared with the long-term mean (1919-2010) (fig.1) (Espeland and Knutsen 2014). Svedäng (2003) also reported that several coastal areas in Skagerrak have been depleted of adult cod over the last decade. Olsen and Moland (2011) found that $50 \%$ of potentially mature cod were removed by fishing each year, suggesting that the fishing pressure is very high. The mortality rate on the Skagerrak coastal cod is comparable to the rate on Canadian cod stocks prior to the major collapses in the late 1980s - early 1990s (Hutchings and Myers 1994). In 2009 the fisheries authorities increased the minimum size from 30 to 40 cm and introduced a minimum mesh size for bottom nets of 63 mm . Many of these regulations is directed at commercial fishing, but on the Skagerrak coastline it is documented that $72 \%$ of harvested coastal Atlantic cod is caught by recreational fishers using a variety of different gear (Kleiven et al. 2016). From 2010, these regulations also included recreational fishing (Forskrift om utøvelse av fisket i sjøen 2005). Despite these regulations, the Atlantic cod population is still decreasing. Ecosystem-based management approaches such as introducing a maximum size limit or establishing marine protected areas, may be more effective management tools than traditional management (Conover and Munch 2002).


Figure 1: The amount of juveniles ( 0 - group cod (upper)) and adult cod ( $1+$ - group cod (lowest)) from a long-term beach sein series conducted along the Skagerrak coast by IMR. Blue points represents the average numbers of individuals based on all hauls in Skagerrak a given year. The red line is a floating five-year average, the black horizontal line is the long-term average based on the blue points. The green line illustrates 10\% of the long-term average (Espeland and Knutsen 2014).

In 2012, the Ministry for Fisheries and Coastal affairs proclaimed the establishment of four marine protected areas and one no-take reserve in the municipality of Tvedestrand, southern Norway. This is the first and only no-take reserve in Norway. Marine protected areas (MPAs) are geographically distinct zones of the marine environment in which various of extractive activities are excluded. (Pauly et al. 2002). No-take marine reserves are an important subset of MPAs, and in these reserves all forms of extraction, particularly fishing, are banned permanently, except if necessary for monitoring or research (Roberts and Polunin 1991; Dayton et al. 2000; Gell and Roberts 2002). This form of management has been advocated as a solution to many important problems within the marine environment (Dayton et al. 2000; Gell and Roberts 2002), such as biodiversity loss (Jackson et al. 2001) and overexploitation (Pauly et al. 1998, 2002; Hutchings 2000; Jackson et al. 2001).

As of February 2016, marine protected areas constitute 2,07\% of the global ocean, and only $1,03 \%$ of the ocean is protected in no-take reserves (Marine Conservation Institute 2016). In order to meet global marine conservation targets, protecting marine
ecosystems will be critical. Aichi target 11 states that by 2020, 10\% of costal and marine areas will be conserved through effectively managed, economically representative and well-connected systems of protected areas (Convention on Biological Diversity 2010).
Numbers of studies have documented how population densities and biomass, organism size, species richness, reproductive potential, and/or community structure are affected by reserve protection (Halpern and Warner 2002; Palumbi 2002; Gell and Roberts 2003; Halpern 2003). Ideally, marine reserves will maintain segments of populations and ecosystems in natural states. When protecting a portion of an exploited stock, it is expected that the biomass of targeted species within protected areas will rebuild to approach unfished densities (Willis et al. 2003). Significantly higher mean size/age, and significantly higher production of propagules of target species are also major expectations (Russ 2002). Density-dependent processes might then result in net export of adult fishes from the reserve to fished areas, termed the "spillover effect". This may occur either by passive diffusion or by displacement of individuals caused by space limitation (Willis et al. 2003). The above mentioned effects may also result in net export of propagules which will enhance supply of recruits to fished areas, known as the "recruitment effect" (Russ 2002).

Using marine protected areas for fisheries management is controversial. Critics argue that reserve areas in some cases are chosen because they have good quality habitats and then there is a possibility that differences observed are habitat rater then protection effects (Gell and Roberts 2003). Many authors have also suggested that temperate reserves might result in smaller or no changes at all, compared to tropical reserves. The main reason for this assumption is that exploited species in temperate regions tend to be more mobile (Shipp 2003; Kaiser 2004) and, temperate species tend to have longer larvae durations and thus greater larvae dispersal potential and gene flow than tropical species (Laurel and Bradbury 2006; O’Connor et al. 2006). It is also suggested that small MPAs are less effective at protecting exploited populations than large ones, and that reserves in temperate systems may need to be larger than tropical reserves to achieve comparable results. In several meta-analysis it was found that the level of recovery of fished populations is not correlated with the size of the MPA (Côte et al 2001; Halpern 2003; Claudet et al. 2008). In addition, fish capable of moving long distances with presumably wide home ranges, are not expected to benefit from the protection (Palumbi 2004; McCook et al. 2010). However, in many fish species a
proportion of the population might be sedentary, whilst others undertake significant movements. This allows the sedentary ones to build up biomass inside the reserve, while the mobile individuals ensure that benefits are exported outside the reserve (Claudet et al. 2010). Even for species with very large scale of movements, reserves can offer protection at vulnerable stages (Roberts and Sargant 2002). The Atlantic cod (Gadus morhua) is a temperate and highly mobile species and recent studies revealed that this species home to specific coastal spawning sites (Begg and Marteinsdottir 2000; Robichaud and Rose 2001). On the Skagerrak coast, it is proven that the coastal cod is genetically structured into local populations on a scale of 30 km or less (Jorde et al. 2007; Knutsen et al. 2003). Behavioural studies also demonstrate that cod in this area have a high degree of site fidelity and restricted home ranges, stretching a few tens of kilometers along the Skagerrak coast (Espeland et.al. 2008; Knutsen et.al 2011), and would therefore benefit from reserve protection.

As of today, only few studies are conducted regarding response to protection for Atlantic cod. Murawski et al. (2000) reported a slightly increase in spawning-stock biomass after protection, primarily attributed to increased survival of adults, combined with relatively high rates of somatic growth. Moland et al. (2013) were the first to report that cod benefit from small-scale northern MPAs in a pilot study on the Norwegian Skagerrak coast. The MPAs in this study did not include a no-take reserve as in our study and therefore only gave partly protection for cod. However, they reported that after four years of partly protection, cod density and body size had increased compared to control areas.

In this study, a BACI (before-after, control-impact) experimental design is used to assess the effect of MPAs on Atlantic cod on the Norwegian Skagerrak coast. The effects of the marine protected areas are evaluated by addressing three main questions: 1) Are cod populations increasing inside the MPAs compared to fished areas (measured in catch per unit effort (CPUE))?. 2) Is protection from fishing leading to the occurrence of larger fishes inside the MPAs compared to control areas? 3) Is it possible to estimate an effect on CPUE and size of the fish from where it is caught relatively to the border of the MPAs?

## 2. Methods

### 2.1 Study species

The Atlantic cod (Gadus morhua) (fig.2) has a wide North Atlantic distribution and is a highly fecund batch spawner, with multiple spawning events during February-April (Kjesbu 1989). After two to three weeks the eggs hatches and the age 0 juveniles settle in shallow water nursery areas in early summer (April-June) (Dhal and Dannevig 1906; Knutsen et al. 2007). The duration of egg stages, larvae stages and growth of larvae and juveniles is highly affected by water temperature (Pepin et al. 1997). In the Skagerrak region, cod grows about 10-15 cm per year and reach maturity at an age of two to three years with a body length of $30-50 \mathrm{~cm}$ (Olsen et al. 2008). Atlantic cod may attain an age of more than 20 years, with a body length of more than 130 cm and weigh more than 30 kg (Hutchings 1999). However, these large individuals are rarely seen, most likely due to longevity overfishing (Beamish et al. 2006).


Figure 2: Atlantic cod (Gadus morhua). Photo: Øystein Paulsen, IMR.

Studies has proven that cod on the Skagerrak coast is genetically structured into local populations (Knutsen et al. 2003; Knutsen et al. 2011), separated from each other by as little as 30 km (Jorde 2007). Age at $50 \%$ maturity in these small-scale populations varies from two to four years, with a body length varying from 35-60 cm (Olsen et al. 2004). The sheltered inshore basins in this fjord system is protected from coastal currents and have low water circulation. This, combined with egg characteristics and site fidelity of older fish, is likely mechanisms contributing to this fine-scale population structure (Espeland et al. 2008; Ciannelli et al. 2010). However, it is observed a low
level of genetic differentiation among cod populations in the Skagerrak-North Sea system, which can be explained by egg and larval drift from the North Sea, rather than adult dispersal (Stenseth et al. 2006). Thus, a segment of the North Sea cod stock inhabits the skerries outside the fjords every year (Knutsen et al. 2011). Natural predators for the Atlantic cod is Harbor seals (Phoca vitulina L.) and great cormorants (Phalacrocorax carbo L.), but it is not known to what extent these species affects the cod population on the Skagerrak coast (Olsen and Moland 2011).

### 2.2 Study area

This study was conducted in two different fjord systems (Tvedestrandsfjorden and Sømskilen) on the Skagerrak coast in southern Norway. This coastline is rugged, with many islands and fjords creating suitable habitats for coastal Atlantic cod. The area is also a popular tourist destination and there is a lot of recreational fishing activity along the coastline (Julliard et al. 2001). The Tvedestrand fjord consists of several sills and basins, and extends eight kilometers inland from the coastline (Ciannelli et al. 2010). The outer southern areas is shallow, while the inner northern area is deeper, with a maximum depth of 93 meters. Variation in habitat, such as eel grass beds, mud flats and kelp forest (Knutsen et al. 2010), contributes to several inshore spawning and nursery sites for coastal cod (Knutsen et al. 2007). However, especially the inner part of Tvedestrandsfjorden has high contamination of organic matter, which causes low oxygen levels at depths of 30-40 meters. At 60-70 meters, there is high concentrations of hydrogen sulfide and the sediments contains quite high loads of pollutants, especially PCB and TBT (Kroglund et al. 2003).

This study is part of the project active management of marine values in the coastal zone at the Institute of Marine Research Flødevigen, started in 2009. From 2009-2012 the main focus for the project was to map the seabed, collect basic documentation of biological value and get an overview of activities along the coast. In fall 2010, conflict analysis was conducted together with meetings with both recreational and commercial fishers, to discuss potential MPA areas based on the conflict analysis. In 2011, the project proposed five MPA areas with two no-take areas in the municipality of Tvedestrand (Bodvin et al. 2012). In 2012, the Ministry for Fisheries and Coastal
affairs proclaimed the establishment of four marine protected areas and one no-take reserve in the municipality of Tvedestrand (fig.3). These are small protected areas with a no-take area of $1,5 \mathrm{~km}^{2}$, and the rest of the MPAs together constitute $7,4 \mathrm{~km}^{2}$, witch in total equals $14 \%$ of the sea area in the municipality of Tvedestrand. In the no-take reserve only research sampling is allowed, whereas in the remaining MPAs, hook and line fishing of cod are allowed (Forskrift om bevaringssoner i Tvedestrand 2012). As controls, the area just outside the MPAs were used, but also an area approximately 30 km from the MPAs. This fjord system (Sømskilen) is a semi-sheltered basin with numerus small islands. Sømskilen has a maximum depth of approximately 30 m and there are several large eelgrass beds in the shallow ( $2-7 \mathrm{~m}$ depth) areas (Espeland et al. 2010). The minimum legal size, both for commercial harvest and recreational harvest in these regions, is 40 cm . Outside the MPAs the fishery regulations ban bottom trawling within 12 nautical miles from the coast, except from small scale coastal trawling for shrimp. It is not required that these small trawlers have sorting grids or other bycatch reduction devices.


Figure 3: The study areas, located along the southern coast of Norway (left panel) and a more detailed map (right panel) of Tvedestrandsfjorden (large square) and Sømskilen (Small Square).

### 2.3 Data collection

To avoid as much bias as possible in the results, a good study design is important. When measuring effects of MPAs it is essential to know something about the fish density and size distribution before MPA implementation, so that the results observed after implementation can in fact be related to the MPA and not just natural variations. Therefore, a BACI (before-after control-impact) study design is used, meaning that data is collected both before and after MPA implementation, in both MPA sites and control areas. This method is considered one of the most optimal methods for assessing effects of protection (Russ 2002; Osenberg et al. 2011). Form 2012-2010 "before data" was collected, data from 2013 and onwards is "after data" (fig.4). In this thesis, data from 2010 and onwards is used to compare my fieldwork data from 2015.

201020112012201320142015


Figure 4: overview of methods and data used in this study.

Three different methods are used when collecting data (fig.4). A standardized fishing method are conducted at the same time each year (first week of June), and the fishing locations are mapped out on advance and randomly selected. This method is used inside the MPAs in Tvedestrandsfjorden and at the control site nearby in the same periode. The goal with this method is not to get the most fish, but to fish as equal as possible so that the method is as person independent as possible. Fyke nets (fig.5) are set on the bottom in shallow water and are not baited, but have a leading net that guide the fish into the trap. All traps is checked every day, meaning that the soak time is approximately the same for each trap. The fishing effort varies between years, but usually 30-40 fyke nets were used each day for five days. In 2015, two boats were used simultaneously and therefore increased the fishing effort to 50 fyke nets each day.


Figure 5: Fyke net and device set up.

This study also uses data form another project (PROMAR) at the Institute of Marine Research Flødevigen. In this project, they use a non-standardized fishing method where the goal is to get as much fish as possible. This will affect where they put out fyke nets meaning that the locations are not random but selected because they are known good fishing locations. The fishing period starts in mid-May until June and the method is used in the no-take reserve in Tvedestrandsfjorden. The soak time is also different form the standardized method, varying from one up to nine days. Longer soak time will affect how many cod we get relative to the number of traps (the catch per unit effort (CPUE)), and is less affected by weather conditions. In the standardized method, all traps should be checked every day but some days the weather conditions made it impossible to haul the gear at the most exposed locations.

In 2011-2013 PROMAR also fished in Sømskilen using the same method with varying soak time, and we conducted this fishing again in 2015 equivalent to the one in 2012 with a non-standardized method. Sømskilen were therefore used as a control for the results in the no-take area collected by the non-standardized method. The fishing in Sømskilen is conducted in late April and throughout May.

Large cod traps (fig.6) were also used in the outer parts of Tvedestrandsfjorden in 2012, and repeated in 2015, but to a lesser extent. This because the outer MPA allows hook and line fishing and does not give the same protection for cod, as the no-take reserve. These traps are baited and were put out on locations varying from five to 50 meters deep. This fishing is conducted in April and May and the soak time varies from two to eight days.


Figure 6: Large cod traps.

The body length of all individual cod was measured to the nearest cm, a DNA-sample were collected and individuals over 25 cm were marked using T-bar anchor tags parallel to the anterior dorsal fin. After data collection fish were released at the capture location.

### 2.4 Data analysis

Microsoft Excel (2013 Ink) was used for plotting raw field data. GPS data was downloaded with the Garmin specific software Mapsource (version 6.16.3). All data were then imported into the R software (version 3.2.2; The R Foundation for Statistical Computing 2015) for statistical analysis and plotting of results.

The catch per unit effort (CPUE) were calculated by dividing number of cod caught, on number of traps used. These results are compared between years, and between the different fishing methods.

When fishing with fyke nets using the standardized method, the traps is hauled every day, meaning that the soak time is one day. However, due to weather conditions, two of
the traps in 2012 was left for three days and one trap for two days. In 2015, two of the traps was also left for two days. These results are included in the analysis even though they have different soak time than the rest of the data. In 2012, there was also six fishes where length measures is not taken. Also in 2014 three fishes missing length measures. These fishes is not included in the analysis. When comparing mean size distribution for the different years, data from the non-standardized and the standardized method are combined. It is assumed that the different methods did not have an effect on size distribution.

In the non-standardized method, the control area used to compare with the no-take reserve is in Sømskilen, but in 2014, a control in Tvedestrand was used to compare with and should maybe not be included in the analysis.
Evidence for spillover are not investigated further because we can not document an abundance effect inside the MPAs.

In the outer MPA were we conducted fishing with cod traps the fishing effort was different in 2015, compared to 2012. The traps also covered a larger area in 2012 than in 2015. To compensate for the different extent of fished areas and to investigate if some localities consequently was better than others, localities that were fished on both in 2012 and 2015 were selected and compared to each other. To do this a generalized linear model function (GLM) in R were used. GLM techniques are used with categorical response variables and it is not required that the response variable follows the normal distribution (McCullagh and Nelder 1992).

The relationship between location in 2012 and 2015 from the cod trap data was tested using formula (1):

$$
\begin{equation*}
C_{15 i}=\beta_{0}+\beta_{1} C_{12 i}+\beta_{2} M_{i}+\varepsilon_{i} \tag{1}
\end{equation*}
$$

Here $\mathrm{C}_{15 \mathrm{i}}$ is the number of cod caught in 2015 at the $\mathrm{i}_{\text {th }}$ location. $\mathrm{C}_{12 \mathrm{i}}$ is the corresponding catch of number of cods in 2012 at the same location (i). $\beta_{1}$ is a slope parameter tracking the effect of the catch in 2012 onto the catch of 2015. A significant positive parameter would indicate that good fishing locations had a high catch both in 2012 and 2015, as well as locations with low catch in 2012 also ha low catch in 2015, regardless of the absolute magnitude of the total catch. $\mathrm{M}_{\mathrm{i}}$ is variable indicating wether the location I is inside what was established as MPA or outside. The variable will take
the value 1 if location I is inside and 0 if the location is outside the MPA. $\beta_{2 \mathrm{i}}$ is a factor variable mapping the effect of the MPA on the catch in 2015. This variable will take a positive value if the expected catch inside the MPA is higher in 2015 than what would be expected if only the location effect was included. $\beta 0$ is a study specific intercept and $\varepsilon_{\mathrm{i}}$ is the site specific error term being independent and identical normally distributed.

## 3. Results

### 3.1 Fyke nets

During 2010-2015 a total of 1390 cod were captured and measured using two different fishing methods (tab.1), in the inner and outer parts of Tvedestrandsfjorden (fig.7). The mean body size was 39 cm , ranging from 4 to 80 cm .


Figur 7: Map over fished locations using fyke nets, in Tvedestrandsfjorden. Blue circles are location of the fyke nets. Light green areas are MPAs with partly protection for cod and the dark green area is the notake reserve.

Table 1: Data used in this study. The MPA area used when fished by the non-standardized method is the no-take reserve in Tvedestrandsfjorden, and the control area is Sømskilen.

| Year | Cod catch/numb. of traps <br> (non-standardized fishing <br> method) |  |  | Cod catch/numb. of traps <br> (standardized fishing method) |  |
| :--- | :--- | :--- | :--- | :--- | :---: |
|  | MPA | Control | MPA | Control |  |
| 2010 | - | - | $11 / 68$ | $71 / 172$ |  |
| 2011 | $47 / 185$ | $58 / 46$ | $4 / 93$ | $24 / 89$ |  |
| 2012 | $183 / 123$ | $276 / 112$ | $47 / 67$ | $83 / 52$ |  |
| 2013 | $25 / 39$ | $48 / 20$ | $6 / 74$ | $15 / 47$ |  |
| 2014 | $134 / 273$ | $8 / 52$ | - | - |  |
| 2015 | $83 / 97$ | $182 / 140$ | $34 / 143$ | $51 / 185$ |  |

After three years of protection, the density of cod is not higher inside the MPAs than in the control areas, and the catch per unit effort (CPUE) inside the MPAs are higher with the non-standardized method (fig. 8 and 9).

2012, stands out as a very good year with high CPUE in both the MPAs and control areas in Tvedestrandsfjorden, but also in Sømskilen. In 2013, the catches decreased in Tvedestrand, but remained stable in Sømskilen. Apart from 2012, the fish density is higher inside the MPAs than former years, but it is increasing in the control areas as well.

The CPUE in the MPAs has consistently been lower than in the control areas. However, figure 10. shows that in 2015 the CPUE inside the MPAs, in percentage of CPUE in the control areas is higher than former years, for both methods. CPUE in the MPAs in the non-standardized and the standardized method for 2015 was $66 \%$ and $61 \%$ respectively of the CPUE in the control areas, while corresponding results for 2011 was $20 \%$ for the non-standardized fishing method and $15 \%$ for the standardized fishing method. In 2012, the CPUE in the MPAs was $65 \%$ of the CPUE in the control areas with the nonstandardized fishing method.


Figure 8: Catch per unit effort conducted through the standardized fishing method. The blue triangles represents catch inside the MPAs and the red circles represents catch in the control areas. The vertical lines represents the $95 \%$ confidence interval based on a negative binominal distribution, parametrized with number of cod and number of gear used. A $95 \%$ interval means that the probability of observing a value outside of this area is less than 0.05 Data for 2014 is missing.


Figure 9: Catch per unit effort conducted through the non-standardized fishing method. The blue triangles represents catch inside the MPAs and the red circles represents catch in the control areas. The vertical lines represents the $95 \%$ confidence interval based on a negative binominal distribution, parametrized with number of cod and number of gear used. Data for 2014 in the control area is based on very few traps and is thus of great uncertainty. The non-standardized fishing started in 2011, thus no data for 2010 exists.


Figure 10: CPUE inside the MPAs divided on CPUE in the control areas. The blue points represents the standardized method and the red points represents the non-standardized method.

In 2012, a larger proportion of small fishes were caught, especially in the control areas, leading to a decrease in mean cod length this year (fig.11). In the control area in Sømskilen, the mean size was low also in 2013 while the catches remained high. In Tvedestrand the portion of large fishes caught in 2013 was higher, leading to an increase in mean cod size, while the total catches decreased the same year.

The average cod size inside the MPAs has increased steadily except for a slight decrease in 2015, due to a larger portion of small fishes caught inside the MPAs. Prior to the designation, cod from the MPA were among the smallest in the study. From 2014 and onwards, the MPA cod had the highest average size. In 2015, cod in the no-take reserve were on average 10 cm longer than cod in any of the control areas (fig. 12 and 13).


Figure 11: Average cod length (mm). The blue circles represents the size of cod inside the MPAs and the two different fishing methods is combined. The gray triangles represents the mean cod length in the control areas for the standardized fishing method, while the red triangles represents fish size from the control area in the non-standardized fishing method (Sømskilen). The vertical lines represent the estimate confidence interval based on a normal distribution.
control 2012

control 2015



MPA 2015


Figure 12: Size distribution for control areas and MPAs in 2012 and 2015 (standardized fishing method).

Control (Sømskilen) 2012




Figure 13: Size distribution for control areas and MPAs in 2012 and 2015 (non-standardized fishing method).

### 3.2 Large cod traps

In 2012, 236 large cod traps were used during the field season. Since these traps are mainly used in the outer MPA (fig. 14) that are less protective for cod, the fishing effort in 2015 was much lower with 146 traps out during the field season. The CPUE in 2015 was approximately the third of the CPUE in 2012, and together with the fyke net data, this suggests that 2012 was a good year regardless of the type of gear.


Figure 14: Map over fished locations in Tvedestrandsfjorden in 2015. The large green polygon is the outer MPA. In the outer parts of the fjord, only large cod traps was used. Red points represents location of the gear.

Even though the total catches in 2012 were higher, there was a significant correlation between fishing locations. Figure 15. shows that locations that were good with high catches in 2012, also were good locations for catching cod in 2015 (GLM; p < 0.001). As seen in table 2, cod density in the outer MPA is also significantly higher than in the control area.


Figure 15: Comparison of number of cod caught in 2012 and 2015 in virtually identical
localities/stations. Red points represents stations in the control area, while blue points represents stations inside the MPA. The red line shows the correlation for the control area, while the blue line shows the correlation inside the MPA. That the blue line is parallel shifted upwards indicates that given the catch on a location in 2012, we will expect to get more cod in 2015 if the location is inside the MPA.

Table 2: Summary statistics of the generalized linear model (formula 1). Significance: * $\mathrm{p}<0,05,{ }^{* * *} \mathrm{p}$ $<0,001$.

| Factor | Parameter | Estimate | Std. Error | P-value |
| :--- | :--- | :--- | :--- | :--- |
| Intercept | $\beta_{0}$ | 0.555 | 0.139 | $* * *$ |
| Effect of catch in | $\beta_{1}$ | 0.087 | 0.025 | $* * *$ |
| 2012 |  |  |  |  |
| Effect of MPA | $\beta_{2}$ | 0.329 | 0.162 | $0.044^{*}$ |
| R-sq adj.: 0.1014 |  |  |  |  |

Unlike cod caught in the inner MPAs, large fishes has disappeared from the outer MPA from 2012 to 2015. In 2015 most of the fish caught are 45 cm or smaller (fig. 16).


Figure 16: Length distribution of cod (mm). Clear bars represents cod caught in 2012 and dashed bars represents cod caught in 2015.

## 4. Discussion

This study investigated the effects of marine protected areas on a highly mobile and temperate species, the Atlantic cod (Gadus morhua).

Many factors may influence biological response to protection: the time since reserve establishment, the size of the reserve, life history and ecological traits of the target species and habitat diversity and complexity. Direct effects of MPAs, like increases in commercial fish density, biomass and individual size, often takes time to accrue (Molloy et al. 2009; Guidetti and Micheli 2011). Most MPA studies are done in tropical areas, and few studies are conducted regarding Atlantic cod response to marine reserves, thus there are few studies to compare the results with.

While fisheries target the largest individuals in a population, natural selection favors the large ones (Olsen and Moland 2011), therefore, an increase in individual body size is often one of the first effects observed in many MPA studies.

In the inner MPA, cod were on average 10 cm longer than in any of the control areas after three years of protection. However, fish density in these MPAs has not increased to any extent. Similar to our study, Edgar and Barrett (1999) also reported that the number of large Tasmanian reef fish inside the MPA increased significantly, and was consistent over time. While total abundance of fish did not change significantly during the study period. In another study conducted in a small-scale northern reserve, Moland et al. (2013) found that Atlantic cod inside the MPA were on average 5 cm longer than cod in any of the control areas after four years of protection.

An increase in individual cod size was not the case for the outer MPA, where numbers of large individuals has decreases compared with data from 2012. This reserve is less protective for cod, since hook and line fishing is allowed and may be one of the reasons why we do not see the same increase here. There was a small peak of cod around 40-45 cm , and with a minimum size of 40 cm in this area, larger cod may be fished out from the population. Rod and line fishing is reported to have very high impact on cod, accounting for $60 \%$ of total fishing mortality (Kleiven et al. 2016).

When closing an area from any fishing activities the fish inside this area have the chance to grow and get larger and older.

In marine ecosystems, size selective fishing is common, and there is evidence that such selective harvesting has negative impact on growth rate, timing of maturation, and reproductive investment in target species (Heino and Godø 2002; Kuparinen and Merilä

2007; Allendorf and Hard 2009). Change in maturation and growth rate is documented for the Atlantic cod and many other exploited natural populations (Olsen et al. 2004). Selection for earlier maturation may result in smaller fish of a give age because of earlier investment of resources in reproduction rather than growth, which in turn will reduce biomass yield (Law 2000). The combined effect of reduced size and sizedependent fecundity may also lower the reproductive potential, which in turn may reduce the ability to recover from large anthropogenic or natural disturbance (Ratner and Lande 2001). Older individuals of both sexes tend to have a longer spawning period than young individuals, and older and bigger females produce more and larger eggs, which will enhance the chance of offspring survival (Hixon et al. 2014). Results represented herein supports the contention that MPAs can help to counter fisheriesinduced evolution of life-history traits by increasing individual size (Dunlop et al. 2009; Miethe et al. 2010). However, it is important to consider when designing MPAs that they may set up new selection pressures on fish behavior, favoring individuals that tend to have restricted movement and thus stay within reserve boundaries (Parsons et al. 2010). This behaviour may not be representative for the population norm.

There were no significant increase in fish density inside the inner MPAs compared to the control areas. Density-dependent processes, like passive diffusion or displacement of individuals caused by space limitations, appears to be the main reasons for net export of adult fishes (termed "spillover") (Willis et al. 2003). Without a severe increase in cod density, it might be too early to investigate evidence for spillover.

Apart from 2012, the density inside the MPAs is increasing more than former years. 2012, was a year with very high CPUE both inside the MPAs and in the control areas. However, the mean cod length decreased the same year. In 2013, the average size was higher and the CPUE decreased. This indicates that a big portion of small fishes migrated into the areas, pulling the average size down, and disappeared from the area before the fieldwork season in 2013.

For the outer MPA there was a significant higher density of cod inside compared to the control area. In the inner parts of Tvedestrandsfjorden, the water is anoxic from 30-40 meters deep which is an unsuitable habitat and will exclude cod from the deepest parts of the fjord (Kroglund et al. 2003). This may be one of many reasons why we do not see an increase in density in this area but a little increase in the outer MPA where fish can migrate to deeper water. The outer MPA is also known to have better feeding grounds
for cod (Espeland pers comm). Inflow of water masses from the North Sea are also transporting a portion of North Sea cod (eggs and larva) into the Skagerrak cod stocks (Stenseth et al. 2006). The outer area is more exposed and will be more affected by larval drift. This may also explain why the outer MPA have a higher CPUE compared to the control areas than the inner MPAs.

The CPUE is not just affected by density but also the catchability. In this study the fishing effort is varying between years and sites. It is expected that higher effort would result in bigger catches. However, in 2015 the fishing effort was a bit higher in the inner MPAs compared to 2012 without an effect on CPUE. The different fishing methods are also conducted in different periods, and may affect the catchability. Fishing in the control area in Sømskilen is conducted in April-May and these results are compared with results from the no-take area were the fishing is carried out in May-June. There may be a considerable rise in seawater temperature from April to June, and water temperature combined with food availability has an impact on cod behaviour (Espeland et al. 2010). Cod is found in deeper, colder waters when surface temperature increases. The fyke nets were put out in shallow water, while the cod traps were put out on locations varying from five to 50 meters. However, the gear was left for a day or more and it is reported than during the night, which is the primary feeding period; cod migrate to shallower water, whereas daytime is the resting period in deeper water when temperature is unfavorable (Espeland et al. 2010).

The location and soak time of the gear is also different with the different approaches. Gear put out on only good locations compared with randomly selected locations will have a higher CPUE. The CPUE is also increasing with increased soak time. Location and soak time are probably the main explanations why the non-standardized method consistently have a higher CPUE than the standardized method.

It is only been three years since the reserves were implemented in this area. In some cases significant differences can be observed rapid (within 3 years, e.g. (Claudet et al.2006; Halpern and Warner 2002)), but are more likely observed when the reserve has already been in place for several years (Paddack and Estes 2000). Especially for long lived, slow growing fishes the effects may take years, decades or even longer to accumulate (Guidetti and Micheli, F. 2011; Russ and Alcala 2004). Few studies are
monitored over time (usually less than four years) and McClanahan (2000) predicted that 30 years or more might be required to achieve full recovery of an important food fish on Kenyan coral reefs. A study of the Georges Bank Atlantic cod reported that cod responded more slowly to protection than other species studied. The reason for this slow response was most likely that they are more mobile than the other species studied, and had been driven down farthest. However, there are signs that their biomass is also rebuilding (NEFSC (Northeast Fisheries Science Center) 2001; O’Brian and Munroe 2001)). One Cape Cod, fishermen reports improvements in catches as they travel less than half the distance and catches nearly twice as much cod as they did before the closures (Gell and Roberts 2002).

Several factors seems crucial for the ecological effectiveness of MPAs. Even though human activities are prohibited within the reserve, activities that occur outside the reserves, e.g. overfishing of the spawning stock biomass in the surrounding fishing areas may limit adult immigration or larval dispersal into the reserve, leading to smaller effects when stocks are more severely overfished (Lloret et al. 2008; Denny et al. 2004). Negative interaction with other species through competition or predation is another factor to consider regarding potential for recovering species (Willis and Anderson 2003).

Another major factor to consider that may affect the results is the location of both MPAs and control areas. MPAs are often selected through political processes that bias their location, and may not be representative. Good control areas are also very difficult to find because reserves can potentially export larvae tens of kilometers away. Sites within this range might also be affected by the reserve through spillover and will not represent true controls (Gell and Russ 2003). In this study, one of the control areas is approximately 30 km away from the MPAs and is also a more open system than the other areas. The other control areas are located just outside the MPAs and may be affected by the MPAs, which will bias the results.

To separate the effects of protection from those of habitat, the recommended study design BACI is used. With sufficient "before" data it is easier to investigate if effecte are due to reserve protection. Without such data, it is difficult to tell if the observed effects may be caused by natural variation, rather than protection. To make sure that marine reserve status was the cause of higher fish densities, some researchers has conducted experiments where reserves are opened to fishing again after a while. They
reported that removal of reserve status caused significant decreases in density much faster than the rate of gain when the reserve was first closed (Russ and Alcala 2003).

## 5. Conclusion

Based on the BACI-approach, the findings reported in this study provide evidence that protection has resulted in increased individual size and age of Atlantic cod inside the inner MPA compared to the control areas. However, without any new big year class immigrating into the fished population, the density has not increased to any extent. A small increase in fish density are also seen in the outer MPA. However, further investigation is necessary to fully understand the effects of reserve protection in these small-scale northern MPAs.

When the MPAs in Tvedestrand were implemented in 2013, a five years protection period was accepted, meaning that in 2017 the protected areas can be opened to fishing activities again. It is highly recommended that these areas maintain reserve status as the signs of recovery may take many years to observe.

For Marine protected areas to work as a management tool they should in the long term compensate for the loss of fishing area. If they not fully compensates for this loss, they will still act as a reserve of spawning stock from which to start a recovery. They also create great opportunities to study marine ecosystems in absence of harvest mortality. MPAs are not advocated as the only solution, but as an insurance against overfishing and fish stock collapses, in other ways a healthy dose of the precautionary principle.

## References

Allendorf, F.W. \& Hard, J.J. (2009). Human-induced evolution caused by unnatural selection through harvest of wild animals. Proc Natl Acad Sci USA, 106: 9987-9994.

Beamish, R.J., McFarlane, G.A. \& Benson, A. (2006). Longevity overfishing. Prog Oceanogr, 68: 289-302.

Begg, G.A. \& Marteinsdottir, G. (2000). Spawning origins of pelagic juvenile cod Gadus morhua inferred from spatially explicit age distributions: potential influences on year-class strength and recruitment. Mar Ecol Prog Ser, 202: 193-217.

Bodvin, T., Kleiven, A.R., Espeland, S.H., Steen, H. \& Moy, F. (2012). Aktiv forvaltning av marine verdier i kystsonen - årsrapport 2012. Havforskningsinstituttet.

Ciannelli, L., Knutsen, H., Olsen, E.M., Espeland, S.H., Asplin, L., Jelmert, A., Knutsen, J.A. \& Stenseth, N.C. (2010). Small-scale genetic structure in a marine population in relation to water circulation and egg characteristics. Ecology, 91: 29182930.

Claudet, J., Osenberg, C.W., Benedetti-Cecchi, L., Domenici, P. et al. (2008). Marine reserves: size and age do matter. Ecol Lett, 11: 481-489.

Claudet, J. Osenberg, C.W., Domenici, P., Badalamenti, F., Milazzo, M., Falcon, J.M. et al. (2010). Marine reserves: fish life history and ecological traits matter. Ecol Appl, 20: 830-839.

Claudet, J., Pelletier, D., Jouvenel, J.Y., Bachet, F. \& 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. Biol Conserv, 130: 349-369.

Conover, D.O. \& Munch, S.B. (2002). Sustaining fisheries yields over evolutionary time scales. Science, 297: 94-96.

Convention on Biological Diversity. (2010). Strategic Plan for Biodiversity 2011-2020:
Target 11-Technical Rationale Extended. Available: http://www.cbd.int/sp/targets/rationale/target-11/ [Accessed 04.01.16].

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

Côte, I.M., Mosqueira, I. \& Reynolds, J.D. (2001). Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis. J Fish Biol, 59: 178-189.

Dayton, P.K., Sala, E., Tegner, M.J. \& Thrush, S.F. (2000). Marine protected areas: parks, baselines, and fishery enhancement. Bull Mar Sic, 66:617-634.

Denny, C.M., Willis, T. \& Babcock, R.C. (2004). Rapid recolonisation of snapper (Pagrus auratus: Sparidae) within an offshore island marine reserve after implementation of no-take status. Mar Ecol Prog Ser, 272:183-190.

Dhal, K. \& Dannevig, G.M. (1906). Studies on the effectiveness of releasing cod larvae for stock improvement in fjords in eastern Norway. Aarsberetn Norg Fisk, 1: 1-121.

Dunlop, E.S., Baskett, M.L., Heino, M. \& Dieckmann, U. (2009). Propensity of marine reserves to reduce the evolutionary effects of fishing in a migratory species. Evol Appl, 2: 371-393.

Edgar, G.J. \& Barrett, N.S. (1999). Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. J Exp Mar Biol Ecol, 242: 107-144.

Espeland, S.H. \& Knutsen, H. (2014). Rapport fra høstundersøkelsen med strandnot i indre Oslofjord 2014. Rapport fra Havforskningen, 31-2014, Havforskningsinstituttet.

Espeland, S.H., Olsen, E.M., Knutsen, H., Gjøsæter, J., Danielssen, D. \& Stenseth, N.C. (2008). New perspectives on fish movement: kernel and GAM smoothers applied to a century of tagging data on coastal Atlantic cod. Mar Ecol Prog Ser, 372: 231-241.

Espeland, S.H., Thoresen, G.A., Olsen, E.M., Stige, L.C., Knutsen, H., Gjøsæter, J. \&
Stenseth, N.C. (2010). Diel vertical migration patterns in juvenile cod from the Skagerrak coast. Mar Ecol Prog Ser, 405: 29-37.

Forskrift om bevaringssoner i Tvedestrand. 2012. Forskrift om bevaringssoner i
Tvedestrand kommunes sjøområder, Aust-Agder [Online]. Lovdata. Available: http://lovdata.no/dokument/FV/forskrift/2012-06-20-617 [Accessed 05.01.2016]

Forskrift om utøvelse av fisket I sjøen. 2005. Forskrift om utøvelse av fiske i sjøen. [online]. Lovdata. Available: http://lovdata.no/dokument/SF/forskrift/2004-12-221878/KAPITTEL_9\#KAPITTEL_9 [Accessed 17.02.2016]

Game, E.T., Grantham, H.S., Hobday, A.J., Pressey, R.L. et al. (2009) Pelagic protected areas: the missing dimension in ocean conservation. Trends Ecol Evol, 24: 360-369.

Gell, F.R. \& Roberts, C.M. (2002). The fishery effects of marine reserves and fishery closures. WWF-US, Washington, USA.

Gell, F.R. \& Roberts, C.M. (2003). Benefits beyond boundaries: the fishery effects of marine reserves. Trends Ecol Evol, 18: 448-445.

Guidetti, P. \& Micheli, F. (2011). Ancient art serving marine conservation. Front Ecol Environ, 9: 374-375.

Halpern, B.S. (2003). The impact of marine reserves: do reserves work and does reserve size matter? Ecol Appl, 13 (Suppl): 117-137.

Halpern, B.S., McLeod, K.L., Rosenberg, A.A. \& Crowder, L.B. (2008). Managing for cumulative impacts in ecosystem-based management through ocean zoning. Ocean Coast Manage, 51: 203-211.

Halpern, B.S. \& Warner, R.R. (2002). Marine reserves have rapid and lasting effects. Ecol Lett, 5: 361-366.

Heino, M. \& Godø, O.R. (2002). Fisheries-induced selection pressures in the context of sustainable fisheries. Bull Mar Sci, 70: 639-656.

Hixon, M.A., Johnson, D. \& Sogard, S.M. (2014). BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. ICES J Mar Sci, 71: 21712185.

Hutchings, J.A. (1999). Influence of growth and survival costs of reproduction on Atlantic cod, Gadus morhua, population growth rate. Can J Fish Aquat Sci, 56: 16121623.

Hutchings, J.A. (2000). Collapse and recovery of marine fishes. Nature, 406:882-885.
Hutchings, J.A. \& Myers, R.A. (1994). What can be learned from the collapse of a renewable resource? Atlantic cod, Gadus morhua, of Newfoundland and Labrador. Can J Fish Aquat Sci, 51: 2126-2146.

ICES 2014a. Cod in Subarea IV (North Sea) and Divisions VIId (Eastern Channel) and IIIa West (Skagerrak). ICES Advice, 2014. Report of the ICES Advisory Committee 2014, Book 6, section 6.3.3.

ICES 2014b. Cod in subareas I and II (Norwegian coastal waters). Report of the Arctic Fisheries Working Group (AFWG) 2014, ICES, 100-158.

Jackson, J.B.C. et al. (2001) Historical overfishing and the recent collapse of costal ecosystems. Science, 293: 629-638.

Jorde, P.E., Knutsen, H., Espeland, S.H. \& Stenseth, N.C. (2007). Spatial scale of genetic structuring in coastal cod Gadus morhua and geographic extent of local populations. Mar Ecol Prog Ser, 343: 229-237.

Kaiser, M.J. (2004). Marine protected areas: the importance of being earnest. Aquat Conserv, 14: 635-638.

Kjesbu, O.S. (1989). The spawning activity of cod, Gadus morhua L. J Fish Biol, 34: 195-206.

Kleiven, A.R, Fernandez-Chacon, A., Nordahl, J-H., Moland, E., Espeland, S.H., Knutsen, H., et al. (2016). Harvest Pressure on Coastal Atlantic Cod (Gadus morhua) from Recreational Fishing Relative to Commercial Fishing Assessed from TagRecovery Data. PLoS ONE, 11(3): e0149595. doi:10.1371/ journal.pone. 0149595

Knutsen, H., Jorde, P.E., Andre, C. \& Stenseth, N.C. (2003). Fine-scaled geographical population structuring in a highly mobile marine species: the Atlantic cod. Mol Ecol, 12: 385-394.

Knutsen, J.A., Knutsen, H., Rinde, E., Christie, H., Bodvin, T. \& Dahl, E. (2010). Mapping Biological Resources in the Coastal Zone: An Evaluation of Methods in a Pioneering Study from Norway. Ambio, 39: 148-158.

Knutsen, H., Olsen, E.M., Ciannelli, L., Espeland, S.H., Knutsen, J.A., Simonsen, J.H., Skreslet, S. \& Stenseth, N.C. (2007). Egg distribution, bottom topography and smallscale cod population structure in a coastal marine system. Mar Ecol Prog Ser, 333: 249255.

Knutsen, H., Olsen, E.M., Jorde, P.E., Espeland, S.H., André, C. \& Stenseth, N.C. (2011). Are low but statistically significant levels of genetic differentiation in marine
fishes "biologically meaningful"? A case study of coastal Atlantic cod. Mol Ecol, 20: 768-783.

Kroglund, T., Helland, A. \& Lindholm, O. (2003). Tiltaksplan for forurensede sedimenter i Aust-Agder, Fase 1 - Miljøtilstand, kilder og prioriteringer. NIVA.

Kuparinen, A. \& Merilä, J. (2007). Detecting and managing fisheries-induced evolution. Trends Ecol Evol, 22: 652-659.

Laurel, B.S. \& Bradbury, I.R. (2006). ‘Big’ concerns with high latitude marine protected areas (MPAs): trends in connectivity and MPA size. Can J Fish Aquat Sci, 63: 2603-2607.

Law, R. (2000). Fishing, selection, and phenotypic evolution. ICES (International Council for the Exploration of the Sea) Journal of Marine Science, 57: 659-668.

Lloret, J., Zaragoza, N., Caballero, D., Font, T., Casadevall, M. \& Riera, V. (2008). Spearfishing pressure on fish communities in rocky costal habitats in a Mediterranean marine protected area. Fish Res, 94: 84-91.

Marine Conservation Institute. (2016). MPAtlas. Seattle, WA. Available:
http://www.mpatlas.org [Accessed: 03.02.16].
Maxwell, S.M., Hazen, E.L., Bograd, S.J., Halpern BS et al. (2013) Cumulative human impacts on marine predators. Nat Commun, 4 (2688): 1-9.

McClanahan TR (2000) Recovery of a coral reef keystone predator, Balistapus undulates, in East African marine parks. Biol Conserv, 94:191-198.

McCook L.J. et al. (2010). Adaptive management of the Great Barrier Reef: a globally significant demonstration of the benefits of networks of marine reserves. Proc Natl Acad Sci USA, 107: 18278-18285.

McCullagh, P. \& Nelder, J.A. (1992). Generalized linear models. Chapman and Hall.
McRae, L., Freeman, R. \& Deinet, S. (2014). In: McLellan, R., Iyengar, L., Jeffries, B. \& Oerlemans, N. (Eds.), The Living Planet Index in: Living Planet Report 2014. WWF, Gland, Switzerland.

Miethe, T., Dytham, C., Dieckmann, U. \& Pitchford, J.W. (2010). Marine reserves and the evolutionary effects of fishing on size and maturation. ICES J Mat Sci, 67: 412-425.

Moland, E., Olsen, E.M, Knutsen, H., Garrigou, P., Espeland, S.H., Kleiven, A.R., André, C. \& Knutsen, J.A. (2013). Lobster and cod benefit from small-scale northern marine protected areas: inference from an emperical before-after control-impact study. Proc R Soc B, 280: 20122679.

Molloy, P.P., McLean, I.B. \& Côté, I.M. (2009). Effects of marine reserve age on fish populations: a global meta-analysis. J Appl Ecol, 46: 743-751.

Murawski, S.A., Brown, R., Lai, H.-L., Rago, P.J. \& Hendrickson, L. (2000). Largescale closed areas as a fishery-management tool in temperate marine systems: The Georges Bank Experience. Bull Mar Sci, 66: 775-798.

NEFSC (Northeast Fisheries Science Center) 2001. Assessment of 19 Northeast Groundfish Stocks through 2000. A Report to the New England Fishery Management Council's Multi-Species Monitoring Committee. Northeast Fisheries Science Center Reference Document 01-20 Avaiable: http://www.nefsc.noaa.gov/nefsc/publications/crd/crd0120/

O'Brian, L., Munroe, N.J. 2001. Assessment of the Georges Bank Atlantic Cod Stock for 2001. Northeast Fisheries Science Center Reference Document 01-10 Avaiable: http://www.nefsc.noaa.gov/nefsc/publications/crd/crd0120/

O’Connor, M.I., Bruno, J.F., Gaines, S.D., Halpern, B.S., Lester, S.E., Kinlan, B.P. \& Weiss, J.M. (2006). Temperature control of larval dispersal and the implications for marine ecology, evolution and conservation. Proc Natl Acad Sci USA, 104: 1266-1271.

Olsen, E.M., Carlson, S.M., Gjøsæter, J. \& Stenseth, N.C. (2009). Nine decades of decreasing phenotypic variability in Atlantic cod. Ecol Lett, 12: 622-631.

Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Brattey, J., Ernande, B. \& Dieckmann, U. (2004). 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., Knutesn, J.A. \& Stenseth, N.C. (2004). Life history variation among local populations of Atlantic cod (Gadus morhua) from the Norwegian Skagerrak coast. J Fish Biol, 64: 1725-1730.

Olsen, E.M., Knutsen, H., Gjøsæter, J, Jorde, P.E., Knutsen, J.A. \& Stenseth, N.C. (2008). Small-scale biocomplexity in coastal Atlantic cod supporting a Darwinian perspective on fisheries management. Evol Appl, 1: 524-533.

Olsen, E.M \& Moland, E. (2011). Fitness landscape of Atlantic cod shaped by harvest selection and natural selection. Evol Ecol, 25: 695-710.

Osenberg, C.W., Shima, J.S., Miller, S.L \& Stier, A.C. (2011). Ecology: assessing effects of marine protected areas: confounding in space and possible solutions. In: Claudete, J. (ed.). Marine protected areas: a multidisciplinary approach, pp. 143-157. Cambridge, UK. Cambridge University Press.

Paddack, M.J. \& Estes, J.A. (2000). Kelp forest fish populations in marine reserves and adjacent exploited areas of central California. Ecol Appl, 10: 855-870.

Palumbi, S.R. (2002). Marine reserves: a tool for ecosystem management and conservation. Pew Oceans Commission, Arlington, VA.

Palumbi, S.R. (2004). Marine reserves and ocean neighborhoods: the spatial scale of marine populations and their management. Annu Rev Environ Resour, 29: 31-68.

Parsons, D.M., Morrison, M.A. \& Slater, M.J. (2010). Responses to marine reserves: decreased dispersion of the sparid Pargus auratus (snapper). Biol Conserv, 143:20392048

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. \& Torres, F. (1998). Fishing down food webs. Science, 279:860-863.

Pauly, D., Christensen, V., Guénette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J., Watson, R. \& Zeller, D. (2002). Towards sustainability in worlds fisheries. Nature, 418: 689-695

Pepin, P., Orr, D.C. \& Anderson, J.T. (1997). Time to hatch and larval size in relation to temperature and egg size in Atlantic cod (Gadus morhua). Can J Fish Aquat Sci, 54: 210.

Ratner, S. \& Lande, R. (2001). Demographic and evolutionary response to selective harvesting in populations with discrete generations. Ecology, 82: 3093-3104.

Roberts, C.M. \& Polunin, N.V.C. (1991). Are marine reserves effective in management of reef fisheries? Rev Fish Biol Fish, 1:65-91.

Roberts, C.M. \& Sargant, H. (2002). The fishery benefits of fully protected marine reserves: why habitat and behaviour are important. Nat Res Mod, 15: 487-507.

Robichaud, D. \& Rose, G.A. (2001). Multiyear homing of Atlantic cod to a spawning ground. Can J Fish Aquat Sci, 58: 2325-2329.

Russ, G.R. (2002). Yet another review of marine reserves as reef fisheries management tools. In: Sale, P.F. (ed) Coral reef fishes: dynamics and diversity in a complex ecosystem. Academic Press, San Diego, California, pp 421-443.

Russ, G.R. \& Alcala, A.C. (2004). Marine reserves: long-term protection is required for full recovery of predatory fish populations. Oecologia, 138: 622-627.

Russ, G.R. \& Alcala, A.C. (2003). Marine reserves: rates and patterns of recovery and decline of predatory reef fish, 1983-2000. Ecol Appl, 13: 1553-1565.

Shipp, R.L. (2003). A perspective on marine reserves as a fishery management tool. Fisheries, 28: 10-21.

Stenseth, N.C., Jorde, P.E., Chan, K-S., Hansen, E., Knutsen, H., André, C., Skogen, M.D. \& Lekve, K. (2006). Ecological and genetic impact of Atlantic cod larval drift in the Skagerrak. Proc. R. Soc B, 273: 1085-1092..

Svedäng, H. (2003). The inshore demersal fish community on the Swedish Skagerrak coast: regulation by recruitment from offshore sources. ICES J Mar Sci, 60: 23-31.

Willis, T.J., \& Anderson, M.J. (2003). Structure of benthic reef fish assemblages: relationships with habitat characteristics and predatory density. Mar Ecol Prog Ser, 257:209-221.

Willis, T.J., Millar, R.B \& Babcock, R.C. (2003). Protection of exploited fish in temperate regions: high density and biomass of snapper Pagrus auratus (Sparidae) in northern New Zealand marine reserves. J of Appl Ecol, 40: 214-227.

