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Master

Assessing the impacts of marine protected areas on wrasse populations in Norway

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Abstract

Several species of wrasse (Labridae) are increasingly harvested to be used as cleaner fish in salmon aquaculture. The intensity of harvesting wrasse has raised concern regarding sustainability and there is a lack of knowledge on the ecological impacts of such harvesting in Norway. The establishment of marine protected areas (MPAs) could be an effective management tool for maintaining wild wrasse populations. This study investigated the impacts of MPAs on wrasse by comparing body size and catch per unit effort (CPUE) between MPAs and nearby fished areas in Austevoll on the west coast and in Tvedestrand on the south coast of Norway. Age of ballan (*Labrus bergylta*) was also compared between areas in Austevoll. Sampling in Austevoll was conducted during three sampling periods in 2018-2019; and sampling in Tvedestrand was conducted every June from 2010-2019. This study also investigated a possible non-invasive method of aging ballan using scales by comparing scale age to otolith age.

In Austevoll, corkwing wrasse (*Symphodus melops*) were found to be significantly larger in MPAs while CPUE of all wrasse species and age of ballan did not differ between areas. In Tvedestrand, ballan and rock cook (*Centrolabrus exoletus*) were significantly larger in MPAs, while CPUE of rock cook and goldsinny (*Ctenolabrus rupestris*) was significantly lower in MPAs. The larger body sizes found in MPAs indicated a positive effect of protection on size for these species and is consistent with the prediction that there should be larger fish inside MPAs. The lower CPUE of smaller wrasse species in the Tvedestrand MPA contradicted the prediction that there should be more individuals inside MPAs and could possibly be explained by increased predation within the MPA. Furthermore, the scales used to age ballan were found to have a high error rate and a tendency to show a younger age than otoliths, however scales were found to be accurate for aging young ballan (< 6 years). The results from Austevoll demonstrated the ability of MPAs to restore harvested populations within one year of MPA implementation, while the results from Tvedestrand highlighted the potential for indirect effects of protection to occur over a longer period of time. The overall findings suggest that MPAs can be used as a management strategy to maintain natural size structure and abundance of harvested wrasse populations. Recommendations for conservation and management are provided including 1) implementing additional MPAs in Western Norway where intensity of harvesting is highest; and 2) revising current management of the fishery to reflect the life history strategies of wrasse species.

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Preface

I would like to thank my supervisors, Kim Halvorsen and Lars Korslund, for providing invaluable guidance and checking in on me throughout the entire process. Meetings with Kim and Lars were full of enthusiasm and I always left feeling motivated and excited about the next step. Your extensive knowledge and experience with statistical analysis, modelling, and academic writing has been an enormous help to me. Thank you for always being accessible for advice, for reassuring me that no question is too big or too small, for providing feedback on drafts, and for always encouraging me.

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Kristiansand 28.05.20

Molly Reamon

1. Introduction

1.1 Background

Several species of wrasse (Labridae) are increasingly fished in Norway and the British Isles to be used as cleaner fish in the farming of Atlantic salmon (*Salmo salar* Linnaeus, 1758) and rainbow trout (*Oncorhynchus mykiss* Walbaum, 1972) (Halvorsen et al., 2017; Skiftesvik, Durif, Bjelland & Browman, 2015). The wrasse fishery in Norway began in the late 1980s after it was discovered that wrasse may be used in salmon farming to remove sea lice (*Lepeophteheirus salmonis* Krøyer, 1837) (Bjordal, 1988; Skiftesvik et al., 2014). The demand for wild wrasse in Norway has increased substantially since 2009, after the salmon lice began to develop resistance to the pesticides most commonly used to treat salmon lice (Skiftesvik et al., 2014; Nilsen, 2008). Norway is the world's leading producer of salmon (FAO, 2019) and outbreaks of lice are among the greatest challenges facing the industry (Svåsand et al., 2017) suggesting that the wrasse fishery will continue to be relevant in the near future. The intensity of harvesting wild wrasse has raised concern among the scientific community regarding sustainability and there is a general lack of knowledge on the ecological effects of such harvesting in Norway (Espeland et al., 2010; Skiftesvik et al., 2015; Halvorsen et al., 2017; Olsen, Halvorsen, Larsen & Kuparinen, 2018).

1.2 The wrasses

Wrasse are a family of marine fish (Labridae) of more than 500 species that are numerous among inshore areas (Skiftesvik et al., 2015). There are five common species of wrasse found in Norwegian waters including corkwing (*Symphodus melops* Linnaus, 1758), goldsinny (*Ctenolabrus rupestris* Linnaeus, 1758), ballan (*Labrus bergylta* Ascanius, 1767), cuckoo (*Labrus mixtus* Linnaeus, 1758), and rock cook (*Centrolabrus exoletus* Linnaeus, 1758) (Costello 1991; Figure 1). The scale-rayed wrasse (*Acantholabrus palloni* Risso, 1810) also exists in Norwegian waters however it is seldom observed because it inhabits deep waters (50-270 m) (Costello, 1991). Wrasses are intermediate predators that feed on mollusks and crustaceans (Costello, 1991) and are prey for larger predators such as gadoids and seabirds (Nedreaas et al., 2008; Steven, 1933). The wrasses exhibit a variety of life history strategies which will be reviewed in the following paragraphs.

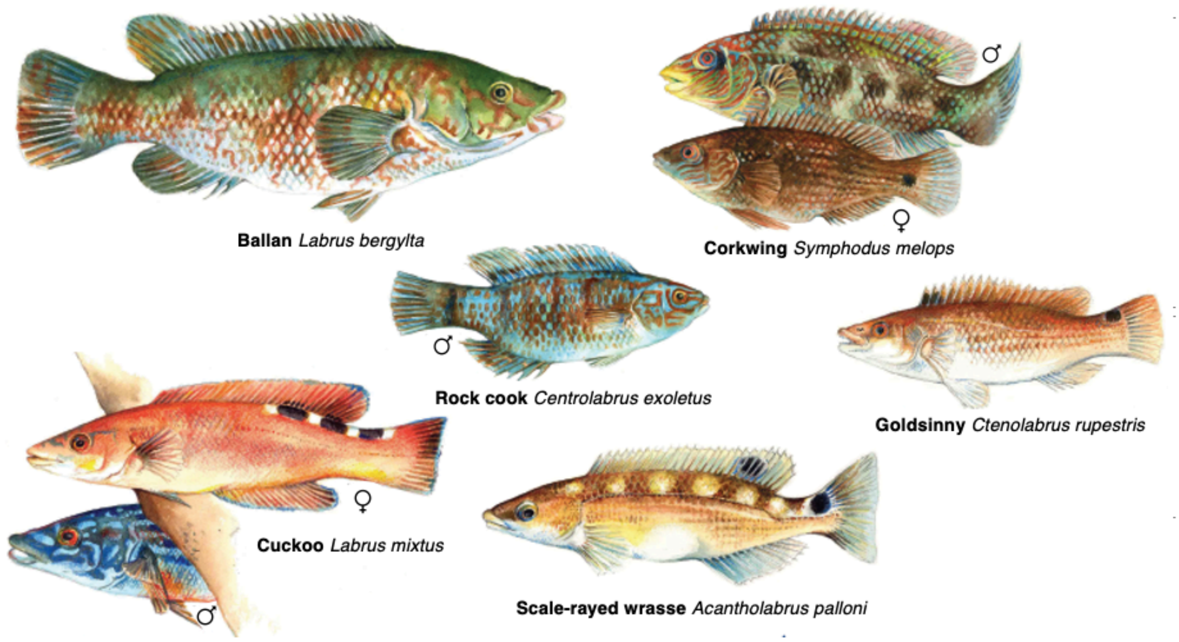

Figure 1: The six wrasse species found in Norwegian waters including ballan, corkwing (top male, bottom female), rock cook, goldsinny, cuckoo (top female, bottom male) and scale-rayed wrasse. Illustration by Stein Mortensen, modified with permission by Marthe Ruud.

The preferred habitat for wrasse is shallow rocky areas with macroalgal cover (Costello, 1991; Darwall, Costello, Donnelly & Lysaght, 1992). The wrasse species have slightly different distributions which vary in terms of exposure, depth and access to refuge (Skiftesvik et al., 2015; Halvorsen, Sørdalen, Larsen, Rafoss & Skiftesvik, 2020; Darwall et al., 1992). Corkwing have been found to occupy sheltered areas, rock cook inhabit more exposed areas, while goldsinny and ballan prefer habitats with intermediate exposure (Skiftesvik et al., 2015). The wrasses have been found to occupy different depth ranges in which corkwing and ballan are primarily found at shallow depths (< 5 m), goldsinny occupies intermediate waters (< 15 m), and rock cook and cuckoo are found more frequently in deeper waters (Halvorsen et al., 2020). It has also been reported that the goldsinny must have access to areas of refuge such as crevices between rocks or caves (Darwall et al., 1992; Sayer, Gibson & Atkinson, 1993). All wrasse species establish territories (Darwall et al., 1992) and exhibit a high level of site-fidelity (Espeland et al., 2010). The goldsinny has been observed to defend territories up to 2 m^2 (Hilldén, 1981) and it is estimated that the ballan occupies a home range of 0.09 km^2 (Villegas-Ríos et al., 2013b). It has been suggested that in species with high site-fidelity, size structure can potentially be an indicator of fishing pressure (Shepherd, Brook & Xiao, 2010).

The wrasses differ substantially in size, growth rate and longevity (Darwall et al., 1992). The ballan is the largest and the longest living of the wrasses, attaining a maximum size of 60 cm and living to be 29 years of age (Costello, 1991; Dipper, Bridges & Menz, 1977). The goldsinny and rock cook are the two smallest wrasse, growing to be 21 cm and 20 cm respectively (Skiftesvik & Halvorsen, 2019). Although similar in body size, the goldsinny has a longer lifespan relative to the rock cook and lives to be 20 years of age as compared to 8 years (Sayer, Gibson & Atkinson, 1995; 1996). The cuckoo attains a maximum size of 35 cm and has been found to live to 17 years of age (Costello, 1991). The corkwing reaches a maximum size of 25 cm and the longevity has been found to vary between regions in which individuals in Northern and Western Norway live longer (9 years) than individuals in Southern Norway (4 years) (Skiftesvik & Halvorsen, 2019). The corkwing inhabiting Western Norway are documented to be genetically distinct populations from those in the south (Gonzalez, Knutsen & Jorde, 2016; Faust et al., 2018).

The wrasses have different reproductive behavior in terms of changing sex, exhibiting sexual size dimorphism, providing parental care and building nests (Darwall et al., 1992). The cuckoo and the ballan are both protogynous hermaphrodites which means that they change sex from female to male (Costello, 1991). All of the ballan change sex when they reach 32-40 cm, while only some of the cuckoo change sex when they reach 22-25 cm (Skiftesvik & Halvorsen, 2019; Costello, 1991). The corkwing and goldsinny consist of two categories of males including territorial males with typical sexual characteristics and sneaker males that are identical to females in their appearance and perform a sneak fertilization (Uglem, Rosenqvist & Wasslavik, 2000; Hilldén, 1981). The territorial corkwing males build and defend a nest during the spawning period and provide parental care for the eggs (Potts, 1985). The corkwing sneaker males have been found to grow slower and mature earlier than territorial males (Halvorsen et al., 2016a). Sexual size dimorphism occurs when there is a difference in body size between the sexes of a species (Parker, 1992) which is evident for ballan (Dipper et al., 1977), cuckoo (Costello et al., 1991), goldsinny (Olsen et al., 2018) and corkwing wrasse (Uglem et al., 2000). The spawning season for all wrasse species begins during the early summer (April/May) and can extend into late summer (August/September) (Darwall et al., 1992). The goldsinny is the only species that has planktonic eggs (Sjölander, Larsson, & Engström, 1972), while all other wrasse species deposit benthic eggs (Darwall et al., 1992).

1.3 Norwegian wrasse fishery

Wrasse were first used as cleaner fish in the aquaculture industry in Norway in the late 1980s after Bjordal's (1988) discovery of the wrasses' ability to remove salmon lice (Skiftesvik et al., 2014). During the period 1998-2005, the use of wild-caught wrasse as cleaner fish was relatively low because chemical pesticides were the primary method for delousing (Jansson et al., 2017). However, around 2007 the salmon lice began to develop resistance to the pesticides that were used (Nilsen, 2008; Besnier et al., 2014) leading to a substantial increase in the demand for wild-caught wrasse (Skiftesvik et al., 2014). The wrasse landings in Norway reached a maximum in 2017 at more than 27 million individuals leading to the establishment of a landing cap at 18 million individuals (Norwegian Directorate of Fisheries, 2020a; 2019b). The 18 million is divided between regions allowing 10 million wrasses to be captured in Western Norway, and 4 million in both Northern and Southern Norway (Norwegian Directorate of Fisheries, 2019b). The wrasses captured in the south are transported to aquaculture farms in mid- and northern-Norway where the local supply of wrasses is inadequate to support the demand for cleaner fish (Skiftesvik et al., 2014).

The species of wrasse that are targeted in the fishery are corkwing, goldsinny, ballan, cuckoo and rock cook (Norwegian Directorate of Fisheries, 2020a). The official landings statistics from the Norwegian Directorate of Fisheries report that goldsinny constitute the largest proportion of the landings (44.8%) followed by corkwing (42.4%), ballan (10.3%), rock cook (2.3%) and cuckoo (<1%) (Norwegian Directorate of Fisheries, 2020a). The cuckoo and rock cook are not targeted in Southern Norway because they have been found to be unfit for transportation (Halvorsen et al., 2020). The wrasses are fished at depths < 7 m because hauling the nets up from deeper waters can destroy the swimming bladders of the fish (Halvorsen et al., 2016b; 2017).

The Norwegian fishing regulations for wrasse include minimum size limits that are species-specific, gear restrictions, fishing quotas, and a seasonal fishing closure from October 20 to July 17 (Norwegian Directorate of Fisheries, 2019b). The minimum size limit was previously the same for all wrasse (11cm), however since 2015 there are species-specific size limits which is 14 cm for ballan, 12 cm for corkwing, and 11 cm for other wrasse species (Halvorsen et al., 2017). Currently both fyke nets and pots are used as fishing gear for wrasse, however fyke nets will be forbidden for recreational fishermen to use from 2020, and for commercial fishermen from 2021 (Norwegian Directorate of Fisheries, 2020b). In addition, from the year 2021 there is a requirement that the entrance of the pots must be ≤60 mm in diameter in order to decrease the amount of bycatch and prevent the capture of large ballan (Norwegian Directorate of Fisheries, 2020b). In addition, it will be required that all wrasse fishing boats are equipped with an automatic identification system (AIS) to report their locations which will provide valuable knowledge regarding spatial patterns of fishing activity (Norwegian Directorate of Fisheries, 2020b).

1.4 Selective fisheries and marine protected areas

The harvesting of wild populations is inevitably selective, whether certain individuals are intentionally targeted due to traits they possess or because they are inherently more vulnerable to be captured (Law, 2000). Fisheries typically target large individuals, as well as certain species, during specific times of the year in order to maximize their profits (Zhou et al., 2010). The selectivity of fisheries is strengthened by management such as minimum size limits or gear modifications that avoid capturing small individuals (Zhou et al., 2010). The selective removal of large individuals over time can lead to a population dominated by small and young individuals, reflected by a left-skew in the population's size structure (Skiftesvik & Halvorsen, 2019). In species where one sex is larger than the other, a size-selective fishery can also disproportionately remove more of the larger sex (Parker 1992; Rijnsdorp, van Damme & Witthames, 2010).

A size- and sex- selective fishery can lead to a population with a truncated size and age distribution as well as imbalanced sex ratios (Fenberg & Roy, 2008; Halvorsen et al., 2016b). These consequences have negative implications for population productivity in terms of reduced reproductive output (Rowe & Hutchings, 2003; Sørdalen et al., 2018). It is documented that older and larger females produce more eggs over a longer period of time, and that these eggs develop into larvae with faster growth and higher survival than those produced by younger and smaller females (Barneche, Robertson, White & Marshall, 2018; Hixon, Johnson & Sogard, 2014). Furthermore, it well recognized that the effects of selective fishing can drive evolution in harvested populations that may be difficult, if not impossible, to reverse (Law, 2000; Zhou et al., 2010; Haugen & Vøllestad, 2001; Fenberg & Roy, 2008). An intense fishery that removes large individuals selects against genotypes with fast growth and late maturation, ultimately leading to a shift towards slower growth and earlier maturation (Zhou et al., 2010; Berkeley, Hixon, Larson & Love, 2004; Haugen & Vøllestad, 2001; Olsen et al., 2004).

Marine protected areas (MPAs), where an area is partially or completely closed to fishing, are increasingly used to restore depleted populations (Halvorsen et al., 2017; Sørdalen, Halvorsen, Vøllestad, Moland & Olsen, 2020). There is growing evidence of the positive effects that MPAs have on abundance, biomass, body size and age of harvested fish populations (Baskett & Barnett, 2015; Fernández-Chacón et al., 2020; Moland et al., 2013; Halvorsen et al., 2017). The benefits that MPAs provide have been shown to buffer fisheries-induced evolution and contribute to fisheries through the spillover of adults and export of eggs and larvae outside the MPA (Sørdalen et al., 2020; Goñi, Hilborn, Díaz, Mallol & Adlerstein, 2010; Harrison et al., 2012). The effectiveness of an MPA to provide benefits to an ecosystem depends on the design of the MPA including its size, location, proximity to other MPAs, and degree of protection (full/partial protection) (Halvorsen et al., 2017). A species' response to protection depends largely on the behavior and ecology of the species, as well as the intensity and selectivity of the fishery (Halvorsen et al., 2017; Baskett & Barnett, 2015). MPAs offer a greater degree of protection to sedentary species that remain within the MPA boundaries than to more mobile species that frequently move beyond the boundaries (Villegas-Ríos, Moland & Olsen, 2017). MPAs also provide a unique research opportunity to study ecological processes in the absence of harvest mortality, which can provide insight into the impact of the fishery on local populations (Moland et al., 2013).

MPAs have been established along the coastlines of Southern and Western Norway with the goal of rebuilding depleted European lobster (*Homarus gammarus*, Linnaeus 1758) populations (Sørdalen et al., 2020; Halvorsen et al., 2017). These MPAs prohibit the use of standing types of fishing gear (e.g. gillnets, pots, fyke nets) which results in a full protection of wrasse that are only targeted using these types of gear (Olsen et al., 2018). A study from Halvorsen et al. (2017) investigates the effects of protection on wrasse in four MPA-control pairs along the Skagerrak coastline and found that there was higher abundance of both corkwing and goldsinny inside MPAs. In addition, the corkwing were found to be larger and older within the MPA while there was no significant effect on size and age for goldsinny (Halvorsen et al., 2017).

These findings suggest that MPAs can be an effective management strategy for maintaining wild wrasse populations (Halvorsen et al., 2017). The wrasse fishery is much larger in Western Norway than in Southern Norway and therefore the impacts of protection for wrasse would likely be greater in the more intensively fished areas. In Western Norway, a network of nine MPA's was implemented in the Hardangerfjord in October 2016 and a single MPA was implemented on the coastline outside of Austevoll municipality in October 2018 (Halvorsen et al., 2016b). This thesis focuses on the MPA in Austevoll and provides the first assessment on the impacts of an MPA in western Norway on local wrasse populations.

1.5 Scale and otolith aging

Information about the age of fish is essential for management as it allows for the estimation of growth and mortality rates, as well as the lifespan of species (Boughamou, Derbal & Kara, 2014; Casselman, 1983; Campana, 2001). Two anatomical structures that are commonly used in determining the age of fish are scales and otoliths (Boughamou et al., 2014; Casselman, 1983). In order for an otolith to be used for determining age, it must grow throughout the entire life of the fish and it must exhibit growth zones that are definable and formed on a regular basis (Fowler, 1990; Villegas-Ríos et al., 2013) The growth zone of a scale is interpreted by their checks (or breaks) formed in their circuli, and the growth zone of an otolith is interpreted by their translucent zones, both of which are formed annually (Casselman, 1983). Aging with otoliths is preferred to scales because scales have been found to grow unevenly or reabsorb when there is a lack of food available or during stressful conditions (Campana & Neilson, 1985). Otoliths are considered to be more reliable because scales have been found to underestimate the age of older fish (Beamish & McFarlane, 1983; Casselman, 1983). The benefit of aging with scales is that they are less time consuming to prepare and examine than otoliths and it does not require killing the fish (Boughamou et al., 2014; Casselman, 1983).

In a study that utilized both the otolith and scale methods to determine the age of the peacock wrasse (*Symphodus Tinca* Linnaeus, 1758), it was found that the two methods yielded similar results (Boughamou et al., 2014). The otoliths were found to have a better fit than the scales (99.61% compared to 91.25% respectively), however the scales were much easier and less time consuming to process and examine (Boughamou et al., 2014). A master thesis (Vik, 2019) tested the scale method for determining age of corkwing in Western Norway by comparing scale age to otolith age and found the error rate to be 13.18%.

Otolith aging has been validated as a method for ballan wrasse (Villegas-Ríos et al., 2013), however the potential to age ballan using scales has not yet been investigated. The validation of the scale method for two other wrasse species, the peacock wrasse and the corkwing, gives reason to believe this could be a valid method for the ballan. One important aspect to consider is that peacock wrasse can live to be 13 years of age, corkwing 9 years, and ballan 29 years (Pallaoro & Jardas, 2003; Costello, 1991; Dipper et al., 1977). With regards to the criticism that the scale method underestimates the age of old fish, the ballan may not be a good fit for the scale method due to its long lifespan.

1.6 Study objective

The primary objective of this project is to compare catch per unit effort (CPUE), size and age of wrasse in two pairs of MPAs and control areas in Austevoll and Tvedestrand respectively. In Austevoll, wrasse were sampled during three periods both before and after the MPA was established in 2018, and sampling took place in protected areas and in nearby control areas where the fishery is active. In Tvedestrand, a nine-year dataset of wrasse sampled in and outside the MPA is analyzed to assess the impact of protection on wrasse populations in this region. The hypothesis is that the wrasse will be more abundant, larger and older in MPAs compared to control areas and that the response will be species specific depending on differences in fishing pressure, depth distribution, life history traits and management. The response is expected to be greater for wrasse species that 1) are subject to higher fishing pressure, 2) primarily occupy the depths where fishing occurs, 3) change sex or display sexual size dimorphism, and 4) are harvested before reaching maturation due to an inadequate minimum size limit. The first two characteristics, fishing pressure and depth, are most relevant for early responses to an MPA while the latter characteristics, regarding life history and management of the species, are mainly relevant for long-term responses. The MPA in Tvedestrand has been implemented longer than the MPA in Austevoll and it is therefore expected that there will be more long-term effects of protection in Tvedestrand. The research in Austevoll, however, will shed light on the early response of protection in the most intensively fished area for wrasse in Norway. A secondary objective is to evaluate the method of using scales for aging ballan wrasse by comparing the age determined by reading scales to the age determined by reading otoliths.

2. Materials and methods

2.1 Study area

The MPA in Southern Norway is located on the Skagerrak coastline outside of Tvedestrand municipality and was established in 2012 (Espeland et al., 2016; Figure 2). The region where Tvedestrand is located (Aust-Agder county) has sustained moderate fishing pressure for wrasse since the 1990's (Halvorsen et al., 2017) and experienced a substantial increase since 2013 (Norwegian Directorate of Fisheries, 2020a; Figure 3). The MPA in Tvedestrand is composed of a network of five protected areas including Inner Oksefjord, Sagesund, Furøya, Kvadstadkilen, and Outer Skjærgård (Espeland et al., 2016; Figure 2). These areas are partially protected and prohibit the use of standing types of fishing gear, except for Furøya which is a no-take zone that prohibits the harvesting of all marine resources (Norwegian Directorate of Fisheries, 2018; Figure 2). The Sagesund and Inner Oksefjord areas together covers 1.97 km^2, the Furøya no-take zone covers 1.48 km^2, the Outer Skjærgård area covers 5.3 km^2, and the Kvadstadkilen area was not included in this study (Table 1). The network of MPAs in Tvedestrand will be collectively referred to as one MPA for the remainder of this thesis.

The MPA in Western Norway surrounds a small group of islands outside of the Austevoll municipality and was established in October 2018 (Norwegian Directorate of Fisheries, 2018; Figure 2). The MPA covers an area of 2.2 km^2 and it prohibits the use of standing types of fishing gear. The western region of Norway sustains a much higher level of fishing pressure than Southern Norway, where the total catch of wrasse in 2019 was 11.5 million individuals in the west and 4.1 million in the south (Norwegian Directorate of Fisheries 2020a; appendix A1).

Table 1: The location, size, and year of establishment of the MPAs in this study (Norwegian Directorate of Fisheries, 2018; 2019a).

Locality	MPA location	MPA size (km^2)	MPA est.
Tvedestrand	Inner area: 58°34' – 36'N, 8°56' – 9°0'E	4.1	2012
	Outer area: 58°35' – 37'N, 9°4' – 7'E	5.3	
Austevoll	60°07' – 08'N, 5°13' – 15'E	2.2	2018

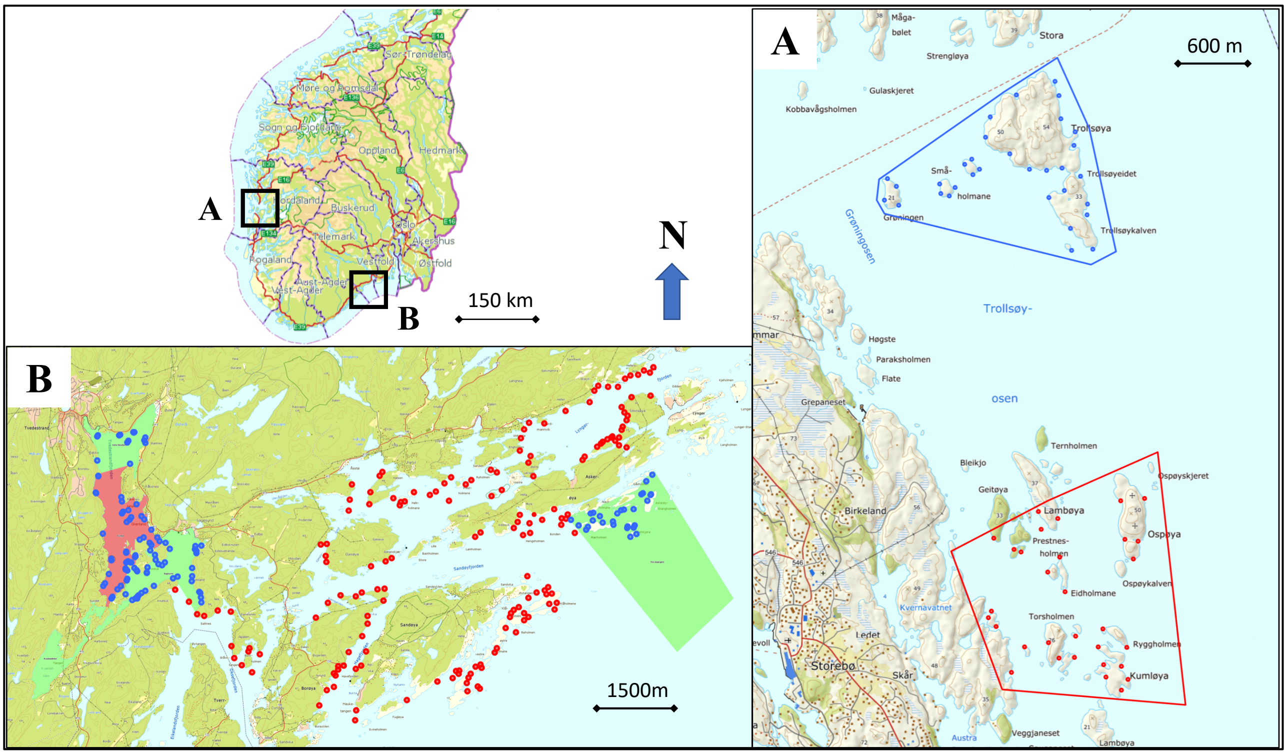

Figure 2: Map of the study area in Austevoll (A) and Tvedestrand (B). In Austevoll, solid lines represent the border of the MPA (blue) and control (red) areas. In Tvedestrand, the shaded areas indicate the boundaries of the partially protected areas (green) and the no-take zone (red). Dots represent sampling stations in the MPAs (blue) and in control areas (red). Map were created using Yggdrasil (Norwegian Directorate of Fisheries, 2020d). Larger images of the maps are available in appendix B.

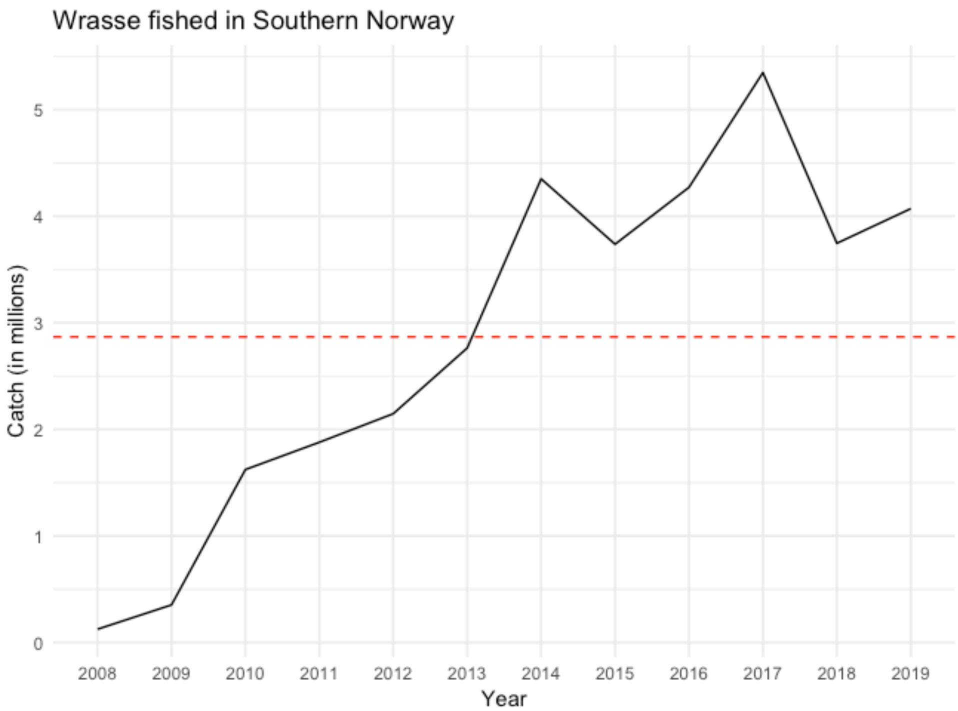

Figure 3: The development of the wrasse fishery in Southern Norway from 2008-2019. The red dotted line indicates mean catch of all the years combined. The data from 2008-2012 was calculated from tonnes to number of individuals captured (Norwegian Directorate of Fisheries, 2020c), and the data from 2013-2019 was provided in number of individuals captured (Norwegian Directorate of Fisheries, 2020a).

2.2 Sampling

This study used a before-after control-impact (BACI) approach that samples in control sites (e.g. outside MPA boundaries) and in impact sites (inside MPA boundaries) both before and after the MPA was implemented (Osenberg, Shima, Miller & Stier, 2011). The changes observed in the impact sites relative to the control sites after an MPA is established can provide a measure of the effects of protection (Osenberg et al., 2011). It was decided that a BACI approach would be most effective for addressing the research question because it is currently considered to be the optimal method for assessing the impacts of MPAs (Moland et al., 2013; Osenberg et al., 2011).

Sampling in Austevoll was conducted during three periods in July 2018, June 2019, and September 2019 (Table 2). The purpose of the 2018 sampling was to collect preliminary data before the MPA had an effect, while the 2019 sampling provides insight into the first year of the MPA both before the fishery began (June) and at the end of the fishery (September). The gear that was used to capture the wrasse was unbaited fyke nets (7.8 m single leader, 70 cm diameter entrance ring, leader mesh size of 11 mm, total length 11.3 m). A data logger was attached at the first ring after the entrance of the net to record soak time, water depth and water temperature. The fyke nets were placed perpendicular to the shoreline in rocky areas with kelp-covered substrate at <8 m depth, and they were hauled the following day (16-29 hours soak time). The location of each sampling station was recorded using a hand-held GPS.

The first sampling period was conducted for 3 days with 24 fyke nets hauled in both MPA and control areas (Table 2). The second and third sampling periods consisted of 4 days each with a total of 32 fyke nets hauled in both MPA and control areas per period (Table 2). At each site all individual organisms were identified and measured to the nearest millimeter. The sex was determined for all wrasse species by visual inspection of coloration, with the exception of ballan which are not possible to visually distinguish male from female. The corkwing can be found either as nesting males, sneaker males, or females (Uglem et al., 2000). The sneaker male is visually identical to the female (Uglem et al., 2000) and therefore it is only possible to distinguish them during the spawning season. The sampling periods in June and July took place during the spawning season, and the spawning status of all wrasse species was determined by gently applying pressure to the abdomen of the fish to release sexual products (milt/roe). Sneaker males were correctly identified during the June and July sampling periods and misidentified as females during the September sampling period. This study does not include sex in the analysis, however information about sex was gathered to be useful for other analyses. For each ballan that was caught during the 2019 sampling (n=89), 2-5 scales were carefully removed and placed in a tube to be used for later age determination.

Sampling in Tvedestrand was conducted by the Institute of Marine Research (IMR) every June from 2010-2019. During the nine-year timespan there were a total of 770 fyke nets deployed in protected areas and 820 fyke nets deployed in control areas. The fishing gear that was used was unbaited fyke nets (5m single leader, 55cm diameter entrance ring and leader mesh size of 30mm) that had a larger mesh size and shorter leading net than those used in Austevoll. The first year the sampling locations were selected by local fishermen, the second year additional locations were supplemented by the researchers, and the following years positions were randomly resampled to avoid subjective bias in catch rates (S. Espeland, personal communication, September 2019). During the first year, the entire municipality was sampled including the Outer Skjærgård protected area, however from the second year the study area was reduced and the outer area was no longer included (S. Espeland, personal communication, September 2019). The fishing locations from sampling in 2014 were not randomly selected and therefore the data from this year was excluded from the analysis (S. Espeland, personal communication, April 2020). The location of the fyke nets were registered when the nets were set, and the nets were hauled the following day. At each site all individual organisms were identified and measured to the nearest millimeter.

Table 2: Number of fishing gear used in MPA and control areas during the sampling periods and the total gear used at each locality. Date of sampling is provided for each sampling period in Austevoll (date format dd.mm.yy) and year of sampling is provided for Tvedestrand.

Locality	Sampling period	Treatment	Fishing gear used
Austevoll	July 2018 (10.7.18-12.7.18)	MPA	24 fyke nets
		Control	24 fyke nets
	June 2019 (18.06.19-21.06.19)	MPA	32 fyke nets
		Control	32 fyke nets

	September 2019 (9.9.19-12.9.19)	MPA	32 fyke nets
		Control	32 fyke nets
	Total	**MPA**	**88 fyke nets**
		Control	**88 fyke nets**
Tvedestrand	Early fishery (2010-2013)	MPA	302 fyke nets
		Control	360 fyke nets
	Late fishery (2014-2019)	MPA	468 fyke nets
		Control	460 fyke nets
	Total	**MPA**	**770 fyke nets**
		Control	**820 fyke nets**

2.3 Age determination

In order to test the reliability of using ballan scales as a method for determining age, 129 ballan were captured at Flødevigen in 2018 and the age determined from their scales and otoliths was compared. The use of ballan otoliths for aging purposes was validated by Villegas-Ríos et al. (2013). In order to test for the effect of MPAs on the age of ballan, scales were collected from each ballan (n=89) captured during the 2019 sampling in Austevoll and aged. The details of testing the scale aging methodology are presented in section 2.3.1 and the details of testing the effect of MPAs on the age of ballan are presented in section 2.3.2.

2.3.1 Flødevigen otoliths and scales

The ballan wrasse (n=129) that were used for comparing age of otoliths and scales were captured by researchers at IMR during a spawning survey in 2018 conducted on the coast outside of Flødevigen in Southern Norway. Of all the ballan that were captured, only individuals >12 cm were retained to be used for age determination. Otoliths were removed from the ballan by a lab technician and stored dry before being placed in black multicell trays with 96% ethanol. The otoliths were photographed by the lab technician with an IS 1000 microscope camera (20x enhancement) using the software IS capture. Scales were removed from the fish, placed into a tube, and stored dry at room temperature until October 2019 when they were analyzed by me. Since the scales were removed when the fish were no longer living, a large quantity of scales (6-20) were taken to ensure that some would be usable. In contrast, when scales were taken from live fish in Austevoll in the field (see section 2.3.2 below), a small quantity of scales (2-5) were taken to limit the amount of stress and damage inflicted on the fish.

In October 2019, the scales were prepared for analysis. First, all of the scales from an individual were placed under a microscope and the highest quality scales (5-6) were selected to be used. The scales were cleaned with soap to remove dirt and residuals, dipped in freshwater, and then patted dry between paper towels. The cleaned scales were placed between two microscope slides and visually inspected under a microscope for remaining dirt or particles. Once all scales were in place, the slides were taped together and labelled with the appropriate ID of the scale. After all scales were prepared on the slides, the scales were photographed using an IS 1000 microscope camera using the software IS capture. The magnification of the camera ranged between 7.11-10x depending on the size of the scale.

Otoliths and scales were analyzed by two independent readers that were previously trained to read otoliths and scales by an experienced lab technician at IMR. The photographs of the scales and otoliths were visually inspected to determine their age and a dot was placed at each growth zone using the open source image-analysis program Image J (plug-in Object J). Otoliths and scales were given a quality rating of 0-3 where 0 represents unreadable and 3 represents high certainty of age. Otoliths and scales assigned a quality rating of greater than or equal to 2 were included in the analysis, while those with a quality rating of less than 2 were excluded from the analysis due to uncertainty. The age of otoliths is determined by counting the clearly defined opaque zones, while the age of scales is determined by counting the breaks, both of which are formed annually (Figure 4). The age determined by scale analysis will be referred to as ‘scale age’, and the age determined by otolith analysis will be referred to as ‘otolith age’ for the remainder of the thesis. An example of otoliths and a scale taken from the same ballan wrasse are shown in Figure 4.

The otoliths and scales were inspected separately to avoid the possibility that aging results from otoliths would influence the aging of scales. In addition, the scales from an individual fish were analyzed independently rather than subsequently to prevent a biased interpretation. To ensure independent analysis, the first scale from all individuals was analyzed, followed by the second scale of all individuals, and so on. The age of scales determined by the two readers was compared afterwards and revealed that the two readers frequently disagreed on scale age by up to 5 years. It was then decided to make a subsample of scales (n=30) to analyze together with the knowledge of the age, based on the otoliths. This allowed both scale readers to learn how to properly age ballan wrasse scales. The scales that were selected for the subsample were those that both readers disagreed on by 2+ years. Then, all scales were analyzed a second time resulting in more frequent agreement of age. After the scale and otolith analyses were completed, their age was compared to discover the relationship between scale readings and otolith readings. In this study, otolith age is assumed to be correct given the fact that otolith reading is a well-established method of aging fish, and because otoliths have been validated as a method for aging ballan (Villegas-Ríos et al., 2013).

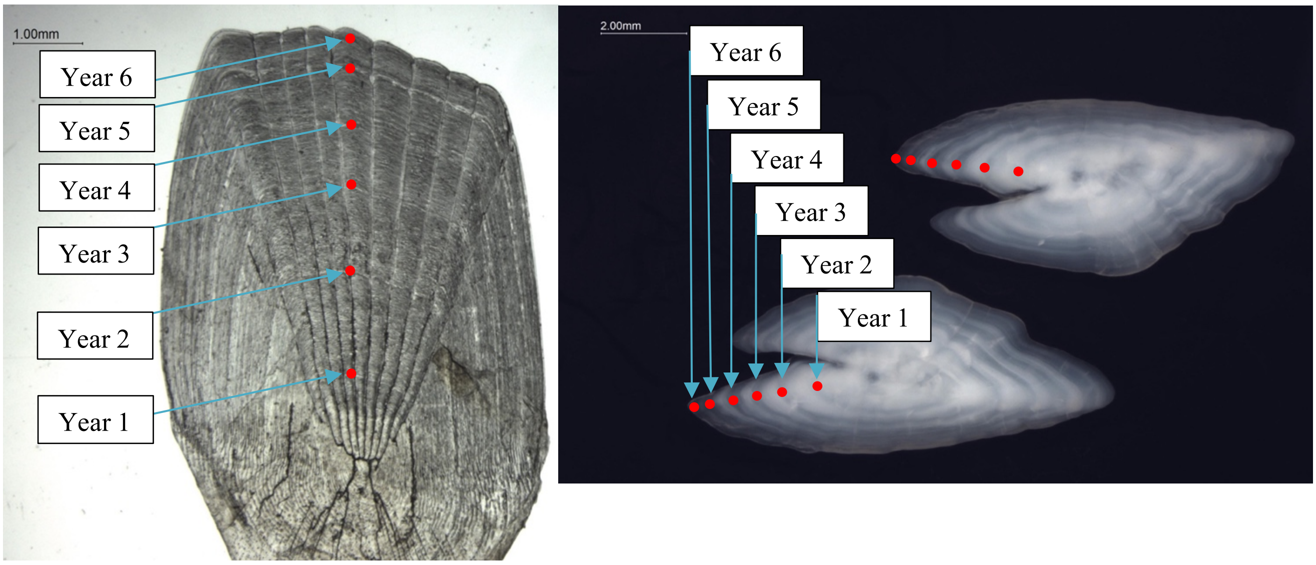

Figure 4: A scale (left) and associated otoliths (right) from a 6-year-old ballan. Growth zones are marked with a red dot and age of growth zone is indicated with a blue arrow.

2.3.2 Austevoll scales

Scales were collected from all of the ballan (n=89) that were captured during the 2019 sampling in Austevoll, including those that were under the minimum size limit (<14 cm). The scales were carefully removed from the abdomen of the fish with tweezers and placed into labelled tubes. The fish were handled with care and released into the same location they were captured after handling. The amount of scales that were taken from the live fish in Austevoll was considerably less (2-6 scales) than the amount of scales taken from the fish in Flødevigen (6-20 scales) during 2018. The procedures for cleaning and preparing the scales were identical to that mentioned above. However, instead of selecting the highest quality scales for analysis, all scales were cleaned and prepared since there were few. The procedures for quality rating, photographing and ageing the scales were the same as those mentioned above.

2.4 Data analysis

All statistical analyses were performed using the R software version 3.5.1 (R Core Team, 2018) and Rstudio (version 1.1.456). The ggplot2-package was used to create all graphics (Wickham, 2016). Generalized linear models were used to test for the effect of protection on age, length, and CPUE. The age and length data were modelled with a gaussian error distribution using the function lm(), while the CPUE data was modelled with a negative binomial distribution using the function glm.nb() from the MASS package (Venables & Ripley, 2002). The gaussian distribution was appropriate for the length and age data because they are normally distributed (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). The linear regression model is based on a series of assumptions such as normality, homogeneity, fixed X, independence, and correct model specification (Zuur et al., 2009). When applying a linear model to your data it is necessary to verify these assumptions through a model validation process. I followed the instructions provided by Zuur et al. (2009) for model validation which included: 1) checking for homogeneity by plotting the residuals vs. fitted values, 2) checking for normality by plotting a QQ plot, and 3) checking for independence by plotting the residuals against each explanatory variable (Zuur et al., 2009). The CPUE data had a variance that was larger than the mean, indicating overdispersion, and Zuur et al. (2009) recommends using a negative binomial distribution to deal with overdispersion.

The models were fitted separately for each species. The response variables in the models include length (mm), age (years), and CPUE (number of individuals caught in fyke net). The explanatory variables in the models include area (MPA, control) and sampling period. The CPUE dataset only includes wrasse that are greater than or equal to 11 cm, which was the minimum size limit for all wrasse before 2015. It was decided to only include wrasse greater than 11cm in the analysis because that is the same standard that was used in a previous assessment of the impact of MPAs on wrasse in Southern Norway (Halvorsen et al., 2017). Using the same standard makes it possible to compare results from the previous assessment.

There are three sampling periods for the Austevoll data which are July 2018, June 2019, and September 2019. The first sampling period in July 2018 represents pre-MPA effects because it occurred before the MPA was established in October 2018. The second sampling period, June 2019, is also considered pre-MPA effects because it takes place at the beginning of the first wrasse fishing season since the MPA was established. It is assumed that there are no effects of protection yet since there has been no fishing pressure in the control areas. The third sampling period in September 2019 is considered to be after MPA effects because it occurs at the end of the wrasse fishery, when we expect to see differences between protected and fished areas. The sampling in Tvedestrand took place over nine years from 2010-2019 and it was decided to split the sampling periods into two groups: early fishery (2010-2013) and late fishery (2014-2019). This is because the wrasse fishery in Southern Norway intensified after the year 2013, and this was the year that the catch began the exceed the average yearly catch (Figure 3, Norwegian Directorate of Fisheries, 2020a).

In order to detect if there is an impact of protection on age, length, or CPUE there must be a significant interaction effect between area and sampling period. This is because I assume there will be differences between areas (MPA, control) and there will be differences between sampling periods due to seasonal variation. In order to conclude that the differences are directly related to protection, there must be a significant interaction between area and sampling period. For this reason, two models were chosen a priori which included one with an interaction effect and one with only an additive effect:

$$Response = Area + sampling\ period$$

$$Response = Area \times sampling\ period$$

Model selection using the Akaike Information Criteria or AIC (Akaike, 1973) was used to select the best fit model between the two models. The AIC measures goodness of fit and model complexity, and the model with the lowest AIC score is considered to be the model that fits the data best (Zuur et al., 2009). If the difference in AIC scores (Δ AIC) between two models is less than two, then the model with fewest parameters is selected to be used for statistical inference as it is considered to be more parsimonious (Burnham & Anderson, 2004).

Variables such as depth of the fyke net, number of hours that the fyke net is deployed (soak time), and water temperature can impact the catch rates. To decide if these variables should be included in the models, a two-sided t-test assuming unequal variances was used to determine if these variables were significantly different between MPA and control areas. There was no significant difference between the depth of the fyke nets in control areas (mean = 3.83 m) and protected areas (mean = 3.60 m; t= -1.14, df= 143.60, P= 0.25). The soak time was slightly longer in control areas (mean = 22.49 hours) than in protected areas (mean= 21.42 hours; t= -2.05, df= 143.72, **P= 0.04**). There was no significant difference between the water temperature in the control area (mean= 14.09 ˚C) than in the protected areas (mean= 13.97 ˚C; t= -0.40, df= 143.13, P= 0.69). Since the water temperature and depth of fyke net were not found to be significantly different between areas these were not included in the models. The soak time however was found to be significantly different between MPA and control areas and was therefore included as an explanatory variable in the CPUE models for Austevoll. Including soak time in the model reduced the sample size from 176 fyke nets to 146 because only a portion of the fyke nets were equipped with depth loggers measuring soak time.

The von Bertalanffy (1938) growth model (VBGM) is the most common model used in fisheries for age and length (Haddon, 2011). There are many versions of the VBGM and the most commonly used version is the typical parameterization developed by Beverton (1954) and Beverton and Holt (1957) (Calliet et al., 2006). In this study, growth trajectories of the ballan in Flødevigen and Austevoll were constructed by fitting the typical parameterization of the von Bertalanffy growth model (VBGM) to the age and length data:

$$L_t = L_\infty \times [1 - e^{(-K(t-t_0))}]$$

Where L_t is the expected length at age t, L_∞ is the asymptotic length, K is the von Bertalanffy growth parameter and t_0 is the age at hypothetical length 0. The function vbStarts() in the FSA-package (Ogle, Wheeler, & Dinno, 2016) was used to determine the appropriate starting values for the parameters. For the Austevoll data, the starting value for L_∞ was found to be very different from the observed maximum length and the starting value of K was negative, both signs that indicate a model fitting problem (Ogle et al., 2016). Therefore, the starting value for L_∞ was manually set to the observed maximum length, and the starting value for K was manually set to 0.3 as suggested by the warning message provided in R by the FSA package (Ogle et al., 2016). The von Bertalanffy parameters were estimated using the nls() function (Ogle et al., 2016), and the confidence intervals were obtained by bootstrapping 1000 iterations using the Boot() function from the car package in R (Fox and Weisberg, 2011).

3. Results

3.1 Scale aging methodology

All otoliths (n=128) were assigned a quality rating of greater than or equal to 2 and were therefore included in the analysis (Table 3). A total of 68% of the scales (n=443) met the standards of the quality rating, while 32% of the scales (n=209) were assigned a quality rating of less than 2 and were therefore excluded from the analysis due to uncertainty of age (Table 3). The reduction in scales due to the quality rating reduced the number of ballan in the sample from 128 to 122 individuals.

Table 3: Quality rating for otoliths and scales used in age determination of ballan, including the number (and percentage) of otoliths and scales in each quality group. The otoliths and scales from Flødevigen are used for the scale aging methodology while the scales in Austevoll are used to test for the impact of protection on age of ballan.

Quality	Meaning	Otoliths Flødevigen	Scales Flødevigen	Scales Austevoll
3	High certainty	99 (77.3%)	309 (47.4%)	131 (49.4%)
2	Moderate certainty	29 (22.7%)	126 (19.3%)	38 (14.3%)
1	Uncertain	0 (0.0%)	185 (28.3%)	23 (8.6%)
0	Unreadable	0 (0.0%)	32 (4.9%)	73 (27.5%)
	Total:	128	652	265

The age of the ballan ranged from 3-14 years, with a mean age of 7.77 years. Percentage agreements between otolith and scale readings were higher for Reader 1 (63.3% agreement) than for Reader 2 (44.6% agreement). Although the percentage of agreement between scale and otolith age was low, the scale age was often within 1-2 years of the otolith age. Scales from individuals that were 3-5 years old were aged with high accuracy, and both readers aged all of the scales within one year of the otolith age (appendix C). Scales from ballan that were 6-7 years old were aged with good accuracy, and both readers aged all of the scales within two years of the otolith age (appendix C). Scales from ballan that were 8-10 years old were aged with moderate accuracy, while Reader 1 aged all of the scales within two years of otolith age and Reader 2 aged 88% of the scales within two years of otolith age (appendix C). Scales from ballan that were 11+ years old were aged with poor accuracy, and the scale age was often 3 or more years lower than the otolith age for both readers (appendix C). The relationship between scale and otolith age is shown in Figure 5. Trend lines from both readers are below the reference line after age 6, and the distance between the trend lines and the reference line increases with increasing age (Figure 5).

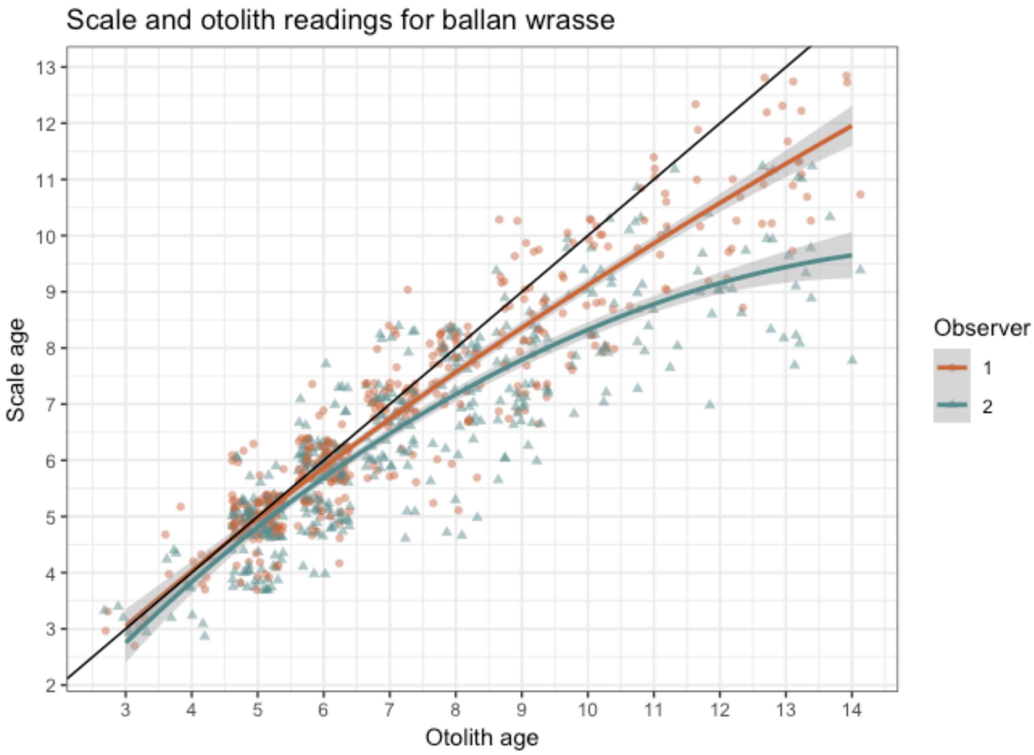

Figure 5: Age of ballan as determined by scales (y-axis) compared to otoliths (x-axis). Trend lines for the two independent observers are included as well as a black reference line indicating where scale age equals otolith age. Each point represents a scale reading (n=652 per observer).

3.2 Austevoll

3.2.1 Age

The Austevoll sample consisted of 265 scales that were analyzed from 87 ballan. A total of 64% of the scales (n=169) were assigned a quality rating of greater than or equal to 2 and were therefore included in the analysis, while 36% of the scales (n=96) were assigned a quality rating of less than 2 and were excluded from the analysis due to uncertainty of age (Table 3). The reduction in scales due to the quality rating reduced the number of ballan in the sample from 87 to 72 individuals. Mean age of ballan was 2.63 years and maximum age was found to be 16 years. The oldest ballan was excluded from the von Bertalanffy growth model due to a model fitting problem, and therefore the age range of ballan included in the model was 1-8 years old (Figure 7, right).

The model results show that there is no significant effect of protection on age of ballan in Austevoll (Table 5). There are significant differences in age between sampling periods in which ballan were found to be significantly younger in September than in June (Table 5, Figure 6).

Given the 14 cm minimum size limit for ballan wrasse, only 1-year-old individuals are fully protected in Austevoll according to the von Bertalanffy growth model (Figure 7, right). In their second year, ballan wrasse captured in June are below the minimum size limit, but most individuals seem to grow out of protection during their second summer as they become larger than 14 cm (Figure 7, right).

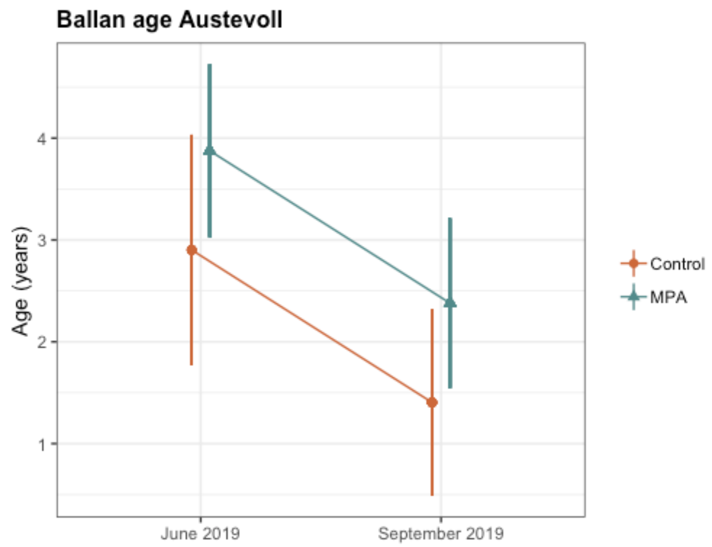

Figure 6: Predicted effect of protection (MPA or control) on age of ballan in Austevoll as estimated by linear models. Error bars show standard error around the predicted means.

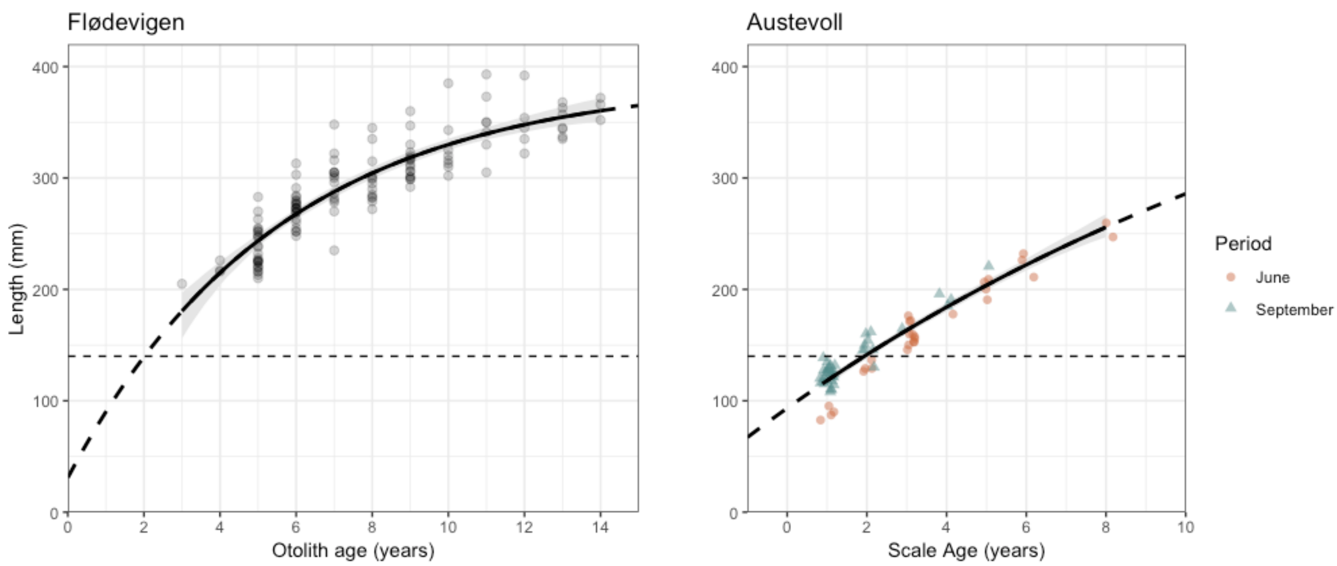

Figure 7: Fitted line plot of the von Bertalanffy growth model for ballan wrasse captured in Flødevigen (left) and Austevoll (right) with approximate 95% bootstrap confidence bounds. Points represent all ballan included in the

analysis (n=128 Flødevigen, n=87 Austevoll). The horizontal line represents the minimum size limit for ballan (14cm). Von Bertalanffy parameter estimates Flødevigen: $L\infty$ = 389.00, k = 0.18, t0 = -0.46; and Austevoll: $L\infty$ = 526.58, k = 0.05, t0 = -3.3.

3.2.2 Body size

In Austevoll, a total of 4748 wrasse were captured and measured for length. A summary of the length of wrasse captured in Austevoll including the sample size for each species, the mean length, and the percentage of individuals above the minimum size limit is provided in Table 4. The length distribution for all wrasse species captured in Austevoll can be found in appendix D1. There are considerable differences in length between MPA and control areas during the three sampling periods (appendix D2). Corkwing is the only species in which it is possible to see a clear shift from larger individuals in the control area before the MPA was implemented (June 2018), to larger individuals in the protected area after the MPA was implemented (September 2018) (Figure 8). This effect was supported statistically, where model selection favored the model with Period x Area interaction (Δ AIC: 71.49) (appendix E1).

Table 4: Summary statistics of the length and CPUE of wrasse in Austevoll and Tvedestrand. Table includes species, sample size for length and CPUE, mean length and range, as well as percentage above minimum size limit which is 14cm for ballan, 12cm for corkwing, and 11cm for all other wrasse species.

Location	Species	Sample size length	Sample size CPUE	Mean length (range)	% > minimum size limit
Austevoll	Corkwing	2577	1479	118 (67-217)	41%
	Goldsinny	1466	586	108 (74-160)	42%
	Ballan	110	90	180 (83-435)	65%
	Rock cook	417	169	110 (70-150)	55%
	Cuckoo	178	144	176 (110-264)	100%
Tvedestrand	Corkwing	3619	3334	141 (50-230)	85%
	Goldsinny	3302	2068	111 (50-210)	63%
	Ballan	635	625	218 (90-410)	94%
	Rock cook	2700	2078	118 (70-190)	77%
	Cuckoo	349	341	192 (90-320)	98%

The model results show that corkwing was the only species found to be significantly larger in the MPA than in control areas after the MPA takes effect (Table 5, Figure 8). The average length of corkwing remained relatively stable in the MPA and dropped in the control area from 131.50 mm before MPA establishment to 110.04 mm after the fishery. The difference in average length between MPA and control areas after the fishery was found to be 11.78 mm.

The model for goldsinny shows that they were significantly larger in the MPA than in control areas, however this was the case in all three periods (Table 5, Figure 8). The models for ballan, rock cook and cuckoo show no effect of protection on length, however there were significant differences in length between sampling periods for ballan and rock cook (Table 5, Figure 8).

Table 5: Summary of generalized linear models on the effects of protection (MPA, control) on length and age of wrasse in Austevoll. The table shows response variable, species, coefficients, estimate, standard error, T value and P value. Significant terms are illustrated with a p-value in bold**.** Reference level is control area and September 2019.

Response	Species	Coefficients	Estimate	Std. Error	T value	P value
Length	Corkwing	(Intercept)	110.05	0.78	140.12	< **0.0001**
		MPA	11.77	1.09	10.77	< **0.0001**
		July 2018	21.42	2.19	9.77	< **0.0001**
		June 2019	8.81	1.71	5.15	< **0.0001**
		MPA: July 2018	-25.08	2.92	-8.59	< **0.0001**
		MPA: June 2019	-7.52	2.52	-2.99	< **0.01**
	Goldsinny	(Intercept)	108.87	0.44	247.31	< **0.0001**
		MPA	1.65	0.55	3.02	< **0.01**
		July 2018	-3.67	0.77	-4.77	< **0.0001**
		June 2019	-4.86	0.64	-7.20	< **0.0001**
	Ballan	(Intercept)	151.95	13.53	11.23	< **0.0001**
		MPA	17.18	14.27	1.20	0.23
		July 2018	60.33	17.78	3.39	< **0.001**
		June 2019	11.07	15.88	0.70	0.49
	Rock cook	(Intercept)	100.28	1.74	57.71	< **0.0001**
		MPA	2.39	1.45	1.64	0.10
		July 2018	11.70	1.77	6.63	< **0.0001**
		June 2019	11.50	2.39	4.81	< **0.0001**
	Cuckoo	(Intercept)	173.63	4.91	35.40	< **0.0001**
		MPA	5.00	5.54	0.90	0.37
		July 2018	1.07	5.95	0.18	0.86
		June 2019	-1.46	8.81	-0.17	0.87
Age	Ballan	(Intercept)	1.40	0.47	3.00	< **0.01**
		MPA	0.97	0.56	1.75	0.09
		June 2019	1.50	0.54	2.75	< **0.01**

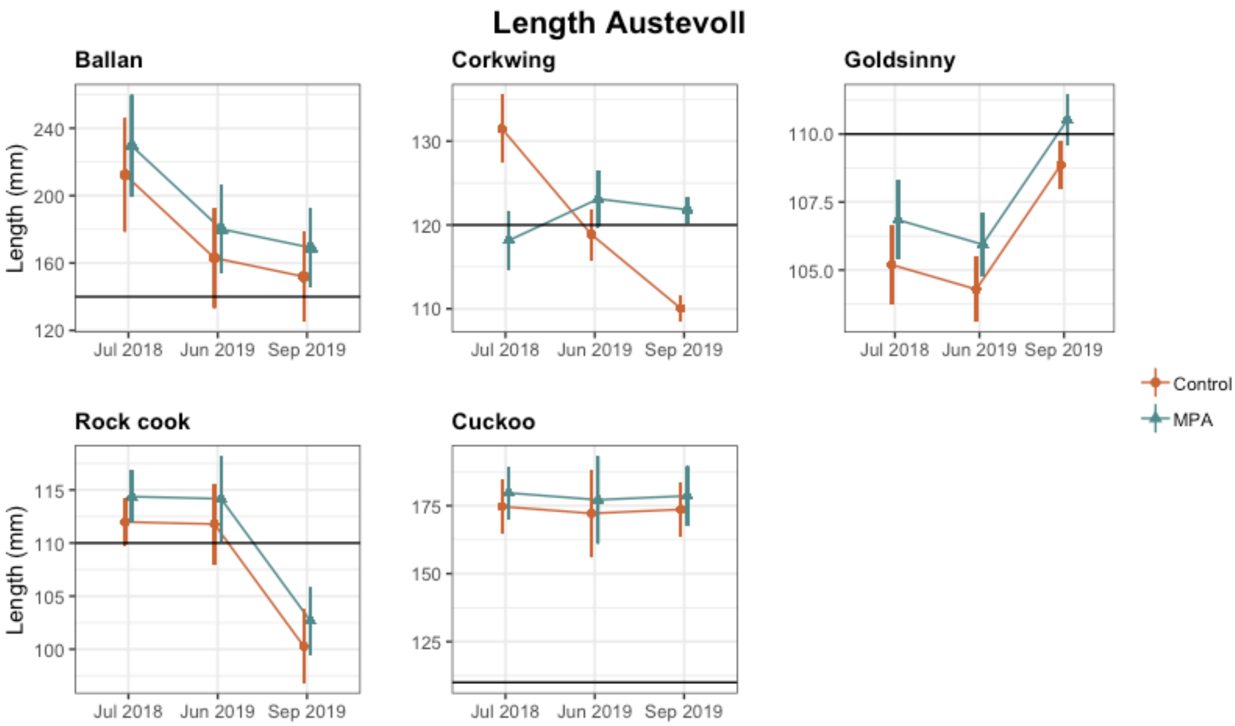

Figure 8: The predicted effect of protection (MPA or control) on length as estimated by linear models for ballan, corkwing, goldsinny, rock cook, and cuckoo wrasse captured in Austevoll during the three sampling periods. Error bars show ±1 standard error around the predicted means. The solid black line represents the minimum size limit for each species.

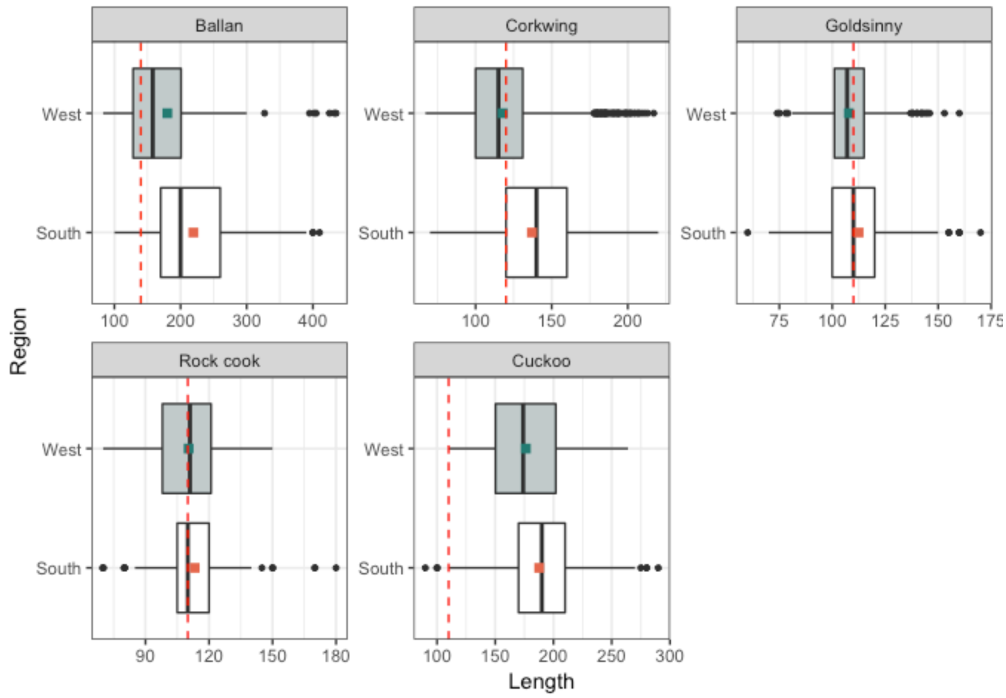

Figure 9: Boxplot showing the median (thick black vertical line) and mean (solid squares) of length (mm) of wrasse captured in Western Norway (Austevoll) and Southern Norway (Tvedestrand) during 2018-2019. The dotted red line indicates minimum size limit for each species (ballan 14 cm; corkwing 12 cm; goldsinny, cuckoo and rock cook 11cm).

3.2.3 CPUE

Of the 4748 wrasse that were captured and measured for length in Austevoll, only 2468 were included in the CPUE dataset after removing individuals <11 cm and including soak time in the models. The inclusion of soak time in the models decreased the number of fyke hauls in the sample from 176 to 146. The sample size for each species included in the CPUE analysis is shown in Table 4. For all species, model selection favored the model without an interaction effect between area and sampling period (appendix E1).

The model results show that there were significant differences in CPUE between the sampling periods for corkwing, goldsinny, rock cook and cuckoo (Table 6, Figure 10). The average CPUE of corkwing and goldsinny was significantly higher during September than in June and July; increasing from approximately 5 corkwing per net in the summer months to more than 15 in September, and from approximately 2 goldsinny per net in the summer months to more than 6 in September (Figure 10). The average CPUE of rock cook and cuckoo was significantly higher during July 2018 than in June and September 2019; decreasing from approximately 4 rock cook per net in 2018 to less than 1 in 2019, and from approximately 2 cuckoo per net in 2018 to 1 in 2019 (Table 6, Figure 10). Soak time was found to have a positive effect on catch rate for ballan, corkwing and goldsinny (Table 6).

Table 6: Summary of generalized linear models on the effects of protection (MPA, control) on CPUE of wrasse in Austevoll. The table shows response variable, species, coefficients, estimate, standard error, Z value and P value. Significant terms are illustrated with a p-value in bold**.** Reference level is control area and September 2019.

Response	Species	Coefficients	Estimate	Std. Error	Z value	P value
CPUE	Corkwing	(Intercept)	2.65	0.18	15.07	**< 0.0001**
		MPA	0.28	0.20	1.42	0.16
		July 2018	-1.14	0.29	-3.93	**< 0.0001**
		June 2019	-1.23	0.21	-5.74	**< 0.0001**
		Soak time	0.29	0.10	2.9	**< 0.01**
	Goldsinny	(Intercept)	1.78	0.12	13.90	**< 0.0001**
		MPA	0.16	0.15	1.07	0.28
		July 2018	-1.03	0.23	-4.57	**< 0.0001**
		June 2019	-1.17	0.17	-7.03	**< 0.0001**
		Soak time	0.19	0.07	2.59	**0.01**
	Ballan	(Intercept)	-0.67	0.25	-2.66	**< 0.01**
		MPA	0.42	0.27	1.53	0.13
		July 2018	-0.04	0.37	-0.10	0.92
		June 2019	-0.36	0.30	-1.21	0.23
		Soak time	0.45	0.14	3.31	**< 0.001**
	Rock cook	(Intercept)	-0.80	0.33	-2.45	**0.01**
		MPA	-0.07	0.34	-0.19	0.85
		July 2018	2.25	0.45	5.01	**< 0.0001**
		June 2019	0.33	0.39	0.86	0.39
		Soak time	0.23	0.18	1.32	0.19
	Cuckoo	(Intercept)	0.16	0.19	0.83	0.41
		MPA	-0.15	0.22	-0.67	0.50
		July 2018	0.71	0.26	2.70	**0.01**
		June 2019	-1.03	0.28	-3.69	**< 0.001**
		Soak time	0.06	0.11	0.53	0.60

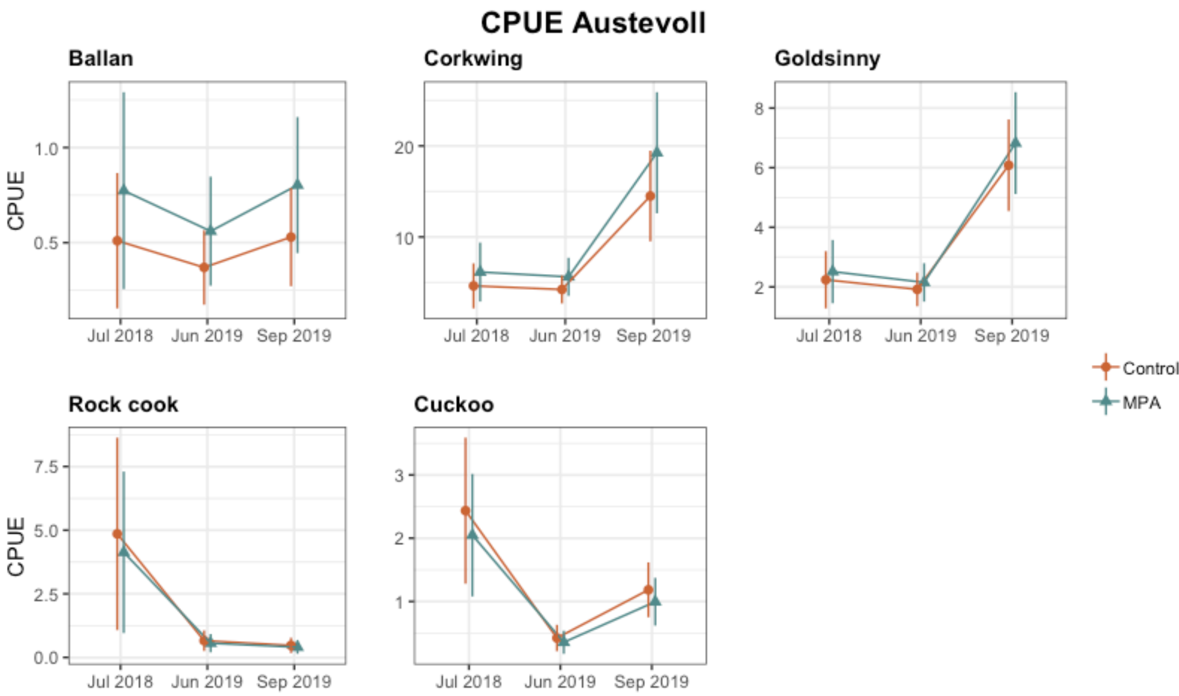

Figure 10: The predicted effect of protection (MPA or control) on CPUE as estimated by generalized linear models for ballan, corkwing, goldsinny, rock cook, and cuckoo wrasse captured in Austevoll during the three sampling periods. Error bars show ±1 standard error around the predicted means.

3.3 Tvedestrand

3.3.1 Body size

In Tvedestrand, a total of 10601 wrasse were captured and measured for length between the years 2010-2019. A summary of the length of wrasse captured in Tvedestrand including the sample size of each species, the mean length, and the percentage of individuals above the minimum size limit is provided in Table 4. The length distribution for all wrasse species captured in Tvedestrand can be found in appendix D3. There were considerable variations in length for all wrasse species between MPA and control areas during the nine-year time span. Ballan were found to be larger in the control areas than in the MPA until the year 2016 when the length of ballan in the control area dropped and the length in the MPA increased as shown in the time series plot (Figure 11). The length of corkwing in MPA and control areas fluctuated greatly during the nine-year time period and there is no apparent trend (Figure 11). The goldsinny were found to be larger in control areas than MPAs in 2012, then they were approximately the same length in both areas until 2016, and since then the goldsinny length has gradually declined in the MPAs (Figure 11). The length of rock cook follows the same pattern in MPA and control areas, however there was a spike of larger rock cook in the MPA during the years 2013-2015 (Figure 11). The cuckoo were approximately the same length in both areas during all years (Figure 11). The length of ballan, corkwing, rock cook, and cuckoo was always found to be higher than the minimum size limit indicated by the black horizontal line in Figure 11.

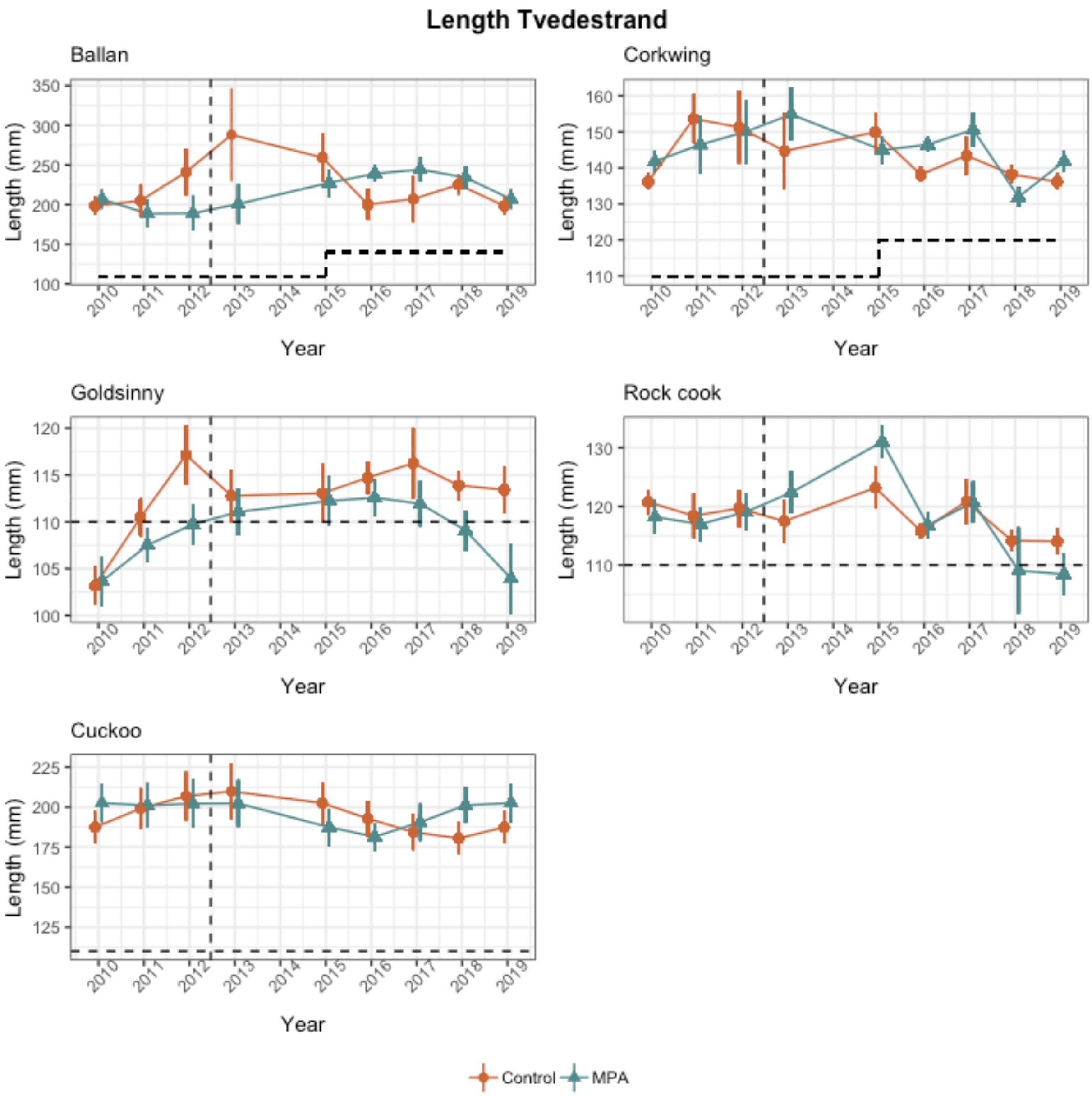

Figure 11: The predicted effect of protection (MPA or control) on length as estimated by generalized additive models for ballan, corkwing, goldsinny, rock cook, and cuckoo wrasse captured in Tvedestrand from 2010-2019. Error bars show ±1 standard error around the predicted means. Vertical black lines represent year of MPA establishment, horizontal black lines indicate minimum size limit which was 11 cm for all species until 2015 when it was increased to 14 cm for ballan and 12 cm for corkwing. The methods and details of the models these plots are based on can be found in appendix F.

Model selection favored the model with Period x Area interaction for both ballan (Δ AIC: 10.7) and rock cook (Δ AIC: 8.76) (appendix E2). The model results show that both ballan and rock cook were found to be significantly larger in the MPA than control areas during the late fishery period (Table 7, Figure 12). The average length of ballan remained stable in the control areas during both periods and it increased in the MPA from 189.75 mm in the early fishery period to 234.60 mm in the late fishery (Figure 12). The difference in average length of ballan between areas in the late fishery period was found to be 21.00 mm. The average length of rock cook remained stable in the MPA during both periods and it dropped in the control area from 119.71 mm in the early fishery period to 115.78 mm in the late fishery (Figure 12). The difference in average length of rock cook between areas in the late fishery period was found to be 3.74 mm. The model results also show that corkwing were found to be significantly larger in the MPA, and goldsinny were found to be significantly smaller in the MPA, however this was the case both in the early and late fishery period (Table 7, Figure 12).

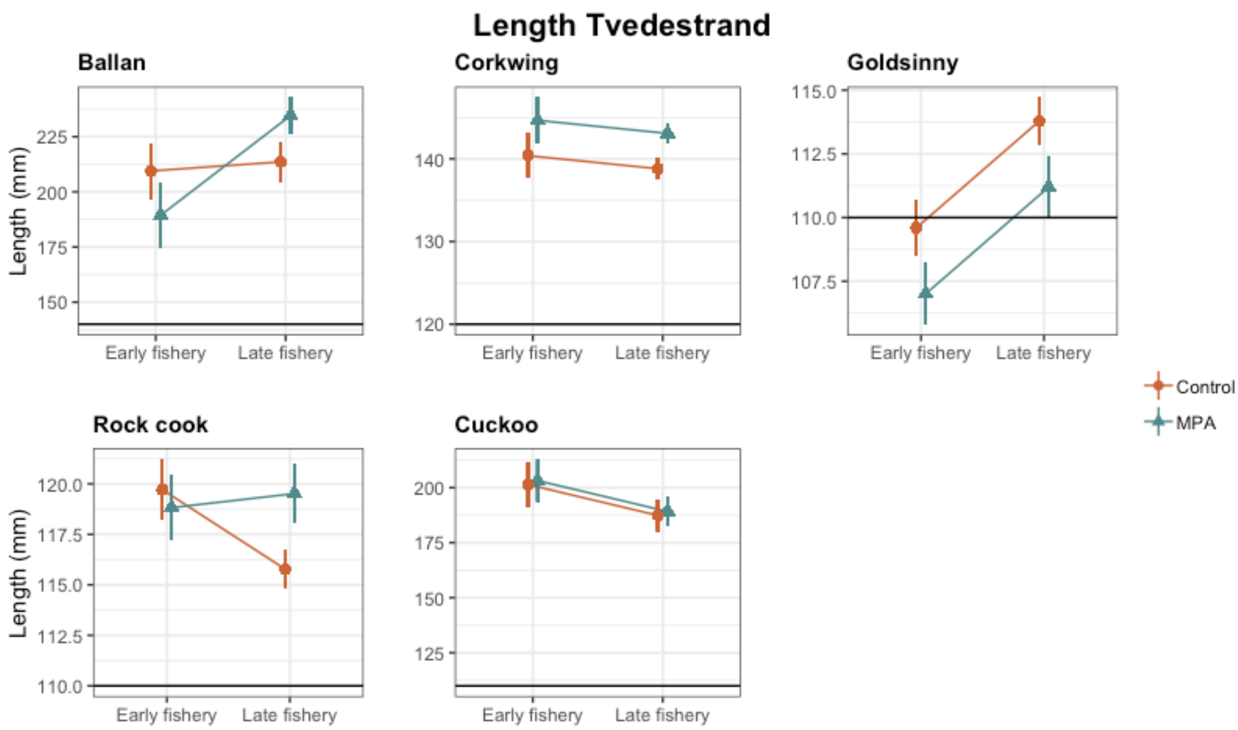

Figure 12: The predicted effect of protection (MPA or control) on length as estimated by linear models for ballan, corkwing, goldsinny, rock cook, and cuckoo wrasse captured in Tvedestrand during the early fishery (2010-2013) and the late fishery (2014-2019). Error bars show ±1 standard error around the predicted means. The black solid line represents the minimum size limit for each species.

Table 7: Summary of generalized linear models on the effects of area (MPA, control) on length and CPUE of wrasse in Tvedestrand. The table shows response variable, species, coefficients, estimate, standard error, T value for models with a Gaussian error distribution (length and age response variables), Z value for models with a negative binomial distribution (CPUE response variable), and p-value. Significant terms are illustrated with a p-value in **bold.** Reference level is control area and late fishery sampling period.

Response	Species	Coefficients	Estimate	Std. Error	T (Z) value	P value
Length	Corkwing	(Intercept)	138.73	0.64	216.28	**< 0.0001**
		MPA	4.35	0.85	5.09	**< 0.0001**
		Early fishery	1.63	1.37	1.19	0.24
	Goldsinny	(Intercept)	113.79	0.46	245.87	**< 0.0001**
		MPA	-2.60	0.66	-3.96	**< 0.0001**
		Early fishery	-4.19	0.64	-6.58	**< 0.0001**
	Ballan	(Intercept)	213.60	4.44	48.15	**< 0.0001**
		MPA	21.00	6.03	3.48	**< 0.001**
		Early fishery	-4.13	7.73	-0.53	0.60
		MPA: Early fishery	-41.08	11.50	-3.57	**< 0.001**
	Rock cook	(Intercept)	115.78	0.46	251.92	**< 0.0001**
		MPA	3.74	0.87	4.31	**< 0.0001**
		Early fishery	3.94	0.89	4.42	**< 0.0001**
		MPA: Early fishery	-4.63	1.41	-3.28	**0.001**
	Cuckoo	(Intercept)	187.38	3.62	51.72	**< 0.0001**
		MPA	1.77	4.46	0.40	0.69
		Early fishery	14.02	5.13	2.73	**0.01**
CPUE	Corkwing	(Intercept)	1.14	0.08	15.22	**< 0.0001**
		MPA	0.04	0.10	0.42	0.68
		Early fishery	-1.76	0.10	-17.35	**< 0.0001**
	Goldsinny	(Intercept)	0.67	0.06	10.37	**< 0.0001**
		MPA	-0.94	0.10	-9.36	**< 0.0001**
		Early fishery	-0.42	0.10	-4.15	**< 0.0001**
		MPA: Early fishery	0.82	0.15	5.30	**< 0.0001**
	Ballan	(Intercept)	-0.74	0.10	-7.61	**< 0.0001**
		MPA	0.04	0.12	0.31	0.75
		July 2018	-0.63	0.13	-4.93	**< 0.0001**
	Rock cook	(Intercept)	0.76	0.10	7.73	**< 0.0001**
		MPA	-0.96	0.14	-6.65	**< 0.0001**
		Early fishery	-0.71	0.15	-4.68	**< 0.0001**
		MPA: Early fishery	1.02	0.22	4.55	**< 0.0001**
	Cuckoo	(Intercept)	-1.46	0.12	-12.56	**< 0.0001**
		MPA	0.31	0.14	2.16	**0.03**
		July 2018	-0.73	0.15	-4.75	**< 0.0001**

3.3.2 CPUE

A total of 10600 wrasse were captured in Tvedestrand and of these, 8446 were above 11 cm and could be included in the CPUE analysis. The sample size for each species included in the CPUE analysis is shown in Table 4. The CPUE for each wrasse species varied considerably between MPA and control areas during the nine-year timespan. The CPUE of ballan was found to be similar between areas up until the year 2016 when it was higher in the MPA (0.75 individuals per net) than control areas (0.25 individuals per net) (Figure 13). The CPUE of corkwing was nearly identical in MPA and control areas during all years with a sharp increase from ~1 individual per net in 2015 to 5 individuals per net in 2016, followed by a gradual decrease in the following years (Figure 13). The CPUE of goldsinny fluctuated greatly during the nine-year time span and although both areas followed the same rise-and-fall pattern, CPUE was consistently higher in control areas than MPAs (Figure 13). The greatest difference in goldsinny CPUE between areas was observed in 2018 when mean CPUE was 3.5 individuals in control areas and 1 individual in MPAs (Figure 13). The CPUE of rock cook was approximately the same in MPA and control areas up until the year 2016 when it was found to be higher in control areas for all of the following years. The CPUE of cuckoo was found to be similar between areas, and although the time-series plot (Figure 13) appears to show higher CPUE in MPA areas, the difference was <1 individual per fyke net (see x-axis).

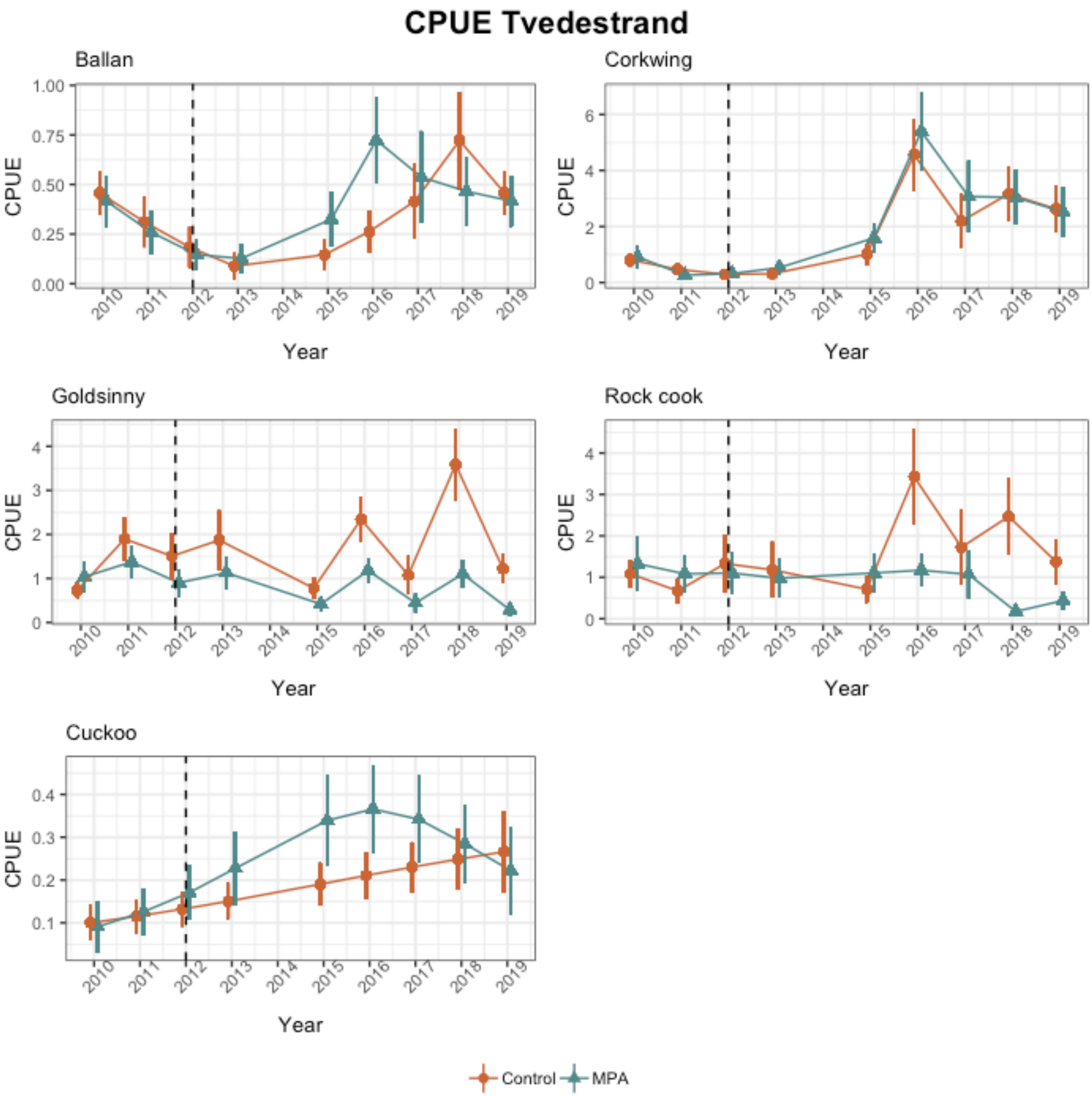

Figure 13: The predicted effect of protection (MPA or control) on CPUE as estimated by generalized additive models for ballan, corkwing, goldsinny, rock cook, and cuckoo wrasse captured in Tvedestrand from 2010-2019. Error bars show ±1 standard error around the predicted means. Vertical black line indicates year of MPA establishment. The methods and details of the models these plots are based on can be found in appendix F.

Model selection favored the model with Period x Area interaction for both goldsinny (Δ AIC: 25.76) and rock cook (Δ AIC: 18.49) (appendix E2). The model results show that there is significantly lower CPUE of goldsinny and rock cook in the MPA relative to the control area during the late fishery period (Table 7, Figure 14). The average CPUE of goldsinny decreased in the MPA area from ~1.2 individuals per net in the early fishery to ~.8 individuals per net in the late fishery and simultaneously increased in the control area from ~1.3 to ~1.9 individuals per net (Figure 14). The average CPUE of rock cook remained relatively stable in the MPA during both periods and it doubled in the control area from ~1.1 to ~2.2 individuals per net (Figure 14). The CPUE of goldsinny was found to be approximately 3.5x higher in the control area than the MPA during the late fishery period, and the CPUE of rock cook was found to be approximately 2.7x higher. The results also show significantly higher CPUE of cuckoo wrasse in the MPA than in control areas, however this was the case during both the early and late fishery period (Table 7, Figure 14). For ballan, corkwing and cuckoo there was significantly higher CPUE during the late fishery period as compared to the early fishery period (Table 7, Figure 14).

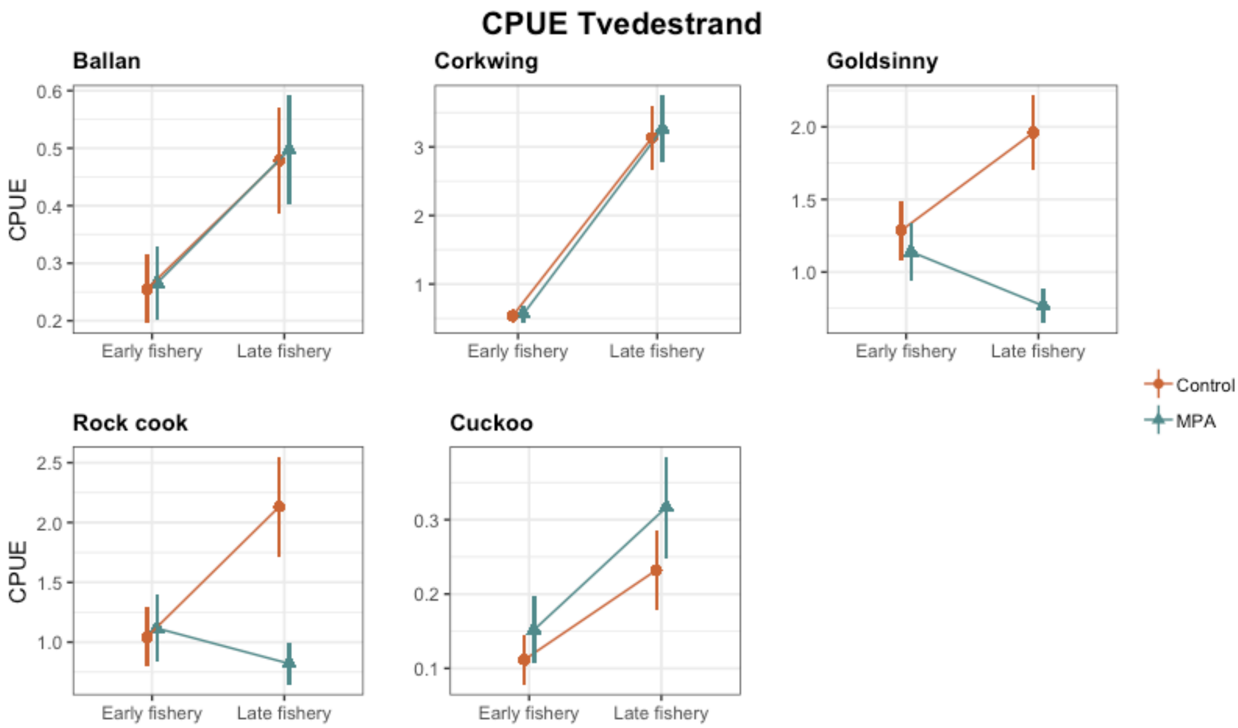

Figure 14: The predicted effect of protection (MPA or control) on CPUE as estimated by generalized linear models for ballan, corkwing, goldsinny, rock cook, and cuckoo wrasse captured in Tvedestrand during the early fishery (2010-2013) and late fishery (2014-2019). Error bars show ±1 standard error around the predicted means.

4. Discussion

This study used a before-after-control-impact (BACI) design to investigate the impact of protection on age, length and CPUE of wrasse both inside and outside of marine protected areas in Austevoll and Tvedestrand. The study sheds light on the effects of harvesting wrasse to be used as cleaner fish in salmon aquaculture on wild wrasse populations in both Southern and Western Norway. The findings demonstrate a positive effect of MPAs on body size of corkwing in Austevoll, and of ballan and rock cook in Tvedestrand supporting the initial hypothesis that there should be larger fish inside the MPA. The abundance of the smaller wrasse, goldsinny and rock cook, was found to be higher outside of the MPA in Tvedestrand which is contrary to the expectation that there should be more fish inside the MPA. The implications of these findings add to the growing evidence that MPAs have the potential to provide direct benefits to harvested marine species (Sørdalen et al., 2020; Moland et al., 2013; Baskett & Barnett, 2015); while they may simultaneously have indirect consequences such as increased predation from recovered predator populations.

This study also investigated a non-invasive method of aging ballan through scale analysis by comparing scale age to otolith age. The findings suggest that there is a high error rate for scales to display the same age as otoliths, and that the error increases with increasing age with a tendency for scales to underestimate age of older individuals. Despite the high error rate, scales were found to be accurate for aging young ballan (< 6 years), and when scale age deviated from otolith age it was often within 1-2 years. These findings imply that the scale aging method can be useful for aging young ballan and in situations when a slight degree of uncertainty can be accepted.

4.1 MPA effects on wrasse

4.1.1 Austevoll

In Austevoll, the corkwing were found to be larger in the MPAs compared to the control areas suggesting that protection has a positive impact on the body size of corkwing in this location. This finding supports the initial hypothesis that there should be larger fish inside the protected area than in control areas. The average length of corkwing remained relatively stable in the MPA area and it decreased sharply in the control area after the fishery, suggesting that the difference in length between areas is due to the removal of fishing mortality in the MPA area.

The fact that corkwing is the first wrasse species to show a detectable response to protection can be related to the species' fishing pressure, depth distribution, life history traits and management. The first two characteristics, fishing pressure and depth, are presumably the most relevant in this situation as they are most important for early responses to an MPA because they are directly related to fishing mortality. The latter two characteristics, related to life history and management, may be more relevant for long-term responses to an MPA which would not yet have an effect in the young MPA in Austevoll. Corkwing is the most commercially targeted wrasse species in Western Norway (Norwegian Directorate of Fisheries, 2020a) and they occupy shallow waters (< 5 m) which overlaps with the depth where fishing occurs (< 7 m). The minimum size limit for corkwing (12 cm) inadequately protects male corkwing before reaching maturity (13-16 cm), indicating a mismatch between management and the species' biology. The goldsinny are also heavily fished in Western Norway which leads to the question of why this species has shown no response to protection. A possible explanation is that goldsinny occupy deeper waters (< 15 m) providing a natural refuge from fishing pressure and their minimum size limit (11 cm) protects individuals until after they reach sexual maturity (6-9 cm) (Halvorsen et al., 2020).

There were no clear effects of protection on abundance of wrasse in Austevoll. This can possibly be explained by the fact that the MPA is newly established, or because changes in body size can occur faster than changes in abundance (Baskett & Barnett, 2015). An increase in biomass due to larger body size is a process that occurs within a generation, while an increase in abundance due to higher reproductive output is a process that takes place over multiple generations (Baskett & Barnett, 2015). An increase in abundance of individuals in response to protection can occur because of a combination of reduced harvest mortality and increased reproductive output (Baskett & Barnett, 2015). Protection from harvesting restores the natural size structure by allowing fish to survive to larger sizes and older ages (Fernández-Chacón et al., 2020), and for species with sexual size dimorphism this implies the survival of more males (Halvorsen et al., 2016a). As the proportion of larger fish increases in the protected area, the reproductive output is expected to increase because there will be more mature individuals and because larger individuals have higher fecundity (Barneche et al., 2018). Although there were no effects of protection on CPUE, the finding that there were larger corkwing in the MPA can be expected lead to an increase in reproductive output and an eventual increase in abundance over time.

There was found to be no effect of protection on the age of ballan in Austevoll. There were differences in average age between sampling periods in which the ballan captured in September were on average younger than those captured in June. This can be expected because the 1-year-old ballan that were too small to be captured in June grew to be large enough for capture in September. This can be seen in Figure 7 (right) where the 1-year-old ballan are larger in September than in June, and there are many more 1-year-old fish captured in September.

4.1.2 Tvedestrand

The results indicate that there are positive effects of MPAs on the body size of rock cook and ballan in Tvedestrand. The average length of ballan increased greatly in the MPA area, and conversely the length of rock cook decreased in the control area while remaining stable in the MPA. Furthermore, the average length of ballan, corkwing, rock cook, and cuckoo was always found to be higher than the minimum size limit (Figure 11) suggesting that the size limit is not adequately protecting these species in Tvedestrand.

While there were positive effects of MPAs on the length of rock cook and ballan in Tvedestrand, there were no clear effects on abundance of wrasse. On the contrary, the smaller wrasse species (rock cook and goldsinny) showed indications of increased abundance outside of MPAs in recent years. This result does not support the initial hypothesis that there should be more wrasse in the protected area than the fished area. This is especially unexpected for goldsinny which is the most commercially targeted species in Southern Norway (Norwegian Directorate of Fisheries 2020a; appendix A1). Hence it seems that protection has a low effect on the wrasse populations in Tvedestrand possibly because the wrasse in this region are too numerous relative to the fishing mortality. The finding that the CPUE of goldsinny and rock cook are lower in protected areas, as well as the lack of differences in CPUE of other wrasse between areas, suggests that overfishing is not an issue in Tvedestrand. Unfortunately, there is no data available on the spatial and temporal distribution of fishing effort in Tvedestrand during the study period to allow a clearer interpretation of the findings.

The lower CPUE of goldsinny and rock cook in protected areas can be caused by other site-specific effects such as increased predation. Goldsinny and rock cook are the two smallest wrasse species, and the increase in Atlantic cod (*Gadus morhua* Linnaeus, 1758) and other large fish can have reduced their abundance in the MPA. The coastal Atlantic cod, a potential wrasse predator (Hop, Danielssen & Gjøsæter, 1993), has been found to be larger and older in the Tvedestrand MPA than in nearby control areas (Espeland et al., 2016). A study that analyzed multiple long-term time series of marine reserves found that the indirect effects of protection, such as increased predation, take longer to develop than the direct effects (Babcock et al., 2010). This may explain why there was no detectable effect of protection on abundance in Austevoll where the MPA has only been implemented for a year, while there was an effect on abundance in Tvedestrand where the MPA has existed long enough to develop indirect effects. A study in Tvedestrand conducted one year after the MPA was implemented found a higher abundance of corkwing and goldsinny inside the MPA as compared to nearby control areas (Halvorsen et al., 2017). The findings from Halvorsen et al. (2017) are inconsistent with the results from my study which could possibly be explained by the duration of time since MPA establishment. The indirect effects of MPAs, such as increased predation from recovered cod populations, would not have occurred within one year of MPA establishment.

4.2 Wrasse populations in Southern and Western Norway

4.2.1 Limitations of comparing regions

Although comparing the wrasse populations of Southern and Western Norway was not an objective of this thesis, it is possible to compare the population parameters from both regions while keeping the limitations of such comparison in mind. There are four main differences between the sampling design in Tvedestrand and Austevoll regarding 1) fishing gear, 2) sampling periods, 3) MPA characteristics, and 4) the use of depth loggers. Fyke nets were used for sampling in both Austevoll and Tvedestrand, however the nets in Austevoll had a longer leading net and a smaller mesh size (7.8 m leading net, 11 mm mesh size) compared to those used in Tvedestrand (5 m leading net, 30 mm mesh size). The fyke nets with the larger mesh size used in Tvedestrand can result in a lower proportion of small fish as they can more easily escape the fyke net. Because the nets in Austevoll can capture smaller fish than those used in Tvedestrand, it is necessary to set a lower limit to the size when comparing CPUE. The CPUE results from both localities in this study only include fish above 11cm, making the results more comparable across localities.

The sampling in Austevoll and Tvedestrand have differences in both duration and seasonality. The duration of sampling in Austevoll took place over two years (2018-2019) during three months (June, July, September), while the sampling in Tvedestrand took place over nine years (2010-2019) during the same month (June). It has been documented that there are seasonal variations in the catch rates and species composition of wrasse (Halvorsen et al., 2017). Catch data from a fisherman in Southern Norway during 2011-2013 reveal that most ballan were captured in June/July, while most corkwing and goldsinny were captured in August/September (Halvorsen et al., 2017). This suggests that the Tvedestrand data which was sampled in June every year, may not truly reflect the status of the wrasse populations in Southern Norway as it may project lower proportions of corkwing and goldsinny. Furthermore, there were found to be large differences in body size and CPUE between sampling periods in Austevoll suggesting the need for studies to sample during different months in order to draw conclusions about the status of a population. While sampling during the same month in Tvedestrand makes it possible to monitor the effect of an MPA on local populations over time, it makes it difficult to compare with other MPA studies conducted during different times of the year.

In addition to the differences in fishing gear and sampling periods between localities, the MPAs in Austevoll and Tvedestrand differ in terms of their size, age, degree of protection (partial vs. full protection), and connectivity (network of MPAs vs. single MPA). The MPA in Tvedestrand is a network of five protected areas, four of which are partially protected and one which is a no-take zone. The MPA in Austevoll is one partially protected area surrounding a group of islands. The MPA in Tvedestrand was established in 2012 and covers 9.4 km^2 in total (4.1 km^2 inside, 5.3 km^2 outside), while the MPA in Austevoll was established in 2018 and covers 2.2 km^2 in total. The size and connectivity of an MPA is important in terms of population connectivity, larval retention, protection of high-movement species, and potential for spillover (Baskett & Barnett, 2015). The decline in abundance of smaller wrasse due to increased predation that was seen in Tvedestrand may be less likely to occur in the MPA in Austevoll due to its smaller size and partial protection. A large reserve network such as the MPAs in Tvedestrand will provide more protection to species with large home ranges such as the Atlantic cod than a smaller single MPA such as that in Austevoll (Villegas-Ríos et al., 2017). Furthermore, a no-take zone will provide more protection to cod than a partially protected zone because recreational rod and line fishing accounts for a large proportion of fishing mortality of cod in Southern Norway (Kleiven et al., 2016). Partially protected areas still permit the use of rod and line fishing and therefore they will protect cod to a lesser degree than no-take zones.

Thus it is expected that the indirect negative effects of predation from cod on small wrasse species would be lower in partially protected areas than in no-take zones.

Variables such as depth of fyke net, water temperature, and soak time can strongly impact the catch rates of the fyke nets. Unfortunately, this data is only available from Austevoll since fyke nets used in Austevoll were equipped with data loggers to measure such variables while fyke nets in Tvedestrand were not equipped with this. In order to compare CPUE between regions, these factors should be included in statistical models to account for environmental variations between regions (Skiftesvik & Halvorsen, 2019).

4.2.2 Geographical variations of the different wrasse species

While the study design in this thesis makes it difficult to compare CPUE between regions, a recent report from IMR (Skiftesvik & Halvorsen, 2019) discusses geographical variations in abundance of wrasse. The report found that there was a higher abundance of ballan in Southern Norway than Western Norway while there were no differences found for corkwing or goldsinny (Skiftesvik & Halvorsen, 2019). A study conducted in 2014 (Halvorsen et al., 2016a) found that Western Norway had 2-3 times higher abundance of corkwing than Southern Norway, however more recent spawning surveys from IMR show a decline in abundance of corkwing in the west and an increase in the south (Skiftesvik & Halvorsen, 2019).

The length of wrasse captured is not as influenced by variables such as water temperature, depth and soak time (Skiftesvik & Halvorsen, 2019) and therefore it is possible to compare body size of wrasse between regions. The mean length of all wrasse species captured in 2018-2019 was found to be larger in Tvedestrand than in Austevoll, with ballan and corkwing having the largest difference in mean length between regions (Table 4, Figure 9). The larger mesh size of the nets used in Tvedestrand can partially explain the higher proportion of large fish captured in this locality. A length distribution that is skewed to the left, with fewer large fish and more small fish, can be a sign of overfishing (Skiftesvik & Halvorsen, 2019). The length distribution of ballan in both Austevoll and Tvedestrand is left-skewed, however it is more severely skewed in Austevoll, indicating overfishing in both regions (Figure 9; appendix D1, D3). The complex life history of the ballan makes this species particularly vulnerable to the wrasse fishery; and the minimum size regulation is low (14 cm) relative to the size at maturation (20-24 cm females; 32-40 cm males) (Skiftesvik & Halvorsen, 2019). The depth distribution of the ballan (0-5 m) overlaps entirely with the depths that fishing occurs (< 7 m) making this species more vulnerable to harvest relative to other wrasse species with a larger depth range (Halvorsen et al., 2020).

The length distribution of corkwing is found to be left-skewed in Austevoll and normally distributed in Tvedestrand, suggesting that overfishing of corkwing may be an issue in Western Norway (Figure 9; appendix D1, D3). The corkwing in Western Norway have been found to mature later and live longer than corkwing in Southern Norway, attaining a maximum age of 9 years and 4 years respectively (Skiftesvik & Halvorsen, 2019). The difference in maturation between regions makes corkwing in the west more vulnerable to overfishing relative to corkwing in the south, with a higher likelihood of being removed before reaching maturity (Skiftesvik & Halvorsen, 2019). The length of goldsinny, rock cook, and cuckoo was found to be relatively similar between regions, with a normal distribution of length in both regions. Although the goldsinny is among the most heavily fished of the wrasse, it is less vulnerable to overfishing because it lives in deeper waters (0-15 m) and matures (6-9 cm) before reaching the minimum size limit (11 cm) (Halvorsen et al., 2020). It is unsurprising that cuckoo and rock cook populations show no signs of overfishing because the fishery for these species is nonexistent in the south and is small in the west (Directorate of Fisheries, 2020a; appendix A1).

4.3 Scale aging methodology

Using scales for age determination is considered to be advantageous compared to otolith aging because it is less time consuming and does not require the killing of fish, however otoliths are considered to be more accurate because scales often underestimate the age of old fish (Boughamou et al., 2014). In this study, the scale readings from ballan wrasse had a high error rate in determining the same age as otoliths in which Reader 1 had an error rate of 36.7% and Reader 2 had an error rate of 55.4%. The error rate in this study is considerably higher than the error rate for age determination of scales for corkwing wrasse (13.18% error) and for peacock wrasse (8.75% error) in other studies (Vik, 2019; Boughamou et al., 2014). Similar to corkwing, the ballan scales had a tendency to underestimate age and the degree of underestimation increased with increasing age (Figure 5; Vik, 2019). The results from this study suggest that using scales to determine age for ballan is not as accurate a method as it is for the corkwing and peacock wrasse. The reason for the greater error rate for ballan compared to the other studies could be because the maximum age of peacock wrasse in Boughamou et al.'s (2014) study was 5 years, maximum age of corkwing in Vik's (2019) study was 7 years, and maximum age of ballan in this study was 14 years. Given the fact that error increases with increasing age, it is no surprise that there is a higher error rate for aging ballan because they have a longer lifespan (maximum 29 years; Dipper et al., 1977) than the corkwing (9 years; Costello, 1991) and peacock wrasse (13 years; Pallaoro & Jardas, 2003)

Despite the high error rate for scales to show the same age as otoliths, the scales were often within 1-2 years of the otolith age (appendix C). This suggests that although ballan scales were found to be unreliable to determine exact age, they can still be used in situations when a degree of uncertainty can be accepted. From the year 2021, the maximum entrance size of the traps used for wrasse fishing is required to be 6 cm in diameter which reduces the ballan catch to < 28 cm (Directorate of Fisheries, 2020b; Halvorsen, Skiftesvik & Jørgensen, 2019). According to the von Bertalanffy growth curves from ballan in Southern Norway (Figure 7), this means that the wrasse fishery is targeting ballan that are < 8 years old. The scale aging methodology was found to age ballan up to 8 years of age with good accuracy, in which both scale readers aged all ballan within 2 years of the otolith age (appendix C). Therefore, the scale method can be useful for aging wrasse that are targeted by the fishery. Scale aging can also be a useful method for monitoring the impact of protected areas by being able to compare the age groups of ballan inside and outside of the MPA. For the purpose of MPA monitoring, it may be sufficient enough to have rough estimates of age groups to be able to compare between areas than to have the exact ages of ballan. For future studies, the benefit of not having to kill ballan to determine their age may outweigh the disadvantage of having to accept a degree of uncertainty in the aging.

4.4 Management implications

The complex and vulnerable life history strategies of the wrasse species must be taken into account when managing the fishery. Before the year 2015, the minimum size limit of all wrasse species was the same (11 cm) despite the fact that the wrasses differ greatly in size and longevity (Costello, 1991). This implies that until recently, management of the wrasse fishery in Norway treated all wrasse as a single species rather than treating them as unique species with stark contrasts in life history traits. Management of the wrasse fishery has made improvements in recent years by increasing the minimum size limit of ballan to 14 cm and of corkwing to 12 cm in 2015, reflecting the fact that these species grow to be larger than the other wrasse species. The decision to prohibit the use of fyke nets for commercial fishermen from 2021 will greatly reduce the amount of bycatch, since fyke nets are documented to retain a significantly higher proportion of bycatch species than pots (Halvorsen et al., 2017). A recent study (Olsen et al., 2018) revealed that individuals with larger asymptotic body sizes are more likely to be captured in fyke nets than pots, suggesting that the prohibition of fyke nets will also help protect large-growing phenotypes such as the corkwing nesting male. Furthermore, the reduction in entrance size of the pots to 6 cm will limit the catch of ballan to < 28 cm (Skiftesvik & Halvorsen, 2019) which will protect larger individuals with higher fecundity and preserve natural sex ratios. Despite the improvements in managing the wrasse fishery, there are further steps that should be taken to reduce the selectivity of the fishery and ensure sustainable harvesting.

The results from my study suggest that the ballan is the species most urgent in need for a change in management. The length distribution was found to be left-skewed in both Tvedestrand and Austevoll, suggesting that the ballan are overharvested in both regions. Furthermore, the current minimum size limit of 14 cm was shown to only fully protect 1-year-old ballan in Austevoll with most ballan growing out of protection during their second year. The von Bertalanffy growth curve from Flødevigen also indicates that the minimum size limit only protects individuals less than 2-years-old. There is a mismatch between the management of the ballan wrasse and the biology of the species, as the ballan reach sexual maturity at a size much larger than the current minimum size limit. It becomes mature at 20-24 cm for females and changes sex to male at 34-40 cm, while the regulations only protect individuals up to 14 cm (Skiftesvik & Halvorsen, 2019). It is recommended to increase the minimum size limit of ballan to a size that protects individuals until after they reach sexual maturity, as well as set a maximum size limit to protect large females with the highest reproductive potential and to preserve natural sex ratios. This recommendation is in alignment with advice from IMR advising that in addition to the reduction in entrance size of pots, a slot-size limit from 22-28 cm should be introduced (Halvorsen et al., 2019).

The findings from this study also indicate the need to revise management practices for the corkwing wrasse. The length distribution of corkwing in the west was found to be left-skewed, indicating that corkwing are overharvested in this region. In the south, the majority of the corkwing that were captured during the entire nine-year timespan were well above the minimum size limit (12 cm) with a mean length of 14.1 cm. The proportion of larger individuals captured in the south compared to the west (mean length 11.7 cm) can be partially explained by the larger mesh size used in the south, or it might be because corkwing in the south grow larger than corkwing in the west (Halvorsen et al., 2016a). The study from Halvorsen et al. (2016a) also found that differences in body size between nesting males, sneaker males and females were significantly larger in the western populations than in the south. The results from this study show large differences in corkwing body size between regions which is consistent with the findings from Halvorsen et al. (2016a). The implication of this finding, in addition to the differences in sexual size dimorphism between regions (Halvorsen et al., 2016a) suggests the need to manage the corkwing in Western and Southern Norway as separate populations. IMR has recommended either increasing the minimum size limit of corkwing in the west to 13 cm or introducing a slot-size limit (12-17 cm) in order to protect the faster growing nesting males (Skiftesvik & Halvorsen, 2019; Olsen et al., 2018). It is deemed less necessary to implement a slot-size limit in the south because 1) there are smaller differences in sexual size dimorphism in this region; and 2) it would only protect large individuals at the end of their life span (shorter longevity relative to corkwing in west) (Halvorsen et al., 2016a).

Similar to the ballan and corkwing, the goldsinny and cuckoo wrasse also display sexual size dimorphism in which males have a larger body size than females (Olsen et al., 2018; Costello, 1991). A minimum size limit alone will disproportionately protect females more than males, which can lead to changes in a population's sex ratio with consequences for overall population productivity (Halvorsen et al., 2016a). Therefore, it has been recommended by IMR to implement a slot-size limit for goldsinny (11-14 cm) and cuckoo (11-20 cm) as well (Skiftesvik & Halvorsen, 2019).

From a conservation perspective, the findings from this study suggest that MPAs can be used as a management strategy to maintain natural size structure and abundance of harvested wrasse populations. This is supported by the results from Austevoll that demonstrated the ability of MPAs to restore corkwing size structure within one year of MPA establishment as well as the positive effects protection was found to have on length of ballan and rock cook in Tvedestrand. The finding that the abundance of rock cook and goldsinny was higher outside of MPAs in Tvedestrand, presumably due to increased predation within the MPA, highlighted the potential for indirect effects of protection to occur over a longer period of time. Therefore, it is recommended to monitor MPAs regularly with a study design that allows for evaluation of the impacts on an ecosystem as a whole rather than focusing on an isolated species. Monitoring with an ecosystem-based approach will facilitate a clearer interpretation of the direct (e.g. biomass and abundance) and indirect (e.g. density of predators and competitors) effects of MPAs. Furthermore, it is recommended to establish additional protected areas in Western Norway where the intensity of harvesting wrasse is highest.

5. Conclusions and future directions

The implications from the results of this study are two-fold. First, the larger body size of corkwing found in the Austevoll MPA after one year of protection demonstrates the ability for MPAs to have a positive effect on harvested populations within a short time period. Second, the finding that there were larger ballan and rock cook within Tvedestrand MPAs as well as lower abundance of goldsinny and rock cook highlights the potential for indirect consequences of protection to occur over a longer period of time. The positive effect that MPAs were found to have on body size of corkwing in Austevoll, and of rock cook and ballan in Tvedestrand, supports the initial hypothesis that there should be larger individuals in MPAs. The finding that rock cook and goldsinny were less abundant in MPAs relative to control areas, possibly due to an increase in predation from recovered cod populations, does not support the initial hypothesis that there should be more individuals in protected areas. The overall response to protection was found to be greater for species such as ballan and corkwing that are subject to high fishing pressure, occupy shallow waters where fishing occurs, display sexual size dimorphism, and are managed by an inadequate minimum size limit.

The findings from this study make contributions to both conservation and management of wrasse fisheries. For conservation, it is recommended to establish additional MPA networks in Western Norway where the intensity of harvesting wrasse is highest. For fisheries management, it is recommended to increase the minimum size limit of ballan wrasse and to introduce a slot-size limit which will simultaneously allow individuals to grow to maturity, preserve natural sex ratios, and increase reproductive output. Furthermore, it is recommended to manage the populations of corkwing in Southern and Western Norway as two separate populations given their differences in body size, longevity, and sexual size dimorphism. The establishment of additional protected areas combined with the revision of current management to reflect the wrasses' biology will help to buffer the effects of selective fishing and ensure sustainable harvesting.

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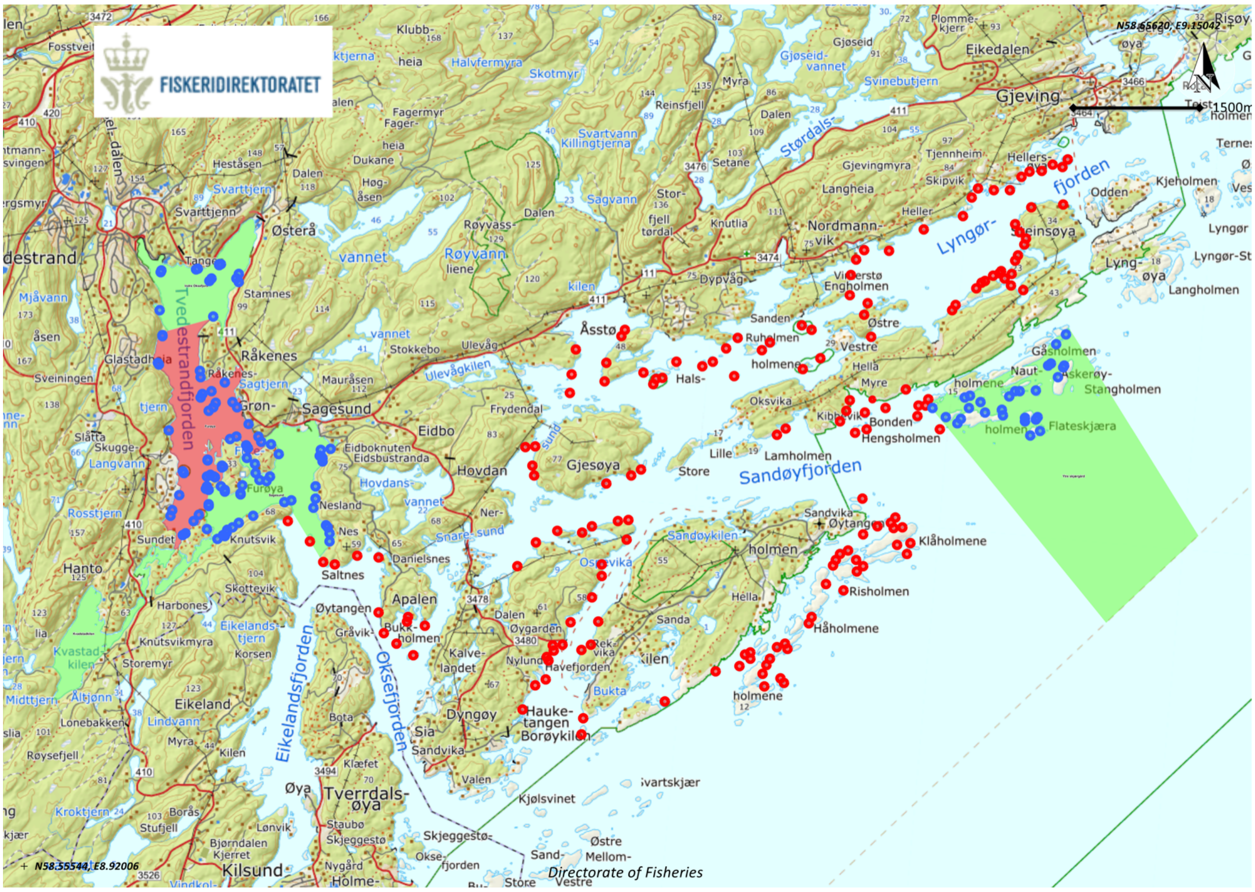
Appendix A

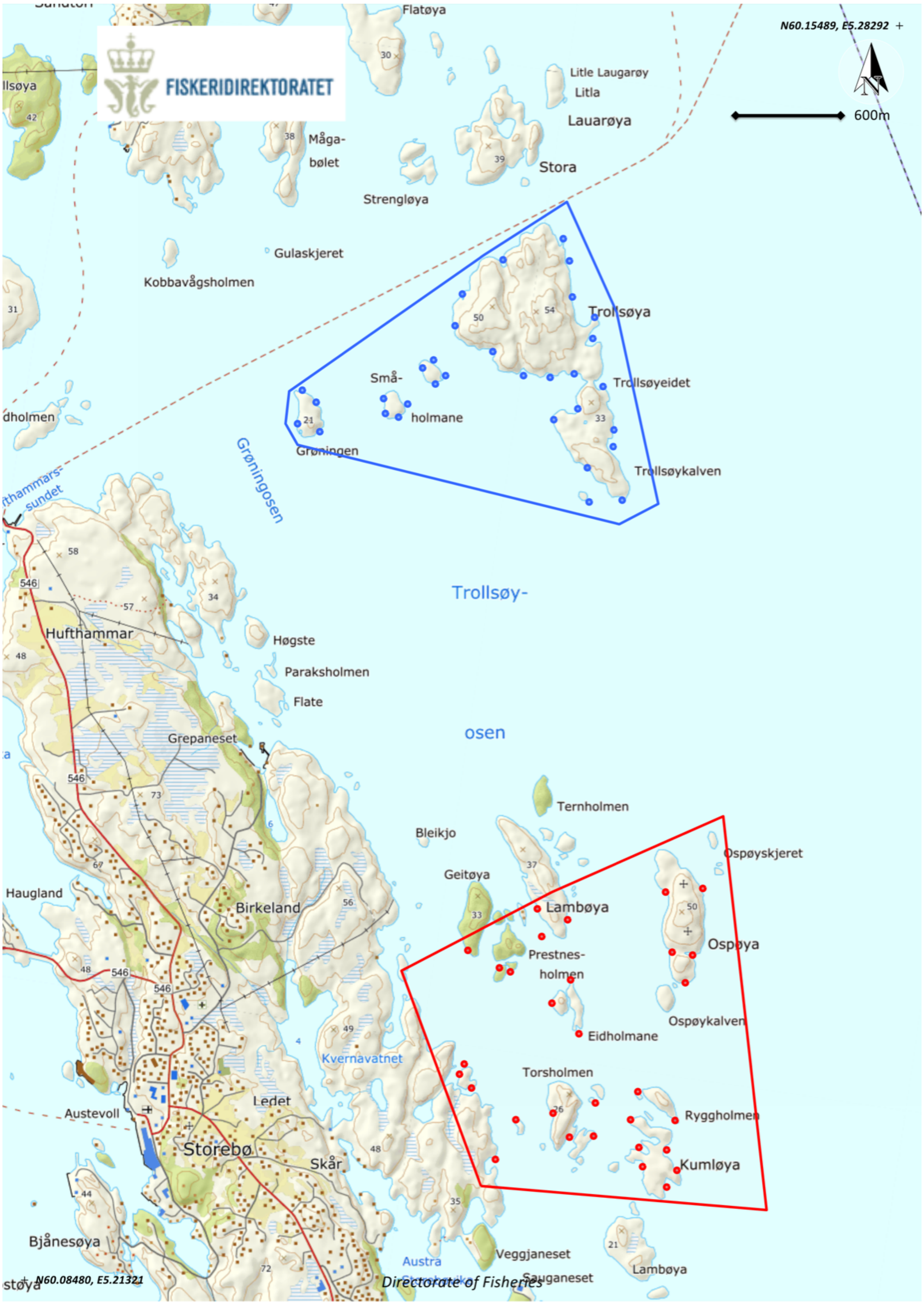
Table A1: Reported landings of each species of wrasse in Southern Norway and Western Norway during the last six years. Source: Norwegian Directorate of Fisheries (2020a).

Region	Species	Year					
		2019	2018	2017	2016	2015	2014
Western Norway	Ballan	1037845	960486	1200156	778563	820690	690604
	Goldsinny	3672027	3192008	5746341	3440747	4426899	4380133
	Cuckoo	12860	0	3487	967	2138	200
	Rock cook	451801	394239	623321	543002	289774	337706
	Corkwing	6358379	6273246	8648910	7862171	7066862	5970459
	Total	**11532912**	**10819979**	**16222215**	**12625450**	**12606363**	**11329102**
Southern Norway	Ballan	283999	336526	352098	246792	202068	335515
	Goldsinny	2642818	2314524	3250319	2103332	1772445	3060769
	Cuckoo	0	0	379	0	0	0
	Corkwing	1150917	1095164	1171698	1921139	1762732	954283
	Total	**4077734**	**3746214**	**5347494**	**4271263**	**3737245**	**4350567**
Total		**15610646**	**14566193**	**21569709**	**16896713**	**16343608**	**15679669**

Appendix B



Appendix B1: Enlarged image of the study area in Tvedestrand. The shaded areas indicate the boundaries of the partially protected areas (green) and the no-take area (red). Dots represent sampling stations in the MPAs (blue) and in control areas (red). Map made using Yggdrasil (Norwegian Directorate of Fisheries, 2020c).



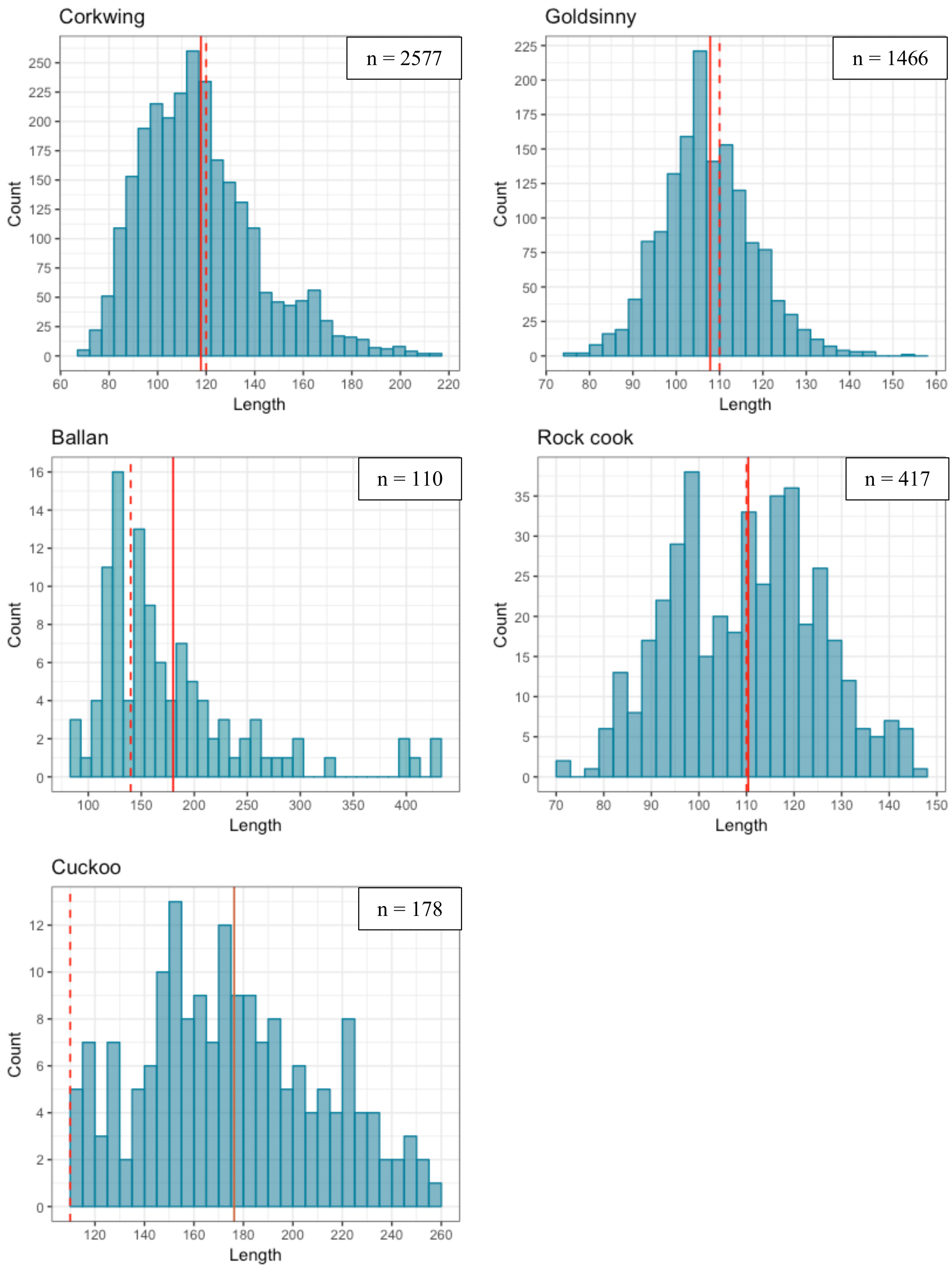
Appendix B2: Enlarged image of the study area in Austevoll. Solid lines indicate the border of the MPA (blue) and control (red) areas. Dots represent sampling stations in the MPA (blue) and control (red) areas. Map created using Yggdrasil (Norwegian Directorate of Fisheries, 2020c).

Appendix C

Table C1: A summary of the accuracy of scale readings for the two scale readers. The left column shows the number of scales that were analyzed for each age group from 3-14 years. The number (and percentage) of correct scale readings are shown for each age group, and the number (and percentage) of correct scales when accepting an error margin of ±1, 2, and 3 years.

		Observer 1				Observer 2			
Otolith age	N scales	Correct	±1 year	±2 year	±3 year	Correct	±1 year	±2 year	±3 year
3	5	5 (100%)	-	-	-	4 (80%)	5 (100%)	-	-
4	10	8 (80%)	10 (100%)	-	-	6 (60%)	10 (100%)	-	-
5	108	90 (83%)	108 (100%)	-	-	73 (68%)	108 (100%)	-	-
6	98	71 (72%)	97 (99%)	98 (100%)	-	52 (53%)	94 (96%)	98 (100%)	-
7	56	42 (75%)	55 (98%)	56 (100%)	-	26 (46%)	53 (95%)	56 (100%)	-
8	43	27 (63%)	38 (88%)	41 (95%)	43 (100%)	20 (47%)	34 (79%)	39 (91%)	43 (100%)
9	41	11 (27%)	29 (71%)	41 (100%)	-	5 (12%)	17 (41%)	36 (88%)	41 (100%)
10	25	10 (40%)	17 (68%)	25 (100%)	-	4 (16%)	13 (52%)	22 (88%)	25 (100%)
11	15	6 (40%)	11 (73%)	15 (100%)	-	2 (13%)	6 (40%)	9 (60%)	14 (93%)
12	12	2 (16%)	5 (42%)	9 (75%)	12 (100%)	0 (0%)	0 (0%)	3 (25%)	8 (67%)
13	17	2 (12%)	6 (35%)	13 (76%)	17 (100%)	0 (0%)	0 (0%)	5 (29%)	9 (53%)
14	3	0 (0%)	2 (67%)	2 (67%)	3 (100%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)

Appendix D



Corkwing
n = 2577
Count
Length
Goldsinny
n = 1466
Count
Length
Ballan
n = 110
Count
Length
Rock cook
n = 417
Count
Length
Cuckoo
n = 178
Count
Length

Figure D1: Length distribution of the corkwing (n=2577), goldsinny (n=1466), ballan (n=110), rock cook (n=417), and cuckoo (n=178) wrasse caught and measured in Austevoll. The solid vertical line indicates mean length of corkwing (118mm), goldsinny (108mm), ballan (180mm), rock cook (110mm) and cuckoo (176mm) and the dotted vertical line indicates minimum size limit.

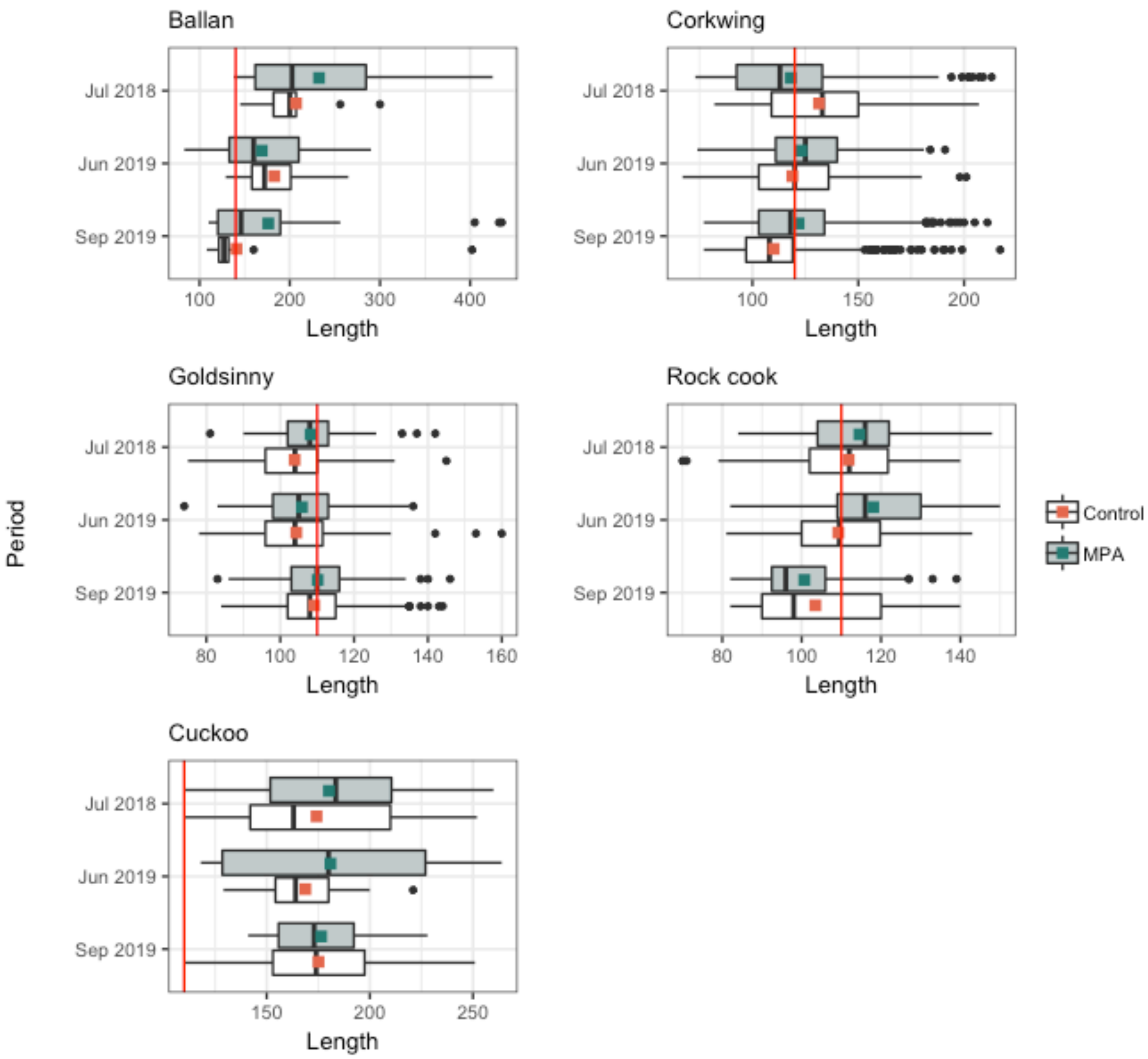


Figure D2: Boxplots showing the median (thick black vertical line) and mean (solid squares) of length (mm) of wrasse captured in Austevoll during the three sampling periods. Shaded boxes are MPAs, open ones are control sites. The right and left edge of the box represents the 25th and 75th percentiles, respectively. Filled dots are outliers, and the red line represents the minimum size limit for each species.

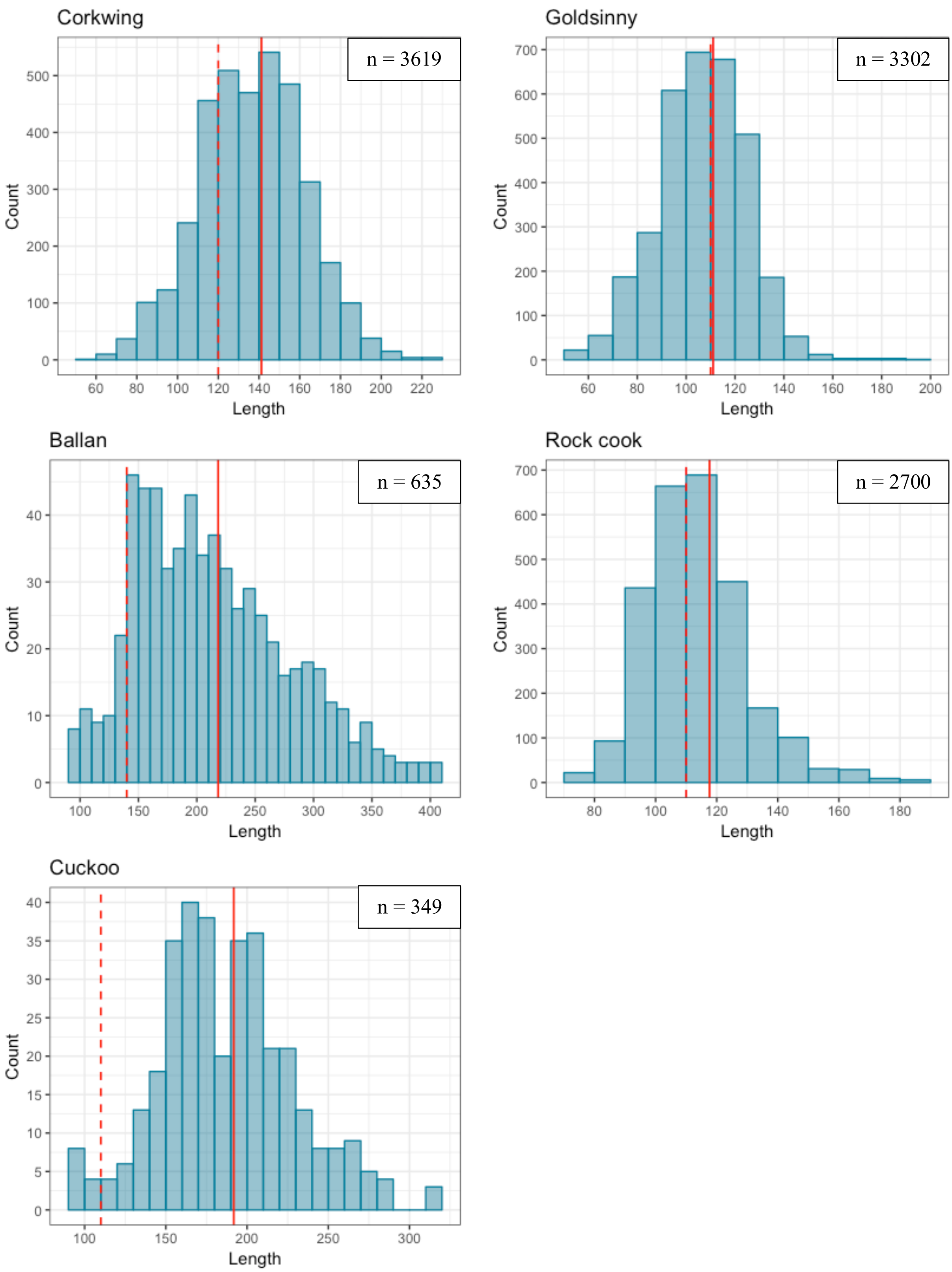

Corkwing
n = 3619
Count
Length
0 100 200 300 400 500
60 80 100 120 140 160 180 200 220
Goldsinny
n = 3302
Count
Length
0 100 200 300 400 500 600 700
60 80 100 120 140 160 180 200
Ballan
n = 635
Count
Length
0 10 20 30 40
100 150 200 250 300 350 400
Rock cook
n = 2700
Count
Length
0 100 200 300 400 500 600 700
80 100 120 140 160 180
Cuckoo
n = 349
Count
Length
0 5 10 15 20 25 30 35 40
100 150 200 250 300

Figure D3: Length distribution of the ballan (n = 635), corkwing (n = 3617), goldsinny (n = 3301), rock cook (n = 2697) and cuckoo (n = 349) wrasse caught and measured in Tvedestrand. The solid vertical line indicates mean length of corkwing (141mm), goldsinny (111mm), ballan (218mm), rock cook (118mm) and cuckoo (192mm) and the dotted vertical line indicates minimum size limit.

Appendix E

Table E1: Model selection of linear models on the effects of protection on the length, CPUE, and age of wrasse in Austevoll. The table shows response variable, species, model structure, number of estimated parameters, AIC score, and difference between the AIC scores of the two models. The selected model for statistical inference is in **bold.**

Response	Species	Model structure	Parameters	AIC	Δ AIC
Length	Corkwing	**Area * Period**	**7**	**23576.89**	**0**
		Area + Period	5	23648.38	71.49
	Goldsinny	Area * Period	7	11035.89	0
		Area + Period	**5**	**11036.70**	**0.81**
	Ballan	Area * Period	7	1261.50	0
		Area + Period	**5**	**1259.94**	**1.56**
	Rock cook	Area * Period	7	3423.91	0
		Area + Period	**5**	**3425.80**	**1.88**
	Cuckoo	Area * Period	7	1796.45	3.58
		Area + Period	**5**	**1792.87**	**0**
CPUE	Corkwing	Area * Period + Soak time	8	941.09	2.75
		Area + Period + Soak time	**6**	**938.34**	**0**
	Goldsinny	Area * Period + Soak time	8	692.49	1.80
		Area + Period + Soak time	**6**	**690.69**	**0**
	Ballan	Area * Period + Soak time	8	314.94	3.66
		Area + Period + Soak time	**6**	**311.27**	**0**
	Rock cook	Area * Period + Soak time	8	359.56	3.36
		Area + Period + Soak time	**6**	**356.20**	**0**
	Cuckoo	Area * Period + Soak time	8	386.76	2.94
		Area + Period + Soak time	**6**	**383.85**	**0**
Age	Ballan	Area * Period	5	319.92	0.27
		Area + Period	**4**	**320.19**	**0**

Table E2: Model selection of linear models on the effects of protection on length and CPUE of wrasse in Tvedestrand. The table shows response variable, species, model structure, number of estimated parameters, AIC score, and difference between the AIC scores of the two models. The selected model for statistical inference is in **bold.**

Response	Species	Model structure	Parameters	AIC	Δ AIC
Length	Corkwing	Area * Period	5	33740.90	1.23
		Area + Period	**4**	**33739.67**	**0**
	Goldsinny	Area * Period	5	28464.75	0
		Area + Period	**4**	**28465.60**	**0.85**
	Ballan	**Area * Period**	**5**	**7095.52**	**0**
		Area + Period	4	7106.22	10.7
	Rock cook	**Area * Period**	**5**	**22833.42**	**0**
		Area + Period	4	22842.18	8.76
	Cuckoo	Area * Period	5	3593.86	1.87
		Area + Period	**4**	**3591.99**	**0**
CPUE	Corkwing	Area * Period	5	5292.61	0.16
		Area + Period	**4**	**5292.77**	**0**
	Goldsinny	**Area * Period**	**5**	**4878.96**	**0**
		Area + Period	4	4904.72	25.76
	Ballan	Area * Period	5	2516.29	0.7
		Area + Period	**4**	**2515.59**	**0**
	Rock cook	**Area * Period**	**5**	**4400.68**	**0**
		Area + Period	4	4419.17	18.49
	Cuckoo	Area * Period	5	1731.88	**0**
		Area + Period	**4**	**1729.88**	**2.00**

Appendix F

Generalized additive models (GAM) were used to create a time series plot showing the predicted effect of MPAs in Tvedestrand on length and CPUE for each wrasse species during the nine-year time span (Figure 10 & 12) The length data was modelled with a gaussian distribution and an identity link, while the CPUE data was modelled with a negative binomial distribution. The models were fitted separately for each species using the function gam() from the mgcv package (Wood, 2017). The response variables in the models include length and CPUE, and the explanatory variables include area (MPA, control) and year as a continuous variable (2010-2019). GAMs are used when there is a non-linear relationship between the response variable and explanatory variables (Zuur et al., 2009). The GAM model was used to create a time series plot showing the predicted effect of protection on length and CPUE for each wrasse species during the nine-year time span (Figure 10 & 12). The maximum number of splines was set to k=9 for all models.