

Selective harvesting and life history variability of corkwing and goldsinny wrasse in Norway: Implications for management and conservation

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Preface

I would like to thank my supervisors at the Institute of Marine Research and University of Agder, Esben Moland Olsen and Halvor Knutsen, for their support and for giving me the freedom to pursue my ideas of the wrasse-fisheries interaction, even though the original project had a different topic. I have been very lucky to have Asbjørn Vøllestad as my supervisor at the University of Oslo. Your extensive theoretical knowledge and experience with how to deal with the difficulties that arises during the course of a PhD has been invaluable. Thanks for always being accessible for advice, thorough comments on my paper drafts and for checking up on me regularly, always ending the emails with “Stå på!”

I am grateful to Anne Berit Skiftesvik, Howard Browman, Reidun Bjelland and Caroline Durif at Austevoll for including me in your group and putting so much effort into my projects. But above all, I would like to thank you for the hospitality and kindness you have shown me. I truly hope I can continue working with you in coming years. I would also like to thank the master and bachelor students I have collaborated with; Torkel Larsen, Torborg Rustand and Benjamin Hanssen.

I have spent most of my time as a PhD student at IMR Flødevigen, and it has been a fantastic place to be. There are too many people that deserve to be mentioned, as all the base staff, scientists, technicians and fellow students has created a great environment for work and friendships. I would also like to thank the staff and colleagues at my second home, IMR Austevoll, for always being helpful and positive.

Before starting this thesis, I believed that finishing a PhD would be the most important thing to happen in my life for the next four years. Fortunately, I was completely wrong. My dearest Tonje – I owe my biggest thanks to you, for bringing love and happiness to my life every day and for being my most trusted field companion and partner-in-science. I am also thankful for the support of my family and friends, for always being there when I needed a break from work.

Lastly, I would like to dedicate this thesis to my son, Julian. More than anything else, I look forward to be able to spend more time with you.

Arendal, 28.10.2016

Kim Aleksander Tallaksen Halvorsen

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Summary

Selective harvesting, where some individuals are actively targeted or possess phenotypes rendering them more vulnerable to capture, is inevitably happening in all commercial and recreational fisheries. Selective harvesting may affect reproduction and recruitment and cause fisheries induced evolution, potentially reducing fisheries yield and resilience to environmental change. Several species of wrasse (*Labridae*) are now being harvested as cleaner fish to reduce salmon lice-infestations in Norwegian aquaculture. The fisheries are regulated by minimum size limits are presumably size-selective, but they may also be sex-selective since these wrasses exhibits sexual size dimorphism. In this thesis, I focus on life history traits of corkwing and goldsinny wrasse in the context of a growing, selective fishery in southern Norway. Specifically, my goals were to: 1) Study spatial and sexual variation in life history traits in corkwing (*Symphodus melops*) and goldsinny wrasse (*Ctenolabrus rupestris*) and elucidate the underlying processes producing such variation. 2) Estimate size and sex selectivity in the corkwing wrasse fishery and assess the effects of fishing on population parameters of corkwing and goldsinny and 3), evaluate the current management and fishing practice in a selective harvesting perspective. In Paper I, we show that sexual dimorphism of corkwing wrasse is more male biased in populations further north on the western coast of Norway. The size limit is therefore selective against males who builds nests and provide parental care. In Paper II; we further explore the male selective fishery in a tagging experiment, finding that the nesting males have higher vulnerability for being captured in the fishery, independent of body size. It is also shown that a small marine protected area reduces fishing mortality, but have similar sex selectivity as the fished site. In Paper III, we assessed the effect of four MPAs on corkwing and goldsinny populations in Skagerrak, finding that MPAs, relative to control areas, have higher abundance of both species and older and larger corkwing, but no consistent differences for goldsinny. Paper IV further explores goldsinny individual growth rate variability in the same four MPA-control pairs. No MPA effect was detected, but there were indications of growth rates being negatively affected by local population density and abundance of Atlantic cod (*Gadus morhua*), a wrasse predator. I have shown that the fishery and the current regulations promote selective harvesting of wrasse at different levels which has implications for management. Some specific advices are proposed: For

corkwing, introducing a slot size limit (protecting both small and large fish) can protect nesting males and females in more equal proportions. A slot size limit should also be beneficial for goldsinny, which has a considerably longer life span and is therefore more prone for truncated natural age distribution as a consequence of size-selective fishing. Moreover, slot limits are likely to reduce selection for slow growth and ensure a more balanced exploitation of populations with different growth rates. Further, I suggest increasing the number of marine protected areas. The results of paper II and III show that MPAs can be effective as a management tool for wrasse, especially considering that these species exhibit high site fidelity and fine-scaled variability in life history traits.

List of papers

Paper I:

Halvorsen, K.T., Sørдалen, T.K., Durif, C., Knutsen, H., Olsen E.M., Skiftesvik A.B, Rustand T.E., Bjelland, R.M., and Vøllestad L.A. (2016). **Male biased sexual size dimorphism in the nest building corkwing wrasse (*Symphodus melops*): implications for a size regulated fishery.** *ICES Journal of Marine Science*

Paper II:

Halvorsen, K.T., Sørдалen, T.K., Vøllestad, L.A., Skiftesvik, A.B., Espeland, S.H., Olsen, E.M. **Sex- and size-selective harvesting of corkwing wrasse (*Symphodus melops*) – a cleaner fish used in salmonid aquaculture.** Manuscript; submitted and revised for *ICES Journal of Marine Science*

Paper III:

Halvorsen, K.T., Larsen, T., Sørдалen, T.K., Vøllestad, L.A., Knutsen, H., Olsen E.M. **Impact of harvesting cleaner fish for salmonid aquaculture assessed from replicated coastal marine protected areas.** Manuscript; submitted and revised for *Marine Biology Research*

Paper IV:

Olsen, E.M., Halvorsen K.T., Larsen, T., Kuparinen, A. **Life history variability of an intermediate predator (*Ctenolabrus rupestris*) in northern European marine protected areas and harvested areas.** Manuscript.

Introduction

Selective fisheries – concept and challenges

The harvesting of natural populations is never random, whether intentionally or not. Since the dawn of hunting and fishing; large individuals have been the most sought after. Moreover, most modern fisheries have implemented measures to reduce or avoid capturing or retaining juveniles. This can be achieved by gear modifications (such as larger mesh size, selective grids) and minimum size regulations, where it is prohibited to retain individuals below a certain size. Active gears such as trawls or purse-seines tend to be positively selective on body size – whereas passive gear, such as gillnets typically have dome-shaped selection curves where intermediate sized fish have the largest capture probability (Millar and Fryer 1999; Kuparinen *et al.* 2009). Selectivity for other passive gear types such as traps, fyke nets and hooks, may be less obvious, where fish behaviour is of particular importance. Individuals which possess traits that induce a more active or risk-taking behaviour tend to be more vulnerable for being captured in such gear types (Uusi-Heikkilä *et al.* 2008, Biro & Post 2008, Diaz Pauli *et al.* 2015, Wilson *et al.* 2015; but see Wilson *et al.* 2011). Harvest selection on diel behaviour and movement patterns has also been demonstrated as fishing activity is often concentrated on certain depths and habitats (Olsen *et al.* 2012). Size-selective harvesting can be sex-selective when one sex is larger, such as in sequential hermaphroditic species (Alonzo and Mangel 2004) and sexual dimorphic species (Rijnsdorp *et al.* 2010; Kendall and Quinn 2013). Several crustacean fisheries are also male-selective through fishing regulations protecting females (Pillans *et al.* 2005; Sato and Goshima 2006; Sato 2012). Sex-selective fishing can also arise independently of body size and harvest restrictions, possibly a result of sexual differences in growth rates or behaviour (Myers *et al.* 2014; Biro and Sampson 2015). Moreover, fishing may be selective on alternative life history strategies and reproductive tactics within sexes (e.g. species with territorial and sneaker males (Taborsky 2008)) (Darwall *et al.* 1992; Drake *et al.* 1997; Thériault *et al.* 2008).

Selective harvesting has a wide range of potential consequences for population dynamics, demography and reproduction. Both selective and non-selective exploitation can truncate age and size distributions. For species with long life-span, depletion of old, large individuals, especially females, can affect recruitment and the resilience to variable or changing environment (Longhurst 2002; Hixon *et al.* 2014). Generally, fecundity

increase with body size for most fishes, and larger and older mothers may produce eggs of better quality with higher larvae survival, spawn for longer periods and at different times and places (Berkeley *et al.* 2004a; Wright and Trippel 2009; Hixon *et al.* 2014). Fisheries induced changes in sex-ratios may lead to sperm or egg limitation, affect the mating behaviour and opportunity for sexual selection (Rowe and Hutchings 2003; Alonzo and Mangel 2004; Kendall and Quinn 2013). Selectivity on behaviour traits may also have consequences for individual fitness. For example, males of largemouth bass (*Micropterus salmoides*) bred for high vulnerability to angling have higher mating success and parental care intensity than males with low angling vulnerability (Sutter *et al.* 2012, Philipp *et al.* 2015).

Human exploitation is now widely recognized as a selective force driving contemporary evolution (Hutchings and Fraser 2008; Darimont *et al.* 2009; Allendorf and Hard 2009). Increased adult mortality, whether natural or not, induces selection for faster life histories; favouring those maturing and reproducing at younger age (Reznick *et al.* 1990; Stearns 1992). Size-selective harvesting may further reinforce such selection, since individuals growing faster and/or maturing later will have less chance to reproduce before being captured (Law 2000; Fenberg and Roy 2008; Heino *et al.* 2015). Fisheries selection on growth rate are not necessarily always towards slower growth, as fast growers may reach the size at maturation earlier (Enberg *et al.* 2012). In addition, fishing may exert direct selection against fast growth independently of selection on body size (Biro and Sampson 2015). Some even argue that passive gear fisheries selection drive widespread selection for timid behaviour, as those individuals with a more risk-taking or active behavioural traits are more vulnerable to such gears (Arlinghaus *et al.* 2016). Harvest selection can both work on opposite (Carlson *et al.* 2007; Olsen and Moland 2010) or in the same direction as natural selection (Swain *et al.* 2007); a relationship which will, together with heritability of the traits under selection, determine the direction and rate of evolutionary change. Moreover, fishing lowering variation in traits under sexual selection (such as body size), has been predicted to increase rates of fisheries induced evolution operating on the same trait (Hutchings and Rowe 2008). Directional changes in life-history traits, as expected under fisheries induced evolution, have been observed in several exploited species with long data series (e.g. Haugen and Vøllestad, 2001; Olsen *et al.*, 2004; van Walraven *et al.*, 2010). Moreover, fisheries induced evolution has been thoroughly demonstrated in

experimental settings (Conover and Munch 2002; Reznick and Ghalambor 2005; Diaz Pauli and Heino 2014), also accompanied by changes at the underlying loci (van Wijk *et al.* 2013; Uusi-Heikkilä *et al.* 2015). There is now little controversy in claiming that fishing can cause evolutionary change. However, the rate of fisheries induced evolution is difficult to measure in the wild and further research is needed on the consequences for population productivity, recovery potential and the wider effects on the ecosystem (Palkovacs *et al.* 2012; Kuparinen *et al.* 2012; Heino *et al.* 2015). Nevertheless, it is being increasingly acknowledged that an evolutionary perspective needs to be integrated in fisheries management and conservation (Jørgensen *et al.* 2007; Kuparinen and Merilä 2007; Laugen *et al.* 2014; Kindsvater *et al.* 2016).

Mitigating the effects of selective fisheries

Given the wide range of potential negative effects of selective harvesting on populations and ecosystems; how can we best avoid them? One option is to minimize selective fishing, rather than promoting selectivity as is the case in many fisheries now. Balanced harvesting is the idea to distribute fishing mortality more equally across species and body sizes in proportion to natural productivity (Garcia *et al.* 2012). This can then have positive effects on biodiversity, ecosystem function and yield and reduce the potential for fisheries induced evolution (Zhou *et al.* 2010; Garcia *et al.* 2012; Breen *et al.* 2016). Despite being appealing in theory, the usefulness of this approach has been questioned (Froese *et al.* 2015) and the implementation poses several practical challenges at many levels (Reid *et al.* 2016). A different approach dealing with the undesired effects of selective harvesting is marine protected areas (MPAs), where some areas are completely or partially protected from fishing. MPAs have been proven effective in increasing age and body size of target species, population sizes and biodiversity, and may therefore buffer against fisheries induced evolution (Berkeley *et al.* 2004b; Baskett and Barnett 2015). MPAs can also aid in maintaining natural states of ecosystems and be beneficial for recruitment and fisheries yield through spill-over of adults and export of eggs and larvae (Goñi *et al.* 2010; Harrison *et al.* 2012; Di Lorenzo *et al.* 2016). However, MPA design and implementation naturally involves multiple stakeholders, which can slow the rate of establishment and efficiency of MPAs (Wood *et al.* 2008; Chuenpagdee *et al.* 2013).

Lastly, a natural way of reducing depletions of old and large fish is to protect them through maximum size limits or slot-size limits (both a minimum and maximum size limit) (Conover and Munch 2002; Berkeley *et al.* 2004b; Gwinn *et al.* 2015). Such measures may buffer or reverse selection for slower growth and earlier maturation (Conover and Munch 2002; Law 2007; Matsumura *et al.* 2011), and although an initial reduction in fisheries yield is inevitable, an increase in yield may be expected with time through maternal effects (Berkeley *et al.* 2004b; Matsumura *et al.* 2011; Gwinn *et al.* 2015). A prerequisite for such regulations to function is that released fish have high survival, and they are therefore most useful for shallow-water, small-scale commercial fisheries or in recreational fisheries (Hixon *et al.* 2014).

Good management demands the necessary knowledge about life history, population structure, ecology, reproduction and behaviour of the species in question. For instance, it is being increasingly evident that coastal fish populations may be genetically structured and display substantial life history variability over small spatial scales (Knutsen *et al.* 2011; Wilson *et al.* 2012; Kuparinen *et al.* 2015). Fishery regulations ignoring this can result in spatial variation in the strength of harvest selection on life history traits (Alós *et al.* 2014). Ultimately, this may lead to loss of specific genotypes, potentially lower the adaptive potential for species facing increasing anthropogenic stress (e.g. climate change, pollution, invasive species) (Kuparinen *et al.* 2015). Similarly, an MPA may not function as intended if not taking into account spatial behaviour of the species targeted for protection (Olsen *et al.* 2012). For example, small MPAs may induce selection for small home ranges, as more mobile individuals have larger probability of being captured outside the MPA (Villegas-Ríos *et al.* 2016).

The Norwegian wrasse fisheries: size selective and lightly managed

Most fish stocks of current commercial interest have been harvested for several decades or centuries. The story of several wrasses (*Labridae*) of Northern Europe is indeed a different one. Here, commercial exploitation of wrasses began as late as in the 1990s in Norway and on the British Isles, when it was discovered that their natural behaviour as parasite cleaners on other fish (Potts 1973) could be used to reduce sea-lice (*Lepeophtheirus salmonis* and *Caligus elongatus*) infestation in salmonid aquaculture (Bjordal 1988; Darwall *et al.* 1992). However, catches remained relatively low throughout the 90-s and 00-s, when wrasses were only complementary to chemical

treatments. The demand for cleaner fish increased dramatically from 2009 and onwards, coinciding with the sea-lice evolving resistance to various pesticides (Skiftesvik *et al.* 2014b; Besnier *et al.* 2014). Wrasses are now being used in nearly all salmon farms in Norway and more than 20 million wild wrasses were reported in the landing statistics of 2014 and 2015 (Figure 1). In western Norway, the salmon farms mainly use local caught wrasse, while in mid and northern Norway; wrasse is also imported from the Skagerrak coast in the south, where salmon farming is virtually absent (Taranger *et al.* 2013; Skiftesvik *et al.* 2014a).

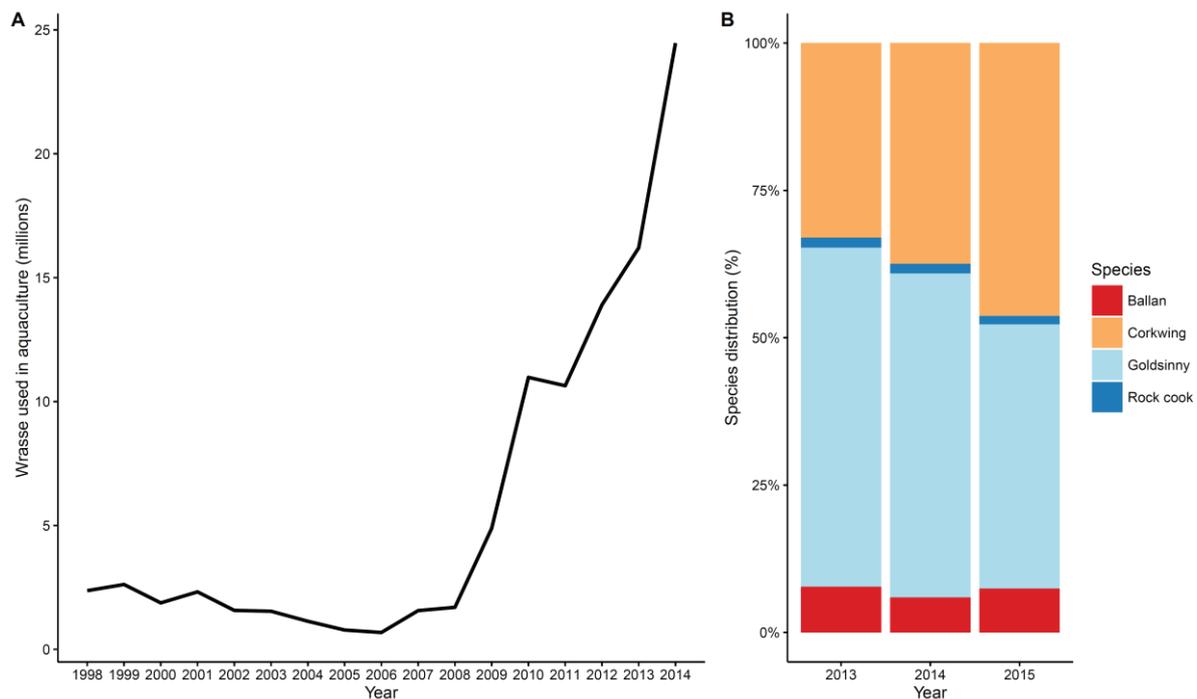


Figure 1:

A: The number of cleaner fish (including both wild caught and farmed wrasse and lumpsucker (*Cyclopterus lumpus*) deployed in salmonid aquaculture 1998-2014.

B: The species distribution in the last three years fisheries of wild caught wrasses; the ballan (*Labrus bergylta*), corkwing (*Symphodus melops*), goldsinny (*Ctenolabrus rupestris*) and rock cook (*Centrolabrus exoletus*). The total landings of wrasse in 2015 was 24.8 millions individuals. Source: The Norwegian Directorate of Fisheries. The figure was developed by Torkel Larsen.

Confined to shallow rocky shores and reefs, the wrasses are caught with small vessels using fyke nets and baited pots. Four different species are being harvested in Norway with corkwing wrasse (*Symphodus melops*) and goldsinny wrasse (*Ctenolabrus rupestris*) holding the largest share of the landings (Figure 1, 2). Ballan wrasse (*Labrus bergylta*) is harvested in a considerably lower proportion, but the demand and value is higher since

it can be stocked with the largest salmon (Skiftesvik *et al.* 2013). Rock cook (*Centrolabrus exoletus*) is only used in a few farms, so their low numbers in the landings does not reflect abundance. Corkwing has two distinct male strategies; most mature as nesting males, which build complex nest of algae and guard the eggs, whereas a minority develops as female mimicking males who performs sneak spawning (Uglem *et al.*, 2000; Kim T. Halvorsen pers. obs.). The determination of the male strategy appears to be linked with juvenile growth patterns, without excluding the possibility of a genetic mechanism (Uglem *et al.* 2000). Sneaker males have larger testes and more motile sperm (Uglem *et al.* 2001) and due to the findings of old and large sneaker males in the populations, the male strategies are presumably fixed for life once determined (Uglem *et al.* 2000; Halvorsen *et al.* 2016). The corkwing may attain 24 cm and 9 years (Darwall *et al.* 1992). The smaller goldsinny spawns in the free water masses. The males hold territories, while younger “accessory” males may perform sneak spawning (Hilldén 1981). It can attain 21 cm (Torkel Larsen; pers. comm.) and reach 20 years (Sayer *et al.*, 1996). The ballan is a protogynous hermaphrodite (female first) with males guarding the eggs until hatching. It can attain 60 cm and reach 29 years (Dipper *et al.* 1977; Darwall *et al.* 1992).



Figure 2: The two focal species of this thesis. Left: Corkwing wrasse nesting male (top), female (middle) and sneaker male (bottom). Photo: Tonje K. Sjørdalen. Right: A goldsinny wrasse. Photo: Even Moland.

In Norway, the first management measures for wrasse were implemented as late as 2011, enforcing a general minimum size limit of 11 cm for all wrasse species. The management ignored the large differences in life history traits when setting the minimum size limit. From 2015, minimum size limits were species-specific (11 cm for goldsinny and rock cook, 12 cm for corkwing and 14 cm for ballan). In addition, selective grids of 12 mm inserted in the gear became compulsory to reduce the catch of fish below the size limit. A spring closure to limit fishing during the spawning period was also implemented as a part of the first regulations in 2011. The length of the closure has gradually been extended, with fishing now being prohibited until the 11 of July in western and southern Norway, or earlier if scientific assessment indicates the main spawning period has passed. Spawning closures for species with complex mating systems could have positive effects on successful reproduction and recruitment (Overzee and Rijnsdorp 2015). With both scientists and fishery managers being concerned of the increasing fishing intensity, total landing caps for southern (4 million), western (10 million) and mid Norway (4 million) were set in 2016, limiting the national landings to 18 million wrasses.

Despite the implementation of the various management measures over the last five years, a considerable lack of knowledge on life history traits, reproduction and mortality of the targeted species and populations remained (Espeland *et al.* 2010; Skiftesvik *et al.* 2014a). Such knowledge is fundamental for proper fisheries management. Of particular concern is whether the size regulations help to sustain healthy spawning populations, or if they promote a fishery that alters sex ratios and skew size distributions towards immature fish (Darwall *et al.* 1992; Sayer *et al.* 1996b; Varian *et al.* 1996). In paper I and II we demonstrate that the fisheries are sex and size selective for corkwing, with intermediate-sized nesting males being most vulnerable for being captured. Moreover, these wrasses are sedentary species with low adult dispersal capacity (Darwall *et al.* 1992; Sayer 1999; Skiftesvik *et al.* 2014a) and are distributed over natural gradients in habitat, exposure and temperature (Skiftesvik *et al.* 2014b). Thus, life history variability reflecting these conditions may be evident on regional and local scales. Assessments of such variation are therefore necessary for designing regulations and scales of appropriate management units. Previous studies have detected considerable differences in life history traits such as life span and age at maturation for corkwing between populations on the British Isles and Sweden; (Dipper and Pullin 1979; Sayer *et al.* 1996c;

Uglem *et al.* 2000) and in lifespan for goldsinny (Hildden 1978; Sayer *et al.* 1995). In addition, goldsinny growth rates have been shown to differ between nearby populations on the Scottish west coast (Sayer *et al.* 1995). In paper I and IV, we present results showing differences in life-history traits at smaller scales than those mentioned for both species. Wrasses are abundant in shallow coastal waters and are important predators on crustaceans and mollusc (Sayer *et al.* 1995; Deady and Fives 1995a) and prey for gadoids and sea birds (Steven 1933; Nedreaas *et al.* 2008), in addition to their role as cleaner fish for other fish (Potts 1973). A sustainable wrasse fishery has therefore high value to the ecosystem as well as for the society. In paper III and IV, we show that MPAs have higher abundance of both goldsinny and corkwing and finds goldsinny growth rate to be negatively related to population density and the abundance of coastal cod (*Gadus morhua*).

Objectives and methodical approaches

My main objectives of this thesis were to:

- 1) Study spatial and sexual variation in life history traits in corkwing and goldsinny wrasse and elucidate the underlying processes producing such variation.
- 2) Estimate size and sex selectivity in the corkwing wrasse fishery. Assess the effects of fishing on population parameters, such as abundance, age and body size and sex ratios for corkwing and goldsinny.
- 3) Evaluate the current management and fishing practice in a selective harvesting perspective. Propose alternative regulations to reduce selectivity and to improve general sustainability in the wrasse fisheries.

I chose to study the corkwing wrasse more closely, primarily because its reproductive biology makes it especially vulnerable to size selective harvest, as the nesting males providing obligate parental care tend to be larger than females and sneaker males (Darwall *et al.* 1992; Sayer *et al.* 1996c; Uglem *et al.* 2000). The goldsinny is also harvested in similar numbers as the corkwing, but it grows slower and is therefore better protected by the size limit (Figure 3). However, the goldsinny has long lifespan and males tend to grow slightly faster, so size selective harvest may particularly affect age structure, but also sex ratios (Sayer *et al.* 1996b; Varian *et al.* 1996).

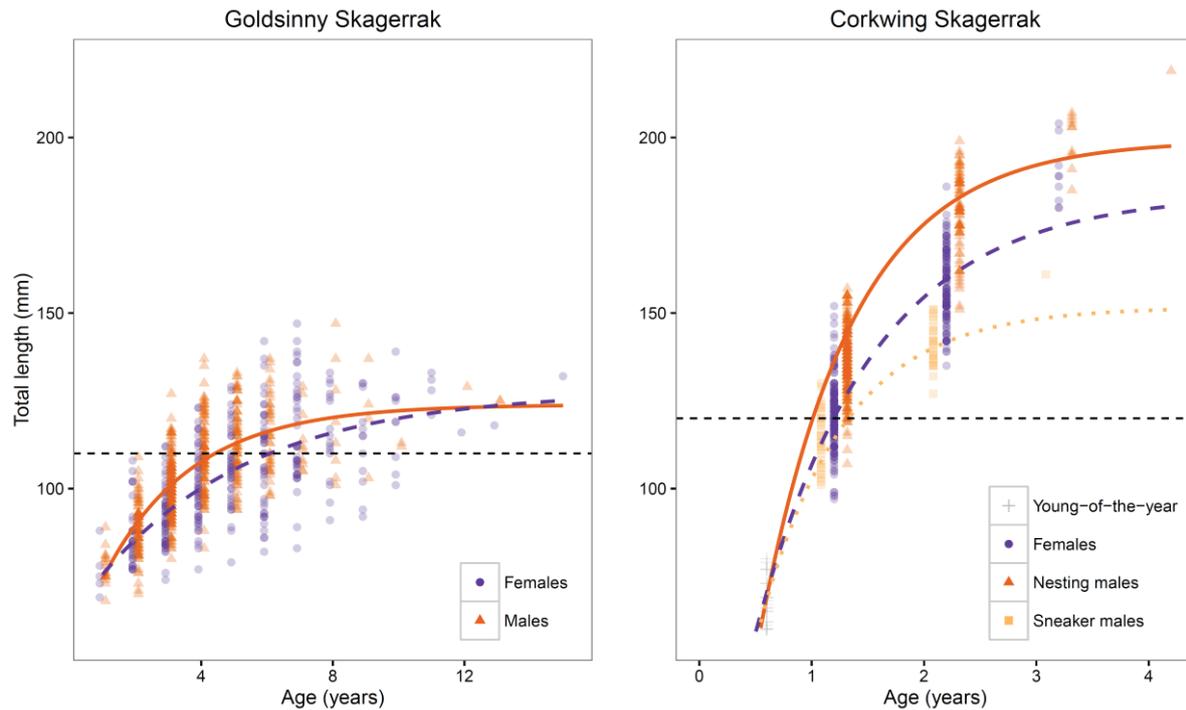


Figure 3: von Bertalanffy growth curves illustrating the different growth trajectories and lifespan between goldsinny (left) and corkwing (right) from Skagerrak populations (2013). The minimum size limit is indicated with the dashed horizontal line. The growth models are constructed using data presented paper III.

The objectives were addressed from different angles in four separate studies conducted in Southern Norway (Figure 4), covering the most important regions for wrasse fisheries. Specifically, we first studied spatial variation and the proximate causes for sexual size dimorphism in corkwing wrasse (paper I) by comparing body size among eight populations during the spawning period. In addition, age, growth and maturation were contrasted for a south-eastern population and a population further north on the western coastline. The effectiveness of the minimum size regulation to protect mature nesting males, females and sneaker males was evaluated. In paper II, we estimated selectivity on sex and body size and fishing mortality in corkwing wrasse in a mark-recapture experiment in Western Norway. We contrasted fishing mortality and capture probability in a fished site and small MPA by recapturing on commercial fishing trips operating in the study area. In paper III, we sampled corkwing and goldsinny in four pairs of MPAs and fished areas in Skagerrak to test whether fishing had affected abundance, age, body size and sex ratios. Lastly, in paper IV, we used back-calculated age-at-length from otoliths to investigate the variability in goldsinny growth rates on small spatial scales in the same MPA-fished areas sampled in paper III.

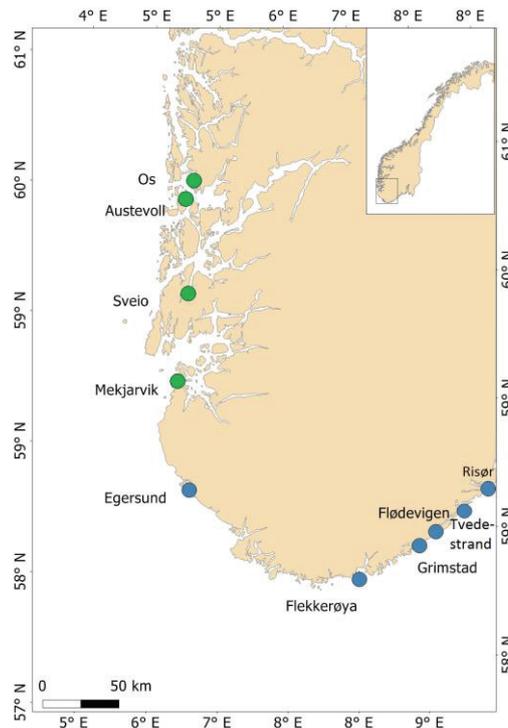


Figure 4: The study locations for this thesis. Circles with green fill represents the northern populations and blue the southern, as defined in paper I. Sampling for Paper I was conducted in all locations except for the two easternmost; Tvedestrand and Risør. The tagging experiment in Paper II was conducted in Austevoll. Paper III and IV used data from the MPA and control sites in in Flødevigen, Tvedestrand and Risør.

The methods and statistical analyses used throughout this thesis are well proven and established for fisheries assessments and for comparing life history parameters. Information on individual age is fundamental in life history studies, allowing for estimation of variation in growth rates, maturation and lifespan (Paper I). In paper IV, we used information of the length of each growth increment to reconstruct age-at-length in previous years of each individual fish. The growth increments on the sagittal otoliths of corkwing and goldsinny wrasse are easy to discriminate and measure under a stereo microscope (Figure 5). In paper II, we used passive integrated transponder (PIT) tags inserted into the body cavity to mark corkwing. These tags allowed us to use a tag reader with an attached antenna to effectively detect recaptures on commercial fishing trips without handling the fish. Often, tag-recovery studies rely on estimating a report rate on tag-returns from fishers, introducing additional uncertainty in parameter estimation (Pine *et al.* 2003). With our study being carried out over a short time period combined with precise information on the individuals caught by fishing, a rather simple logistic regression model could be applied for estimating fishing mortality and the influence of sex and body size on capture probability.

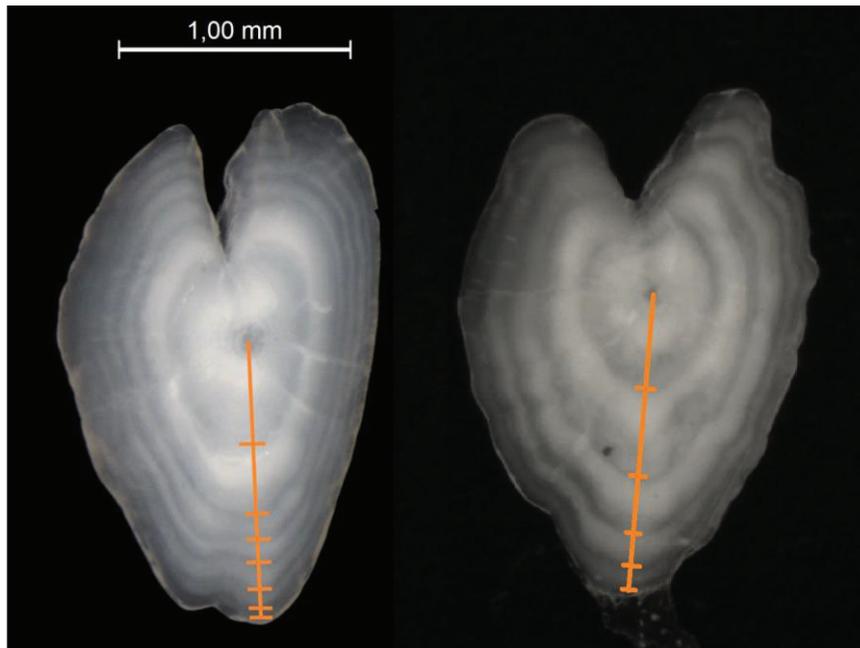


Figure 5: The sagittal otolith of a seven year old goldsinny (left) and a five year old corkwing (right). Summer growth increments (opaque zones) are interrupted by the shorter winter increments (darker bands).

Results and discussion

As opposed to size-selective fisheries, the scientific literature on the occurrence and consequences of sex-selective fishing is limited, most being studies on sequential hermaphroditic species (Alonzo and Mangel 2004; Hamilton *et al.* 2007) or fisheries directed on only one sex (Pillans *et al.* 2005; Sato and Goshima 2006; Sato 2012), which therefore represent more obvious cases. Sexual dimorphism is common across all fish taxa (Parker 1992), but only a few studies have focused on the occurrence and consequences of differential exploitation rates between sexes of dioecious species under more traditional harvest regimes (Rijnsdorp *et al.* 2010; Kendall and Quinn 2013; Myers *et al.* 2014). In **Paper I**, we detected a geographic pattern among corkwing populations in southern Norway, with the four northernmost populations in our sampling having smaller body size, but stronger male-biased sexual size dimorphism (the size differences between mature nesting males and females) compared with four populations further south. Further, two populations (a northern and a southern) were more closely studied and assessed for growth, age and maturation, which provided insight into the proximate causes underlying sexual size dimorphism. The northern population grew slower than the southern, but the sexual growth differences were more pronounced and most nesting males delayed maturation a year relative to females, which was not the case in

the southern. The southern and northern populations have later been confirmed to be genetically distinct (Gonzalez *et al.* 2016). Moreover, the catch per unit effort (CPUE) was consistently higher in the northern sampling locations, indicating higher densities. The nesting males are highly territorial during the reproductive season, and male-male competition is therefore likely stronger at high population densities. Consequently, there may be stronger sexual selection on male body size in the northern populations, which could explain the stronger sexual dimorphism.

In **paper II**, we show that the fishery for corkwing wrasse is sex-selective. For fish tagged during spawning, nesting males had higher capture probability in the fishery than females, independent of body size. After spawning, an interaction effect between body size and sex was evident, with intermediate-sized nesting males being most vulnerable to capture. Sneaker males showed similar capture probabilities as nesting males, but the sample size was too low to draw firm conclusions. A possible explanation for higher capture probabilities of nesting males relative to females could be physiological and/or behavioural differences between the sexes. For instance, nesting males have higher growth rates (Paper I) and most likely a higher feed demand, potentially increasing their attraction to baited traps. Also, due to their territoriality they are more aggressive than females and sneaker males, especially during the nesting period (Potts 1974). Such behaviour differences may persist throughout the year and affect the motivation to enter the traps. Generally, capture probabilities were lowest for the largest individuals, which could have multiple explanations, none being mutually exclusive. First, larger (and older) fish may have higher natural mortality rates. Second, larger individuals may use different habitats or deeper waters not targeted by fishers. Third, large fish could be less attracted to the crustacean bait used in the pots (as previous studies have shown larger fish to predominately graze on molluscs (Deady and Fives 1995b)). Lastly, if vulnerability to passive gear is a consistent behavioural trait, selective fishing in previous seasons may have removed the large individuals with higher capture probabilities. A small protected site (approx. 600 m coastline) reduced fishing mortality significantly, but sex and size selectivity was similar to the site open for fishing. This indicates that MPAs should be larger to protect the sexes evenly. It is concluded that there is a considerable potential for fisheries induced changes in sex ratios and size structure. In turn, this could have negative consequences for mating

system dynamics and the strength of sexual selection and ultimately, for recruitment and evolutionary trajectories.

While paper II demonstrates a relatively high, selective fishing mortality in Western Norway, the question whether fishing has impacted the natural populations was addressed in paper III and IV. Previous studies conducted in Scotland and Ireland in the 1990s observed reduced catch per unit effort and a decline in the proportion of large males concomitant with the emerging wrasse fishery for both species (Darwall *et al.* 1992; Sayer *et al.* 1996b; Varian *et al.* 1996). However, by lacking replicates of exploited and unexploited sites; these studies could not disentangle the effects of fishing from natural fluctuations. In Norway, the lack of reference areas and suitable time series also hampers evaluations of long-term effects of wrasse fisheries. On the Skagerrak coast, four marine protected areas were established in 2006 and an additional two in 2012. These are partially protected areas where passive standing gears are prohibited (gillnets, pots and fyke nets). Wrasse are effectively fully protected in all these MPA's since they are normally not targeted in recreational hook-and-line fisheries. **In paper III**; experimental fishery within four of these MPAs and corresponding control areas revealed a moderate effect of protection on the targeted species. Specifically, abundance was higher within all four MPAs for goldsinny, while in three out of four MPAs for corkwing. Corkwing were generally older and had larger body size within MPAs while no clear pattern was evident for goldsinny. However, goldsinny showed larger variation at these parameters on smaller scales (see also paper IV), possibly reflecting that environmental factors other than fishing have stronger effects on life history traits. Sex ratios did not differ between MPA and control sites in either species, but the potential for size-selective fishing to be sex-selective was found to be limited.

Paper IV further investigates growth variability of goldsinny among four MPA and control pairs on the Skagerrak coast. This revealed large individual and among site variation in growth trajectories. Goldsinny growth appeared to be negatively related with both population density and abundance estimates of coastal cod (*Gadus morhua*). There were no consistent differences between MPAs and fished areas on growth rates, but this possibly could be related to the fisheries effects on population density found in Paper III. For instance, fishing may selectively remove the fastest growing individuals, while simultaneously increasing the average growth rate by reducing the population

density. This may mask any directional selection for slower growth in harvested areas. Males grew faster than females, in agreement with earlier studies on the British Isles (Sayer *et al.* 1995; Varian *et al.* 1996) and sex-selective fishing may therefore also be anticipated for goldsinny. The spatial and individual life-history-variability detected in this study implies that the minimum size limit will protect populations differently such as shown for corkwing in paper I. It has also implications for the translocations of goldsinny to genetically distinct populations northern Norway. For instance, if different growth rates represent genetic adaptations, this may affect fitness and productivity in the recipient areas if escapement and interbreeding with local populations occurs. Lastly, it was found that fyke nets capture faster growing goldsinny than pots. This could be related to fyke nets having larger mesh-size than the pots and therefore retain larger fish, but could also be related to behaviour traits not measured in these studies. Both goldsinny and corkwing appears to be ideal model species for future studies improving our understanding of the interaction between behaviour, physiology and gear selectivity.

The Skagerrak coast has not been as intensively fished as the western coast. This may explain the relatively low, but significant differences between exploited and unexploited areas in paper III and IV. Nevertheless, the reduced abundance of wrasse above the size limit demonstrates that the wrasse fisheries have a considerable potential in affecting ecosystem functioning, as we show that these wrasses are the most numerous fish species in the shallow water communities at the Norwegian coast. It is important to stress that the fishery has increased substantially since these studies were carried out in 2013 (Figure 1), so these results present the situation at the beginning of an intense period of wrasse fisheries. Thus, these studies may prove especially valuable as a baseline for monitoring the impact of fishing in this region in the coming years.

Implications for management and conservation

Sea-lice is one of the largest threats to wild populations of wild salmonids such as Atlantic salmon and sea trout (Costello 2009a; Torrissen *et al.* 2013), with an estimated average cost of 6 % of the annual production value in salmon producing countries (Costello 2009b). The sea lice has quickly evolved resistance to various pesticides and chemical delousing agents (Besnier *et al.* 2014; Aaen *et al.* 2015). In addition, there is

increasing evidence of such treatments having adverse effects on the ecosystems in farming areas (Ernst *et al.* 2001, 2014; BurrIDGE *et al.* 2010; Van Geest *et al.* 2014; Dounia *et al.* 2016). In that perspective, cleaner fish is currently regarded to have less negative environmental impacts compared with chemical treatments (Treasurer 2002; Groner *et al.* 2013; Torrissen *et al.* 2013). However, if wild wrasse populations are overfished; there is a potential for serious ramifications for the coastal ecosystems in which they hold a pivotal position.

I have shown that the wrasse spawning stocks are poorly protected by the current management regulations, especially for corkwing, with a higher fishing mortality for the males providing parental care. Fishing depleting the numbers of large nesting males may affect offspring production (Darwall *et al.* 1992). Altered sex ratios may reduce the encounter frequency of potential mates and could affect the fitness of the alternative reproductive male tactics. In addition, if fishing result in truncated size distributions, the egg production may be reduced as smaller females have smaller gonads. The ballan wrasse has not been studied in this thesis, but depending on the mechanism determining sex-change, overfishing may have serious consequences for reproduction and recruitment of sequential hermaphrodites (Alonzo and Mangel 2004, 2005). The sedentary life-style of all three target species (Sayer, 1999; Villegas-Ríos *et al.*, 2013; Paper II) combined with an increasingly mobile fishing fleet poses a challenge as fishers may gradually deplete the populations without reducing their catch rates. Thus, catch per unit effort and trends in landings statistics does not necessarily reflect the state of the populations, as local populations may be severely overfished with limited possibilities of replenishments of adults from nearby populations. By continuing the mark-recapture survey on corkwing presented in paper II for the two following years, preliminary analyses revealed no indications of directional movement from the protected site to the nearby fished site (K.T. Halvorsen, unpublished data).

The size- and sex-selectivity of the wrasse fisheries indicates a potential for rapid evolutionary change, especially since sexual selection and fisheries selection operating on the same traits may amplify the strength of overall selection (Hutchings and Rowe 2008; Urbach and Cotton 2008). All three target species have genetic structured populations within Norway (Sundt and Jørstad 1998; D'Arcy *et al.* 2013; Gonzalez *et al.*

2016). Thus fisheries induced evolutionary change may happen on relative small scales, threatening the persistence of adaptations to local environments.

To accommodate for the mentioned risks, some specific solutions are proposed. First, in paper I; we advocate for a slot size limit (a combination of minimum and maximum size limits) for the corkwing wrasse fisheries in western Norway, where the species has stronger sexual size dimorphism and a longer lifespan relative to those populations further south on the Skagerrak coast. This would protect the sexes more equally (Figure 6), and by protecting older and larger fish it would therefore increase the reproductive potential and reduce selection pressures for smaller body size and earlier maturation.

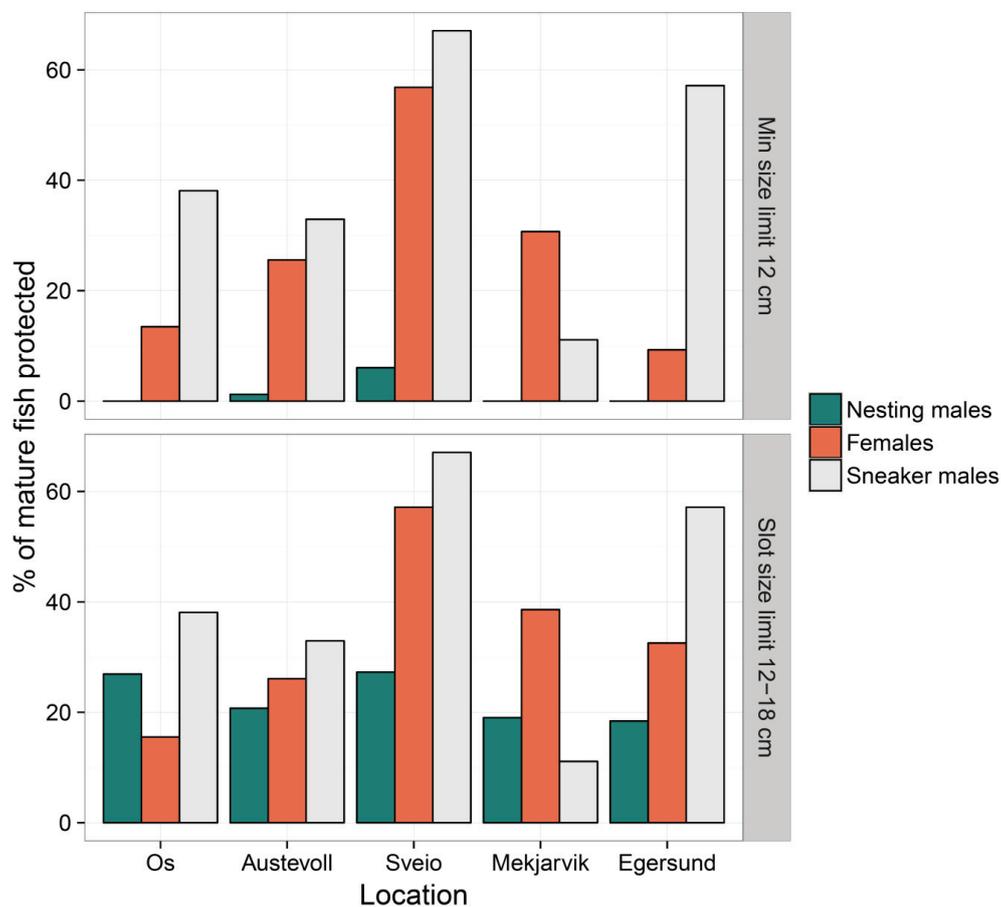


Figure 6: Comparison of the current size limit (12 cm; upper panel) with a slot-size limit (12-18 cm; lower panel) on the protection of mature nesting males, females and sneaker males. The data is size distribution from commercial and scientific fisheries (Austevoll) conducted in 2014 (Paper I).

Using the size distribution of commercial and scientific catches (data from paper I) the estimated loss in yield by implementing a 12-18 cm slot limit for corkwing is only 5.5 %. However, by ensuring a more balanced sex and size structure, an increased yield in a

larger timeframe can be anticipated. The finding of faster growth, earlier maturation and a short life span in the Skagerrak populations indicate that a slot-size limit has little purpose here (Paper I). However, the minimum size limit should be increased to better match the size at maturation for both sexes in Skagerrak.

A slot limit should also be considered for goldsinny due to the relative long lifespan of this species and high individual variation in growth rates. Also, the large degree of individual and spatial differences in growth rates complicates setting an appropriate minimum size limit, whereas a slot size limit could distribute age-specific fishing mortality more evenly in both fast growing and slow growing individuals and populations. It is less clear whether a slot limit would be appropriate for ballan wrasse. Ballan change from female to males at lengths between 34 and 41 cm in Western Norway (Muncaster *et al.* 2013), but better knowledge of the spatial variability in sex ratios, size and age structure is needed. When held in groups in captivity, removal of large ballan males has been observed to induce the smaller females to change sex (Anne Berit Skiftesvik, pers. comm.). Such reaction norms in size-dependency on the onset of sex-change to social environment has been demonstrated in other protogynous hermaphroditic fish (Warner and Swearer 1991; Lutnesky 1994). Thus, it is plausible that fishing may induce changes in the onset of sex-change. Nevertheless, with the current fishery being limited to the smaller fish (<35 cm; Kim T. Halvorsen unpublished data), presumably females, a slot limit for ballan should ensure that both sexes are protected at similar proportions.

Our second recommendation is to establish more marine protected areas (MPAs). Paper III demonstrates positive results of slightly larger MPAs in Skagerrak, particularly on abundance. In paper II we show that even a very small protected site reduced fishing mortality in western Norway. In a meta-analysis with data from 12 European MPAs, Claudet *et al.* (2010) found that positive effects on density for territorial species (such as the wrasses) was not related to the size of the MPA. However, in paper II, sex selectivity for fish tagged in the small MPA and those tagged in the fished site was similar, so larger MPAs should be considered to ensure equal protection of sexes of corkwing. It appears to be a growing recognition of MPAs in Norway. From 2014 to 2016, four new MPAs have been established on the Skagerrak coast and the size of one older MPA has been increased. On the western coast, a network of nine smaller MPAs has been established in

the Hardanger Fjord, effective from 1.10.2016. Although the main purpose of these areas are to protect lobsters, fishing with fyke nets and pots is prohibited, thus excluding commercial wrasse fisheries. For MPAs to be effective in regulating the wrasse fisheries on a national scale, the rate of establishment must be much higher. It should be simpler to implement spatial regulations protecting wrasse only, as it is almost exclusively commercially harvested with specialized gear, thus other commercial and recreational fisheries should not be affected. My experience is that most wrasse fishers are positive to MPAs, since the current situation resembles a classic “the tragedy of the commons” (Hardin 1968) case, where fishers race to the best and less exploited fishing areas. With an increasing number of fishers every year, there is more competition and conflict over fishing areas, driving the fishers to invest in larger, faster vessels that can cover larger areas and increase the catch rates. The implementation of total catch quotas in 2016 may have reinforced this, as the fishery is being stopped as soon as the landing cap is reached and the more effective fishers can naturally receive a larger share of the quota.

Given the strong economic and political interest in further growth in open-pen salmonid aquaculture in Norway, there are no indications of a declining demand for cleaner fish in the near future. However, there is now a viable production of cultured lump sucker (*Cyclopterus lumpus*) and ballan wrasse in Norway, with news reports estimating a production of ten million lumpsuckers in 2015 (<http://ilaks.no/godt-over-ti-millioner-rognkjeks-produisert-i-2015/>). Thus, cultured cleaner fish may be increasingly important and gradually reduce the need for wild-caught wrasse. Nevertheless, the fishery is likely to be carried out at the current intensity for the coming years, which requires a precautionary approach. In addition, the potential risks associated with the large-scale transportation of wild-caught wrasse from Southern Norway and Sweden to mid and northern Norway has only been briefly discussed in this thesis. The fate of wrasses in the salmon pens is poorly documented, but a mortality of at least 33 % has been estimated over six months in a survey of 17 salmon farms (Nilsen *et al.* 2014). The proportion escaping may also be high, and has been shown to reach 50 % for goldsinny (Woll *et al.* 2013). This demonstrates a real potential for genetic introgression of southern wrasse with the local populations in the salmon farming areas which are genetically different (Sundt and Jørstad 1998; Gonzalez *et al.* 2016). In addition, corkwing was not present in North Trøndelag (mid Norway) in the 90s (Maroni and Andersen 1996), but is now reported in the catches in the same area (Per Andersen,

pers. comm.). There are also obvious risks of disease transfers between wrasse populations and for introducing alien species present in the transportation water (Taranger *et al.* 2013). Arguably, translocating millions of wild fish and untreated water several 100 km's away every year is large-scale experiment with the coastal ecosystem for which the consequences are difficult to predict. This certainly merits higher attention from the responsible authorities and further scientific investigations.

Conclusions

In this thesis, I present new knowledge on the spatial and sexual life history variation of corkwing and goldsinny wrasse and provide specific management advice. The corkwing exhibits male-biased sexual size dimorphism in western Norway, which may reflect higher densities and genetic separation from less sexually dimorphic populations in Skagerrak. Nesting males were shown to have higher capture probabilities than females in the fishery, independently of body size. This possibly reflects higher growth rates or different behaviour of nesting males, increasing their attraction to baited pots. Marine protected areas (MPAs) were demonstrated to be effective in reducing fishing mortality and had higher CPUE of both corkwing and goldsinny, with positive effects on effects on age and body size of corkwing. Goldsinny growth rates vary over small geographical distances, which may be related to population density and predator abundance. Both corkwing and goldsinny should benefit from implementation of slot limits, where also the larger and older individuals are protected. This will result in a more even protection of males and females and preserve size and age structure. Several intermediate sized-MPAs specifically protecting wrasse should be established in the most intensively fished regions, which could buffer against the effects of selective harvesting without affecting other fisheries. More studies are needed on the effect of size and sex selective fisheries of ballan wrasse and the consequences of large-scale translocations of wrasse from southern to northern Norway.

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Paper I

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Male-biased sexual size dimorphism in the nest building corkwing wrasse (*Symphodus melops*): implications for a size regulated fishery

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Size selective harvesting can also be selective on sex in species displaying sexual size dimorphism (SSD). This has potential consequences for mating systems and population dynamics. Here, we assessed spatial variation in SSD and body size in eight Norwegian populations of corkwing wrasse (*Symphodus melops*), a species where males either mature as nesting or sneaker males. Corkwing wrasse is increasingly harvested in a size-selective fishery which supplies the Norwegian salmon aquaculture industry with cleaner fish to reduce sea-lice infestations. In our study, mature nesting males had larger body sizes than females and sneaker males, and the size difference was significantly larger in the four northernmost populations. Contrasting life history traits in two of the populations (a southern and a northern), we found that the larger SSD in the north was because of nesting males delaying maturation and growing faster relative to females and sneaker males. Mature northern nesting males also had smaller gonads at smaller sizes relative to their southern counterparts, indicating a trade-off between reproduction and somatic growth in males. Applying the current minimum legal size limit for commercial fishing in Norway (12 cm) would have failed to protect any mature nesting males in five out of the eight populations. Moreover, the findings of more male-biased SSD and female-biased sex ratios in the northern populations imply that there is larger potential for sex-selective harvesting in these populations. To avoid fisheries-induced changes in sex ratios, we advocate for spatially structured management units and to refine the current size-regulations using either sex-specific minimum size limits or a slot limit, also protecting the larger fish and therefore more nesting males.

Keywords: aquaculture–environment interactions, corkwing wrasse, fisheries management, selective harvesting, sexual size dimorphism, *Symphodus melops*.

Introduction

The strength and form of selection on body size or correlated traits is rarely identical between the sexes and result in sexual size dimorphism (SSD) (Parker, 1992; Andersson, 1994; Fairbairn

et al., 2007). For different reasons, sexual dimorphism is often neglected in assessments and management of commercial fisheries (Hanson *et al.*, 2008; Zhou *et al.*, 2010). This is unfortunate, as size selective harvesting of sexually dimorphic populations is

likely to be sex-selective (Rowe and Hutchings, 2003; Fenberg and Roy, 2008; Kendall and Quinn, 2013). Fisheries induced shifts in sex ratios can affect population productivity if the probability of encountering mates is reduced (Rowe and Hutchings, 2003). In species with parental care, selective removal of the caring sex may have direct consequences for offspring survival (Suski *et al.*, 2003; Sutter *et al.*, 2012). Moreover, sex ratio influence intra-sexual competition and mate choice and therefore the opportunity and strength of sexual selection (Kvarnemo and Ahnesjö, 1996; Clutton-Brock, 2007), so size and sex-selective fishing have potential consequences for the direction and rate of evolutionary change (Rowe and Hutchings, 2003; Hutchings and Rowe, 2008).

In both Scandinavia and on the British Isles, the nest building corksling wrasse (*Symphodus melops*) is harvested and used as cleaner fish in the salmonid aquaculture industry to reduce lice infestations from the parasitic copepods *Lepeophtheirus salmonis* and *Caligus elongatus* (Bjordal, 1988; Darwall *et al.*, 1992). Previous studies conducted on the British Isles have found the males, who builds the nests and provide parental care, grow faster, mature later and attain larger sizes than females (Potts, 1974; Darwall *et al.*, 1992; Sayer *et al.*, 1996). In addition, a smaller proportion of males mature as *sneaker males*, which are smaller and mimic the female phenotype to steal fertilizations from the *nesting males* (Potts, 1974; Dipper and Pullin, 1979; Uglem *et al.*, 2000). The wrasse fisheries in Norway and on the British Isles are managed with minimum size limits which therefore may protect nesting males, females and sneaker males unevenly if they differ in body size. During the first wave of wrasse fisheries in Ireland, a reduction of large nesting males and catch per unit effort was observed in a harvested population where nesting males initially were larger than females (Darwall *et al.*, 1992). Given that nesting males provide obligate parental care and are territorial, reducing their frequencies is likely to negatively affect egg survival and the mating system dynamics (Darwall *et al.*, 1992). In Norway, the minimum size limit for corksling wrasse was raised from 11 to 12 cm in 2015, but fundamental knowledge on size distributions, growth and maturation and sexual dimorphism is lacking from Norwegian waters (Skiftesvik *et al.*, 2014a).

This study seeks to investigate spatial variation and proximate causes of sexual differences in body size in harvested Norwegian corksling wrasse populations to provide a basis for evaluating whether the current size regulations may promote sex-selective fisheries. First, we assess sexual differences in body size and sex ratios among eight populations distributed along the coastline South Eastern Norway to Hordaland further north on the Western coast. Second, we analyse sex-specific growth and maturation in a selected northern and southern population. Lastly, we evaluate the potential consequences of failing to address this sexual variation in management and propose possible solutions for reducing sex-selective harvesting.

Material and methods

Scientific sampling

Scientific sampling of corksling wrasse was conducted from 11 June 2014 to 4 July 2014 in two main areas: near the field stations of the Norwegian Institute of Marine Research (IMR) in Austevoll, Western Norway and in Arendal on the South-eastern coast (Figure 1). Corksling wrasse were captured using the same gear types as the commercial fisheries; fyke nets (5 m single

leader, 55 cm diameter entrance ring and leader mesh size of 30 mm) and baited wrasse pots (rectangular prism shaped, 70 cm×40 cm×29 cm, circular entrances (75 mm diameter), two chambers and 15 mm mesh-size), set at 1–7 m depth and hauled every morning. We only included fish sampled in fyke nets when comparing catch per unit effort (CPUE), length and sex ratio data between locations, as pots were not used in the commercial sampling (see below) and the selective properties may differ between the gear types. Fish from both gear types were included when comparing within-population sexual differences in individual growth and age at maturation. Specific sampling sites were selected on the basis of advice from local fishermen (Austevoll) and in areas with documented commercial wrasse fisheries (In Arendal—Gjøsaeter, 2002). Upon capture, total length was measured to the nearest mm and sex and reproductive state (spawning/not spawning) were determined by applying light pressure on the abdomen to check if milt or eggs were extruded from the urogenital papillae (Skiftesvik *et al.*, 2014b). The fish were then released at the site of capture. Certain hauls were selected in which all captured corksling wrasse were immediately euthanized with an overdose of MS222 and then frozen for analysing age and maturation. The method of euthanizing and handling of live fish in this study was in compliance with Norwegian animal welfare Act (LOV 2009-06-19 nr 97: Lov om dyrevelferd). We strived to minimize handling time and stress imposed on the live animals.

Commercial sampling

We collaborated with commercial wrasse fishermen to obtain additional length and sex ratio data from six locations from 14 May to 2 July (Figure 1). Wrasse was captured with un-baited fyke nets set at 0–7 m depths left over night. A trained researcher joined fishing trips and measured total body length to the nearest 0.5 cm and checked for sex and reproductive state as described before. The total number of corksling wrasse per haul was noted to calculate the mean catch per unit effort (CPUE) in each location. Fishermen were to keep or release the fish as during a normal fishing operation. The last commercial sample was obtained from a fisherman operating near Egersund. The fish was here sampled at port; hence catch per unit effort data were not available. He used fyke nets as a capture method and was instructed to retain all size classes.

Determination of age and maturation

Additional data on age and maturation were obtained from a random subsample of the fish in the scientific sampling in Austevoll and Arendal. In the laboratory, gonads were dissected out, blotted dry and weighed to the nearest mg. Gonad wet weight was used as a proxy for reproductive investment and maturity state was determined by macroscopic inspection of the gonads. The mature female gonad is pale or yellow and has clearly visible egg structures, whereas male gonads are opaque and white. Sagittal otoliths were dissected out, cleaned and stored dry. For aging, the otoliths were placed in black multi-celled trays containing 96% ethanol and photographed under a stereo microscope (20×). The otoliths of corksling wrasse have distinct opaque and translucent growth zones, which makes them easy to read without further processing (Uglem *et al.*, 2000). Thus, age was determined by counting winter annuli independently by two trained readers. Disagreements between readings were infrequent and rare, and if it happened, the photographed otoliths were re-examined by a



Figure 1. Corkwing wrasse locations in Southern Norway sampled in scientific surveys (triangles) and during commercial fishing operations (dots).

third reader. No otolith was discarded as unreadable or unresolved.

Statistical analysis

For statistical analysis, the data were grouped into two datasets; first, we explored spatial variation in SSD and sex ratio across the eight populations. Second, we compared life history traits on aged fish between the southern (Arendal) and northern (Austevoll) population sampled in scientific surveys. For convenience, we hereafter refer to Arendal and Austevoll as the **Southern** and **Northern** population, respectively. All statistical analyses were carried out in R (version 3.2.2, R Core Team, 2015).

For estimating SSD and calculating sex ratios of mature fish, only spawning fish (extruding egg or milt) were included. We used Lovich and Gibbons (1992) method to estimate the size dimorphism index (SDI) for each of the eight populations; the mean of the larger sex divided on the mean of the smallest. The SDI was arbitrarily defined as positive when nesting males were larger than females and negative otherwise. To achieve symmetry around zero, 1 was subtracted from the male-biased SDIs (positive) and added if SDI was female biased (negative) (Lovich and Gibbons, 1992). We tested for significant SDIs using two sided t -tests on nesting males and females length, assuming unequal variances.

To compare sexual dimorphism in life history traits between the southern and northern population, sex specific growth trajectories were constructed by fitting the typical parameterization of the von Bertalanffy growth equation to the age and length data:

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

where L_t is the expected length at age t , L_∞ is the asymptotic length, K the von Bertalanffy growth parameter and t_0 the age at the hypothetical length 0. Appropriate starting values for the parameters were determined using the R-Package FSA (Ogle, 2016). Estimates and confidence intervals of t_0 , L_∞ and K were obtained by bootstrapping 1000 iterations. Sexual and population differences in growth were assessed by comparing bivariate 95% confidence ellipses surrounding the estimated K and L_∞ values (Kimura, 1980). Groups displaying non-overlapping ellipses are considered having significantly different growth parameters (Meehan *et al.*, 2001; Villegas-Ríos *et al.*, 2013). Age differences between groups were tested with Wilcoxon rank sum and age at maturity was assessed by comparing the percentage of mature fish for each cohort. If differences in age at maturity were detected within sexes or male type, we tested for the influence of length on probability of being mature within an age class with logistic regression. Logistic regression models including all age classes were fitted to visualize sex-specific size at maturation and to calculate L_{50} ; the length at which 50% of the sample is estimated to be mature. Population differences in sex-specific reproductive investment was tested with multiple linear regression models on log transformed gonad wet weight with log total length and population and their interaction as predictor variables. Models were fitted separately for sex and male type and only spawning fish (extruding eggs/sperm when stroked) were included.

Results

In the combined commercial and scientific fyke net sampling, 1806 out of 3367 corkwing wrasse were classified as spawning and included for assessing spatial variation in SSD. Nesting males were significantly larger than females in six populations and the minimum legal size limit would not have protected any spawning nesting males in five of the populations (Figure 2). A spatial pattern emerged, with the four northernmost populations displaying the most male-biased sexual SDI and had the lowest proportions of nesting males (11–15% of spawning fish) (Table 1). In addition, the mean body size was lower while the catch per unit effort (CPUE) was higher in the northern populations. Nesting males were generally more common than sneaker males, with the relative proportion of nesting males to sneaker males ranging from 49% to 86% (Table 1).

For life history analyses, we determined age and maturity for 403 fish (Northern $n=239$ and Southern $n=164$, Figure 3). Mean and maximum age was twice as high in the northern population (mean = 3.05, range: 1–8) compared with the southern population (mean = 1.49, range: 1–4) (Wilcoxon rank sum test, $W=4497.5$, $p < 0.001$). Moreover, nesting males were on an average younger than females in both populations (Wilcoxon rank sum test, **Southern**: $W=1922$, $p < 0.001$, **Northern**: $W=3354$, $p < 0.001$) (Figure 3).

Growth rates were faster for both males and females in the southern population compared with the northern population (Table 2 and Figure 4). Further, nesting males grew significantly faster than females in the northern population, indicated by non-overlapping 95% confidence ellipses around the growth model parameter estimates (Table 2 and Figure 4). In the southern population the growth rate of females and nesting males did not differ significantly. Growth models were not fitted for sneaker males, because of low sample sizes, nevertheless they corresponded to the smallest individuals in each age class in both populations (Figure 4). In the northern

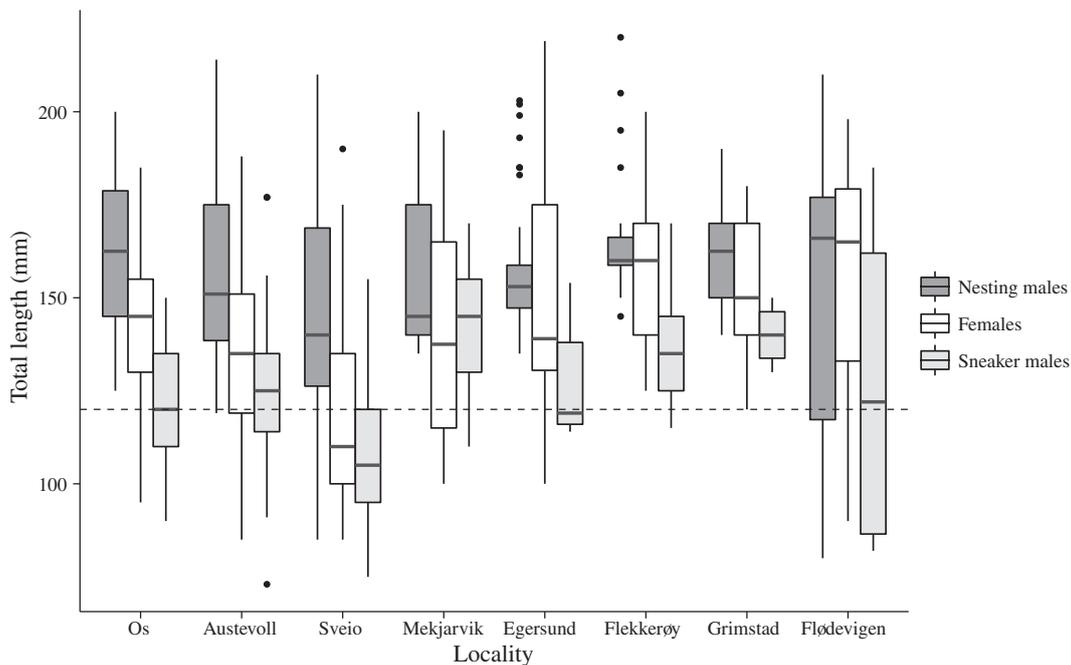


Figure 2. Sex specific length distribution of spawning corkwing wrasse sampled in eight locations in Southern Norway ($n = 1807$), arranged (left to right) in the order they appear along the coastline from North West (Os) to South East (Arendal). Centre line is the median value and the upper and lower edge of box represent the 25th and 75th percentiles, respectively. The vertical lines correspond to the highest value within the range that is 1.5 times the distance between the 25th and 75th percentiles, and filled dots are any individuals outside this range. Dashed horizontal line refers to the minimum legal landing size (120 mm).

Table 1. Sampling summary of corkwing wrasse captured with fyke nets in southern Norway in 2014

Region	Location	Fyke net hauls	CPUE (range)	n (spawners)	Mean length (s.d.) of spawners	SDI	Sex proportion of spawners (% nesting males–sneaker males–females)
South	Arendal	76	3.5 (0–18)	267 (94)	152.0 (34.0)	–0.01	40–9–51
South	Grimstad	26	4.5 (0–22)	118 (89)	155.5 (17.3)	0.06**	27–4–69
South	Flekkerøy	15	9.3 (0–40)	139 (127)	156.1 (20.3)	0.06*	16–15–69
South	Egersund	NA	NA	101 (88)	152.6 (24.7)	0.06	43–8–49
North	Mekjarvik	9	21.3 (0–69)	192 (144)	141.3 (26.1)	0.14***	15–6–79
North	Sveio	45	26.5 (0–228)	1193 (470)	121.1 (25.1)	0.25***	14–17–69
North	Os	25	19.5 (1–83)	488 (240)	136.5 (22.2)	0.15***	11–9–80
North	Austevoll	60	14.5 (0–73)	869 (554)	141.2 (22.1)	0.16***	15–15–70

Both spawning and non-spawning fish was used in estimating mean catch per unit effort (CPUE). The two locations in bold are the northern and southern population compared for sexual dimorphism in life history traits. Values in bold indicates significant sexual sized dimorphism index (SDI— t -test of difference in mean length between nesting males and females). The level of significance is indicated by asterisks:

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

population, all 1-year-old fish would have been protected by the size limit while 35% ($n = 104$) would have been harvestable in their second year, of which 36 were nesting males and 2 were females. In the southern population, 12% would have reached the size limit during the first year (only nesting males), whereas all 2-year-old fish would have been harvestable.

The populations also differed in sex-specific age at maturation. Whereas sneaker males matured in their first year in both populations, nesting males delayed maturation relative to females in the northern population (Figure 3). Here, females were found to mature in their second year, but only 26% of the 2-year-old nesting males were mature. The probability of being mature at age 2 years increased with size for the males (glm, $Z_{45} = 2.87$, $p = 0.003$). In

the southern population, 10% nesting males and 23% females were mature in their first year and all except for one nesting male was found to be mature at age 2 years. There were no significant effects of body size on the probability of being mature in their first year for either nesting males ($Z_{84} = 0.294$, $p = 0.769$) or females ($Z_{28} = 1.83$, $p = 0.07$). The size at maturation was consequently more sexually dimorphic in the northern population (Figure 5). In the northern population, only 3% ($n = 33$) of the mature nesting males were below the minimum size limit ($L_{50} = 136.6$, s.e. = 2.2), compared with 44% ($n = 109$) of the females ($L_{50} = 87.6$, s.e. = 1.4) and 57% ($n = 28$) of the sneaker males (all mature). In the southern population, the minimum size limit would have protected 33% ($n = 24$) of the mature

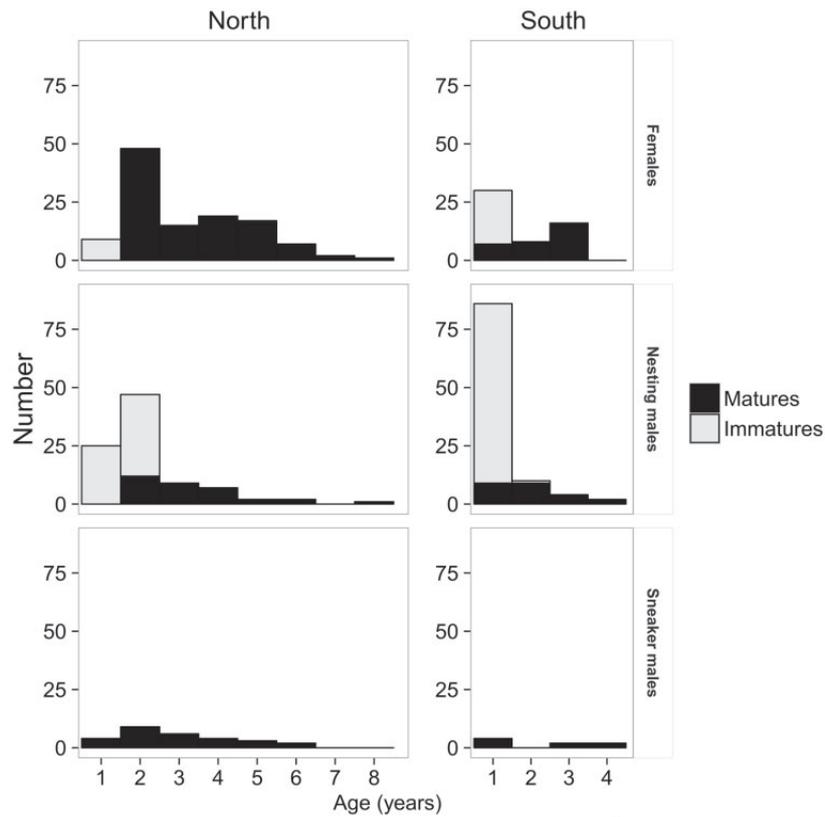


Figure 3. Stacked age histogram of immature and mature corksling wrasse sampled in the northern and southern population.

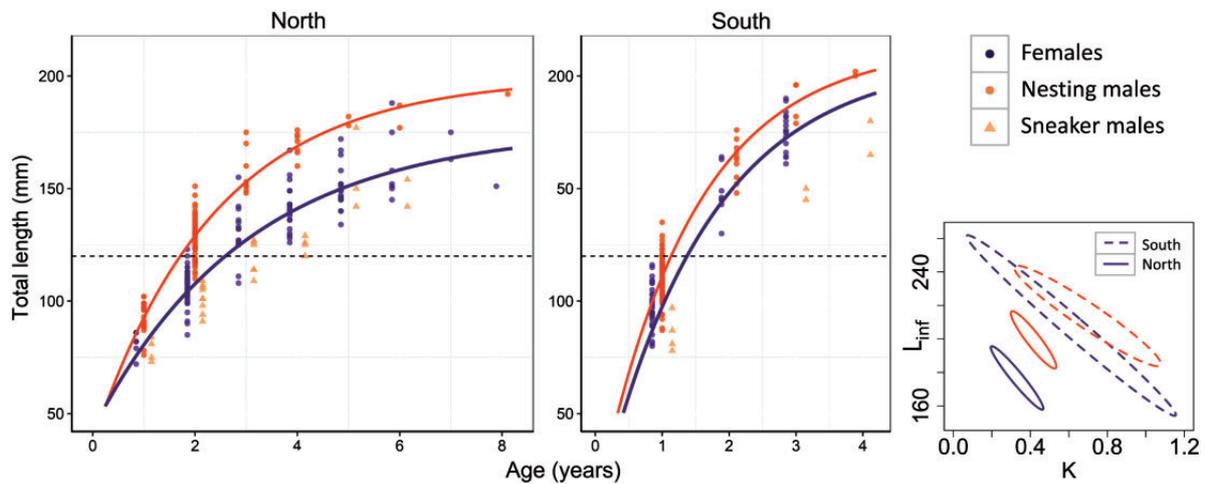


Figure 4. Sex-specific Von Bertalanffy growth curves fitted to length-at-age data of corksling wrasse in the northern (left) and southern population (centre) sampled in Southern Norway. Length-at-age values for individual sneaker males are included (triangles). Dashed horizontal line corresponds to the legal size limit at 120 mm. The right panel displays 95% confidence intervals around K and L_{∞} .

nesting males ($L_{50} = 139.2$, s.e. = 5.7), 23% ($n = 31$) of the mature females ($L_{50} = 109.9$, s.e. = 4.6) and half of the sneaker males ($n = 8$, all sneaker males mature).

The relationship between gonad weight and body size was similar for sneaker males and females in the two populations, but the smaller nesting males in the southern population had relatively larger gonads than in the northern population; a difference that

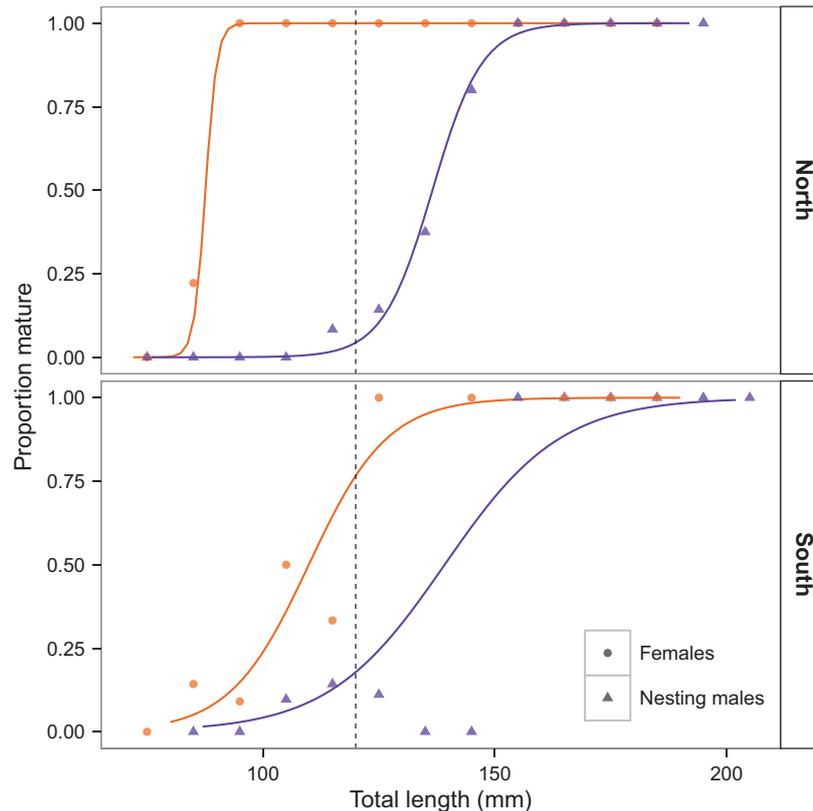
diminished with increasing body size (significant population \times log length interaction; Figure 6 and Table 3).

Discussion

This study demonstrates male-biased SSD in corksling wrasse, which was significant in six out of eight populations in Southern Norway. A clear spatial pattern emerged, with the four

Table 2. Parameter estimates from the von Bertalanffy growth models of corkwing wrasse from two populations in Norway

Population	Sex	L_{inf}	Confidence interval		K	Confidence interval	
			2.5%	97.5%		2.5%	97.5%
Southern	Nesting males	215.46	195.32	246.97	0.71	0.42	1.03
	Females	217.20	183.45	300.47	0.62	0.26	1.04
Northern	Nesting males	199.75	187.09	214.56	0.42	0.33	0.52
	Females	177.68	164.96	197.85	0.33	0.22	0.43

**Figure 5.** The proportion of mature nesting males and females and different body lengths (mm) in the northern and southern populations. Lines show logistic regression model predictions for maturation probability as a function of body length (mm). Sneaker males were mature at all sizes. Dashed vertical line indicates the minimum legal landing size (120 mm).

northernmost populations displaying more male-biased SSDs, lower proportions of nesting males, smaller body sizes and higher catch per unit effort (CPUE). The proximate cause of the SSD in a northern population was found to be higher growth rates and delayed maturation of nesting males relative to females. Sneaker males were smaller and matured earlier than both nesting males and females in both populations. We discuss the possible causes for spatial variation in SSD and the implications for management and sustainability of the fisheries of corkwing wrasse in Norway.

The latitudinal pattern of greater sexual dimorphism in age at maturation in the northern population is not reflected at larger spatial scales in previous studies of corkwing wrasse. In Southern England nesting males was found to mature later (third year) than sneaker males (first year) and females (second year) (Dipper and Pullin, 1979), similar to we detected in the northern population. On the contrary, both nesting males and sneaker males

matured in their first year in western Sweden (Uglem *et al.*, 2000). Intraspecific variation in male-biased SSD in other fish species has been proposed to be result of sex-specific plastic responses to the strength of sexual selection (Lengkeek *et al.*, 2008; Walker and McCormick, 2009). The nesting males of corkwing wrasse are fiercely territorial during the nesting season and larger individuals tend to win aggressive confrontations (Potts, 1974, 1985). Thus, the intensity of male–male competition and sexual selection on body size is likely to increase with population density. The densities of the four northern populations was probably higher, as indicated by higher CPUE, which therefore offer a plausible explanation of the more pronounced SSD. Moreover, the smaller nesting males in the northern population had smaller gonads relative to those in the southern. Since no population differences were detected for females and sneaker males, it appears likely that smaller nesting males in the north trade off sperm

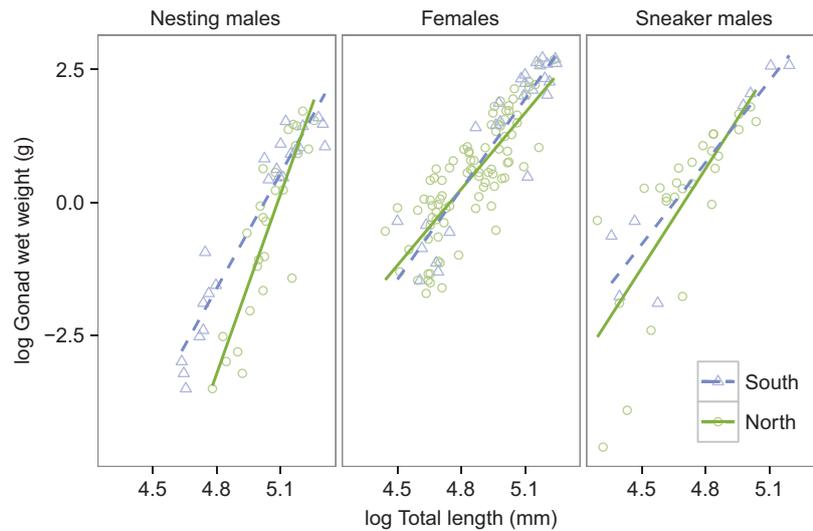


Figure 6. Linear regression of log transformed gonad weight (g) on log transformed total length (mm) of mature corkwing wrasse in the southern and northern population fitted separately for each sex and male type.

Table 3. Summary of the linear models between log transformed gonad wet weight and log total length of corkwing wrasse, fitted separately for mature females, nesting males and sneaker males

	Explanatory variable	Estimate	s.e.	t value	p value
Females multiple $R^2=0.75$	Intercept	-22.68	1.77	-12.81	<0.001
	Log length	4.78	0.36	13.09	<0.001
	Population (south)	-4.22	3.13	-1.35	0.18
	Log length:Population	0.88	0.63	1.39	0.17
Nesting males multiple $R^2= 0.85$	Intercept	-57.21	5.23	-10.94	<0.001
	Log length	11.25	1.04	10.85	<0.001
	Population (south)	21.10	6.06	3.48	0.001
	Log length: Population	-4.06	1.20	-3.37	0.002
Sneaker males multiple $R^2= 0.66$	Intercept	-26.81	4.24	-6.33	<0.001
	Log length	5.70	0.90	6.35	<0.001
	Population (south)	2.98	6.75	0.44	0.66
	Log length: Population	-0.58	1.42	-0.41	0.69

The Northern population (Austevoll) is considered the reference level.

volume for somatic growth to attain larger body size and increase their competitiveness. The northern populations had also consistently smaller mean body sizes than the southern, which possibly is related to gradually decreasing summer temperatures from South-Eastern Skagerrak to further north on the Western Coast (Sætre, 2007). Moreover, the presumably higher density in the northern populations could also contribute to lower growth rates and smaller body size, as density and growth tend to be inversely correlated (Lorenzen and Enberg, 2002). It is possible that the north-south differences in SSD and body size have a genetic basis, because an on-going population genetic study has found large genetic differences between populations on each side of the Jæren sand banks (Enrique Blanco, pers. comm.), which also separates the northern and southern populations in the current study.

The growth analyses showed the minimum size limit (12 cm) to be sex-divisive towards the age classes first entering the fisheries, especially in the northern population. These ages were also clearly the most abundant in our catches, indicating a strong potential for size-selective fishing to alter the relative frequencies of nesting males, sneaker males and females. Nesting males

represented only 15% or less of the spawning fish in the four northern populations with the strongest SSD; implying male-biased harvesting is more likely where the proportion of nesting males is lowest. The Norwegian wrasse fishery first intensified in 2009 and has increased substantially since then (Skiftesvik *et al.*, 2014a, b), so it is plausible that the sex ratios reported in this study have already been shifted by fishing. In a study conducted prior to commercialization of the fisheries in Os (one of the northern sites in this study) during 1997–1999, nesting males constituted 34–39% of the spawning population (Skiftesvik *et al.*, 2014b), which is substantially higher than what we found in the same areas (Os 11% and Austevoll 15%). Pre-fishing data are not available from the more southern populations, but an on-going study finds no differences in sex ratios between two MPAs established in 2006 and the corresponding fished sites (Halvorsen, unpublished). This is consistent with the absence of SSD in the southern population, translating into less opportunity for fisheries induced changes in sex ratios. With the exception of Sveio, the size limit protected less than half of the mature females. Thus, with the current regulations, fishing during the spawning season

may both reduce the egg production and remove the males that guard them. As a conservation measure, fishing is now prohibited until 11 July (2016) and if the main spawning period occurs prior to the opening date, this may allow some nesting males and females to breed at least once before being harvestable. Although previous surveys has found the highest proportions of spawning fish in June and July, a lower proportion of spawners were also present in August (in Arendal) and September (in Os) (Hanssen, 2014; Skiftesvik *et al.*, 2014b). Moreover, nesting males guard and fan the eggs for 11–16 days after spawning (Potts, 1974), and could therefore be vulnerable for a prolonged period after males extrude milt, which is used as an indicator for spawning in the mentioned surveys.

If size-selective fishing reduces the proportion and density of nesting males, this may reduce competition over territories and could therefore weaken the strength of sexual selection on male body size. In addition, sexual selection arising from female choice is also expected to weaken when sex ratios become more female-biased and densities are lowered (Kvarnemo and Ahnesjö, 1996; Kokko and Rankin, 2006; Székely *et al.*, 2014). The combination of size-selective harvesting and sexual selection on body size may produce stronger selection for smaller body size than if reproductive success is independent of body size (Hutchings and Rowe, 2008). In addition, fishing may also induce selection on the mechanism determining the probability of maturing as sneaker male if the relative proportion of sneaker males increases and in that way alters the relative fitness of the two male tactics. Whether selective harvesting can affect sexual selection and fitness of male tactics directly and indirectly are interesting questions that can be addressed in future studies using corkwing wrasse as a model.

On the basis of the clear differences in SSD and body size between northern and southern populations, we suggest to manage these regions separately and to reevaluate the size limits. To reduce the potential of sex selective harvesting in the northern populations, raising the minimum size limit further has limited effect, as the sexual size differences are maintained as body size increase. Alternatively, sex-specific minimum size limit with basis in the male and female size at maturation is a possible and feasible solution. The distinct colouration of nesting males makes it easy for fishermen to distinguish them from females and sneaker males. Another, and perhaps better, option is to use slot limits; a combination of a maximum size and minimum size limit (Gwinn *et al.*, 2015). The faster growth of males implies that they would reach a maximum size limit at a younger age than females. In addition, protecting large and more fecund individuals of both sexes can benefit recruitment and reduce the risk of evolutionary downsizing (Conover and Munch, 2002; Birkeland and Dayton, 2005). The economic consequences of implementing a slot limit are likely to be small as wrasses are sold per individual and not per weight. In the southern populations, a slot size limit is probably less needed because of weaker SSD and shorter longevity which then would protect large individuals near the end of their natural life span. Increasing the size limit so the 1-year-old fish is fully protected and ensuring that the opening date is protecting the population during the nesting season appears to be a better solution. Ideally, growth and maturation data from more locations combined with the information on spatial genetic structure would be beneficial for determining the appropriate distribution of spatial management units and the specific size regulations.

In conclusion, this study has demonstrated spatial variation in sexual dimorphism and life history traits in corkwing wrasse in Norway. There was a particularly strong mismatch between sexual dimorphism and management practices in the northernmost populations in our sampling. To reduce the risk associated with sex-selective harvesting, we suggest spatially structured management regulations with sex-specific size limits or slot-limits reflecting the regional sex-specific growth and maturation patterns.

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Paper II

Sex- and size-selective harvesting of corkwing wrasse (*Symphodus melops*) – a cleaner fish used in salmonid aquaculture

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Abstract

Fisheries-induced changes in sex ratios can have negative effects on reproductive rates and affect sexual selection and evolutionary trajectories. Here, we investigate sex- and size-selectivity of the fishery for corkwing wrasse (*Symphodus melops*) in Western Norway. The males which build and guard nests (nesting males) grow faster than females and sneaker males. Corkwing wrasse were tagged (n=1057) during (May-June) and after (July) the spawning period in 2014 within a no-take site and in a nearby site open for fishing. We monitored the fishery within and nearby the tagging sites from June to October and sampled recaptures on all commercial fishing trips. Fishing mortality was higher for nesting males than females (open site; tagged *during spawning*: 36 % vs. 29 %; *after spawning*: 49 % vs. 36 %), and was found to be caused by nesting males having higher capture probabilities than females, independently of body size. The fishing mortality of sneaker males did not differ from nesting males, but the sample of sneaker males in the study was small. The probability of being retained by fishers once captured depended on size, but not sex. The small no-take site reduced fishing mortality and the sex- and size-selectivity was similar to the open site. By demonstrating the capture process to be male-selective in a commercial fishery, our study highlights the importance of assessing sex-selectivity in similar fisheries. If detected, management measures protecting the sexes more equally should be implemented, such as slot-size limits and marine protected areas large enough to account for sexual differences in spatial behaviour.

Keywords: *Selective fisheries, Sex-selective harvesting, Marine protected areas, Aquaculture-environment interactions, Western Norway.*

Introduction

Fisheries often selectively target large individuals (Fenberg and Roy, 2008; Zhou *et al.*, 2010; Gwinn *et al.*, 2015). Many commercial fisheries are regulated with minimum size limits or gear modifications to limit exploitation on immature fish. In addition, large fish tend to be higher valued and targeted, especially in recreational fisheries (Lewin *et al.*, 2006). In species with sexual size dimorphism, the larger sex may therefore be harvested at higher rates than the smaller (Rijnsdorp *et al.*, 2010; Kendall and Quinn, 2013). Moreover, passive fishing gears (e.g. gillnets, pots, hook and line, fyke nets) can select against fast growth and active and risk-taking behaviours (Uusi-Heikkilä *et al.*, 2008; Biro and Sampson, 2015; Arlinghaus *et al.*, 2016). Thus, sex-selective harvesting may happen independently of body size if other traits that affect capture probability differ between sexes. Fisheries-induced changes in sex-ratios may have consequences for reproductive output and sexual selection (Fenberg and Roy, 2008; Kendall and Quinn, 2013; Rowe and Hutchings, 2003). Quantifying sex-selectivity is therefore necessary in order to understand how populations will respond to fishing and to design optimal management strategies.

In this study, we used tag-recovery data to estimate sex-selectivity in the commercial fishery for corkwing wrasse (*Symphodus melops*) in Western Norway. Together with other wrasse species, the corkwing wrasse is increasingly harvested in Scandinavia and the British Isles to be deployed as cleaner fish in salmonid aquaculture net pens, where salmon lice (*Lepeophtheirus salmonis*) infestations can be a major issue (Darwall *et al.*, 1992; Skiftesvik *et al.*, 2014a; Halvorsen *et al.*, 2016). Corkwing wrasse is found in shallow, rocky coastal habitats from North Africa to Norway and may attain a total

length of 28 cm and a maximum age of nine years (Quignard and Pras, 1986; Darwall *et al.*, 1992; Sayer and Treasurer, 1996). Most males develop as colourful nest-building males, growing faster and maturing later than females (Potts, 1974; Halvorsen *et al.*, 2016). A small proportion of males adopt an alternative sneaker strategy. These males are indistinguishable from females in appearance and perform sneak fertilizations during pair spawning between a nesting male and female (K.T. Halvorsen, pers. obs.). The sneaker strategy appears to be fixed throughout their lifespan, and sneaker males grow more slowly and mature earlier than the nesting males (Uglem *et al.*, 2000; Halvorsen *et al.*, 2016). The wrasse fishery is conducted with baited pots or fyke nets set at shallow reefs or rocky shorelines. In Norway, it is managed by a spring closure (lasting until 17 June in the year of study) to restrict fishing during the main spawning period, which has been shown to peak in June (Skiftesvik *et al.*, 2014b). In addition, a minimum legal size is enforced, which was 11 cm in 2014 when this study was conducted, but increased to 12 cm in 2015. The undersized wrasses are released alive on site of capture. The wrasse fishery in Norway could therefore be expected to be sex-selective for two reasons; first – the higher growth rates of nesting males means they reach the minimum size limit before females and sneaker males (Halvorsen *et al.*, 2016). Second, the sexes may have differential capture probabilities in passive gears. Size-selective gear will catch sexes at different rates if they differ in body size. Moreover, the higher growth rates of nesting males imply higher feeding intensity which can increase attraction to baited traps (Biro & Sampson 2015). In addition, other sexual behaviour differences can affect capture probability. For instance, males are investing in nesting and territory defence and feed less than females during the spawning period (Potts, 1974; Deady and Fives, 1995). Combined, the two independent selective processes of

size regulations and gear selectivity interact to produce either stronger or weaker overall sex selectivity.

In this study, we tested whether fishing mortality on corkwing wrasse differs between sexes and male types and also investigated the combined effect of sex and body size on capture probability and on the probability of being retained once captured. A secondary objective was to assess whether a small marine protected area (MPA) would reduce fishing mortality and whether sex and size selectivity differed relative to that in the open site. MPAs can maintain natural sex ratios, size and age structure (Pillans *et al.*, 2005, Claudet *et al.*, 2010, Baskett and Barnett, 2015), but a recent study has highlighted the possibility of MPAs inducing selection for individuals with small home ranges which are more likely to stay within the protected area (Villegas-Ríos *et al.*, 2016). Thus, if spatial behaviour differences between sexes or size classes exist, a relatively small MPA may protect these groups differently. We tagged corkwing wrasse with passive integrated transponder (PIT) tags during and after the spawning period in a small protected site and a nearby open site with a wrasse fishery representative for the area located in a semi-enclosed bay. The fate of tagged fish in the fishery was determined by recording recaptures on all commercial fishing trips occurring within the bay over a three month period. We then decomposed size- and sex-selectivity in two separate analyses, estimating (1) the probability of being captured and (2) the probability of retention given captured. This allowed for testing for sex-selectivity adjusting for body size and evaluating how these different processes affect the overall selectivity of the fishery.

Material and Methods

Study area

The study was carried out on the Huftarøy Island in Austevoll municipality, western Norway (**Figure 1**). There are several salmon farms on the archipelago, mainly using locally caught wrasse for delousing. Based on consultation with local fishers, the Storebø bay was selected as study area representative of the wrasse fisheries. The bay is a semi-sheltered basin with a maximum depth of 40 meters and some freshwater discharge into the southern and northern part. The local fishing community agreed to inform us whenever traps were set inside the bay or up to 1 km outside the bay inlet. In addition to the commercial fishery, corkwing wrasses were sampled for tagging at two sites within the bay: (1) a temporary no-take zone of approximately 600 meters coastline, defined in agreement with the local fishers, and (2) a similar sized study site on the opposite side of the bay with no restriction on fishing activity (**Figure 1**).

PIT tagging

Passive integrated transponder (PIT) tags were used to monitor the fate of individual corkwing wrasse in their natural environment in the bay. PIT tags are small glass-encapsulated passive transponders inserted into the body cavity or muscle tissue and are well proven and widely used as an identification method for studies of fishes (Prentice *et al.*, 1990; Gibbons and Andrews, 2004; Bolland *et al.*, 2009). We used half duplex PIT tags (12.0 mm x 2.12 mm, Oregon RFID) inserted in the body cavity with a needle fitted to a tag injector. Individuals measuring less than 95 mm in total length were not tagged. The fish were first anaesthetized in a solution 50-100 mg l⁻¹ tricaine methanesulfonate (MS-222) in volume of 8-10 L of seawater. As sea temperature varied

throughout the season, we determined the dosage used each sampling day based on a target time of 1-3 minutes until loss of equilibrium of the fish. Post-tagging, the fish was allowed to completely recover before release (2-5 minutes). The injector needles were cleaned and disinfected in 96 % ethanol or replaced between each tagging operation. We carried out a pilot experiment to assess post-tagging survival under controlled conditions the year prior to the field study. To this end, 51 randomly sampled corkwing wrasse were length measured, tagged as described above, and held in a 5 x 5 meter fish pen with artificial shelters in the sea for 59 days (6 June to 4 August, 2013). No tag-loss or mortality was evident by the end of the period. The method of capture, tagging and handling of live fish in this study was approved by the Norwegian Animal Research Authority (Application ID: 6428).

Data collection

Corkwing wrasse were tagged in two sampling periods during the summer of 2014 (Period 1: 20 May – 26 June; Period 2: 18 - 22 July). The first period coincided with the reproductive season, while the second sampling was conducted after the reproductive season (see results). We considered it important to compare fishing mortality and capture probability for fish tagged both during and after spawning due to the large sexual differences in behaviour during the nesting period (Potts 1974), which is likely to influence the vulnerability to the passive gears used for sampling. During the spawning period, nesting males are occupied by nest building and territory defence, whereas females and sneaker males may move freely between nests. Thus, by tagging both before and after spawning, this provided an opportunity to investigate this potential source of bias in our own sampling and whether this affected estimates of fishing mortality and

capture probability in the fishery. A drawback of sampling after spawning was that sneaker males could not be distinguished from females.

Sampling during the first period was conducted in three shorter sub-sessions (May 20-24; June 9-12 & 21-26). When analysing fishing mortality these sessions were pooled since the commercial fishing did not happen to occur in the area before July 2. In order to reduce selectivity in our own sampling we used both baited wrasse pots and unbaited fyke nets. In the first period, the sampling effort was slightly higher in the fished site (fished site: 25 fyke nets and 49 pots; no-take site: 20 fyke nets and 42 pots), while the effort was identical the second period (18 pots and 18 fyke nets per site) (**Table 1**). To be captured in pots, the fish have to be attracted to the bait and actively enter the gear, whereas fyke nets are set perpendicular to the shoreline to create a physical barrier leading passing fish into the collecting chamber (Gear descriptions: **pots**: rectangular prism shaped, 70 x 40 x 29 cm, 15 mm mesh-size, two 75 mm diameter entrances and two chambers, **fyke nets**: 5 meter single leader, 55 cm diameter entrance and leader mesh size of 30 mm). The gear was randomly placed within the two study sites at 1-7 meters depth with 10-30 meter spacing between each trap and left over night and hauled the following day (soak time: 12-24 hours). Corkwing wrasse were measured for total length (to the nearest mm) and checked for reproductive state by applying gentle pressure on the abdomen and examining the sexual products (egg/sperm). A fish was classified as spawning (reproductively active) if any eggs or milt was extruded. Nesting males could easily be distinguished from females and sneaker males based on coloration, whereas the sex of sneaker males and females could only be determined during the spawning season by stripping as described above. All sneaker males (n=19) observed more than once within the first tagging period extruded milt at

every encounter, proving high accuracy of this sexing method during the spawning season. In the second tagging period we could not distinguish sneaker males and females, but individuals of female appearance were classified as females, which were much more common than sneaker males in the first period (**Table 1**). This implies that the majority of sneaker males first encountered in period 2 have been sexed as females, since only six out of 22 sneaker males had running milt when recaptured in period 2 (being tagged and sexed in period 1). After checking each individual for presence of PIT tag, new encounters were tagged as described before and gently released at the site of capture.

Commercial fishing activity in and around the bay was monitored from 17 June (the opening date of fishing in 2014) to 31 October 2014 in agreement with the local fishers who allowed researchers on-board for detecting recaptures. The study area and the surrounding coastline can be visually assessed from the facilities of the Institute of Marine Research and was daily surveyed by boat or by binoculars from the shoreline to ensure that all fishing activity was accounted for. The fishers used pots of the same type used in the scientific sampling baited with 2-3 prawns (*Pandalus borealis*) or crushed edible crab (*Cancer pagurus*). The pots were linked in chains of 7-23 and set on 1-7 meters depth with approximately 5 to 10 meters spacing between each pot. Upon capture, the catch was emptied in a container with running sea water for being sorted on size. Wrasses that were to be retained were transferred to a holding tank, while by-catch and wrasse below the size limit were discarded close to shore. A PIT-tag reader with an external antenna attached was used to detect any tagged fish present by continuously passing the antenna through the container where the catch of each pot was placed. We were able to infer whether an individual was discarded or retained by scanning the

container with the remaining fish before release. In addition, the holding tank was thoroughly scanned after the end of each fishing trip to confirm the individuals being retained. The scanner stores time and tag number for each observation and we noted exact position for each recapture and the start and end point of each pot chain. This method for tag detection allowed for minimal interference with normal work procedure for the fishers.

Data analysis

First, we compared the mean body size between sexes, sites and sampling periods. Within each period, we used linear models to test for sex differences in body size (total length) independently for each study site (i.e. including an interaction effect between sex and site in the model). Due to low sample size, sneaker males were not included in the model for period 2. Linear models were also used to compare body size between the two periods, independently of site and separately for nesting males and females. In all models, a likelihood ratio test (LRT) was applied to compare the goodness-of-fit of the model including interactions against a reduced model with additive effects and to select the model for statistical inference. Wald's tests were used to assess significance between factor levels.

Second, we estimated sex- and site-specific fishing mortality as the proportion of tagged fish harvested (captured and retained) in the commercial fishery at any point later in the study. Although all retained fish were kept alive to be transported to salmon farms, we adhere to the term *fishing mortality* since the fish can be regarded as dead from the perspective of the natural population. We tested for differences in fishing mortality between sexes (nesting males, females and sneaker males) and the two sites (fished or

no-take) using logistic regression with *harvested* (0,1) as the response variable. Even though no commercial fishing took place within the no-take site during the study, some individuals dispersed out in the bay and were subsequently recaptured (**Table 1, Figure 1**). The two sampling periods were analysed separately, since the behaviour during spawning, when males are territorial and guard nests, is likely to influence the selectivity in the sampling and as well in the commercial fishery. Individuals were assigned to the period they were first encountered (tagged), thus disregarding that some were recaptured in the second period. Moreover, sneaker males were excluded in the models for the second period, when only three of the tagged fish could be classified as sneaker males. As before, a likelihood ratio test was used to test whether an interaction was supported in the model. A significant interaction would indicate that sex-specific fishing mortality differs between the no-take site and the fished site.

Lastly, since fishing mortality has two components; the probability of being captured in the fishing gear and the probability to be retained once captured, we conducted separate analyses of these two sources of selectivity. Capture probability was modelled with similar logistic regression models as with fishing mortality, but with body size (total length) included as a trait in addition to sex to test for sexual differences in capture probability independent of body size. We ignored that some individuals were captured and discarded more than once. The starting models included the three covariates (sex, body size and site) with interactions and were compared against six reduced candidate models. We used the Akaike Information Criterion corrected for small sample size (AIC_c) for selecting the optimal model and if the difference in AIC_c between two models were less than two units, the model with less estimated parameters was selected for statistical inference (Burnham and Anderson, 2002). Logistic regression was also used to model

the probability of being retained once captured with sex and body size as covariates, including fish from both sites and periods. Since the fish was not measured for length when captured in the fishery, the length at time of tagging was used. As with capture probability, AIC_c was used for model selection. To facilitate interpretation of the capture probability and retention probability models, the length variable was scaled and mean centred with standard deviation of one. All statistical analyses were carried out with the software R, version 3.2.2 (R Core Team 2015).

Results

A total of 1057 corkwing wrasse (fished site=565, no-take site=492) were tagged during the two sampling periods (**Table 1**). Of these, 260 were recaptured at least once in the scientific sampling. Those recaptured in the second period had on average increased their total length with 5.5 mm (range 0-23 mm) since being measured and tagged in the first period. The first sampling period coincided with the spawning season, with the percentage of fish releasing eggs or milt when stripped being 75 % at the start of the period (20-24 May), dropping to 45 % towards the end (21-26 June; data not shown). In comparison, only 3 % released eggs or milt in the second period (of these, only one nesting male), indicating the spawning season had, or was close to have ended.

The nesting males were larger than females (Linear model; Wald's test: $\beta = -7.52$, $t = -4.04$, $p < 0.0001$) and sneaker males (Linear model; Wald's test: $\beta = 16.28$, $t = -5.39$, $p < 0.0001$) in the first period, while nesting males and females were of similar size in the second period (Linear model; Wald's test: $\beta = 4.39$, $t = 2.35$, $p = 0.063$). There were no significant interactions between site and sex in either period (LRT: Period 1: $Df = 5$, $X^2 = 5.08$; Period 2: $Df = 4$, $X^2 = 1.64$, $p = 0.20$). Both nesting males and females were considerably smaller in

the second period than in the first (Linear model; Wald's test: Nesting males: $\beta = -22.23$, $t=5.31$, $p<0.0001$; Females: $\beta = -7.41$, $t= 1.70$, $p<0.0001$). The females were also smaller in the no-take site relative to the fished site (Linear model; Wald's test: $\beta = -3.78$, $t=-2.48$, $p=0.013$), whereas nesting males were of similar size in the two sites (Linear model; Wald's test: $\beta = 2.27$, $t=0.80$, $p=0.42$). The interaction between site and period was not significant for neither nesting males (LRT: $Df=4$, $X^2=0.83$, $p=0.36$) nor females (LRT: $Df=4$, $X^2=1.59$, $p=0.21$).

The commercial fisheries involved four fishermen who set a total of 820 pots in and around the Storebø bay from 2 July – 26 August. Scientific personnel participated on all fishing trips. Fishing intensity was highest after the second sampling period (710 pots). A total of 280 fisheries recaptures were recorded of 253 uniquely tagged wrasses. A total of 223 recaptures were retained and sold to salmon farms (**Table 1**). The majority (238) of the fisheries recaptures were caught after the second sampling, thus including recaptures of fish tagged in both sampling periods. Moreover, most recaptures were caught within or close to the fished site (**Figure 1**). One nesting male that had been tagged in the no-take site was recaptured in the fished site. Mean time between tagging and harvesting was 45.6 days (range: 6- 98) for those tagged in period 1, while 8.8 days (range: 3- 39) for those tagged in period 2.

The overall fishing mortality was higher in the fished site relative to the no-take site in both periods (Period 1 - Fished: 36 %; No-take: 6 %; Period 2 - Fished 42 %; No-take 9 %, Logistic regression; Wald's test: Period 1: $\beta=-2.14$, $z= -7.91$, $p<0.0001$; Period 2: $\beta = -2.07$, $z= -6.26$, $p<0.0001$). For modelling fishing mortality, the interaction between sex and site was not significant in either period (LRT: Period 1: $Df=4$, $X^2= 4.67$, $p=0.097$; Period 2: $Df=3$, $X^2= 1.11$, $p=0.29$). Adjusted for site, fishing mortality was significantly

higher for nesting males than for females in both tagging periods (Logistic regression; Wald's test: Period 1: $\beta=-0.62$, $z= -2.608$, $p=0.009$; Period 2: $\beta= -0.74$, $z= -2.498$, $p=0.013$, **Table 1**). There were no differences in fishing mortality between nesting and sneaker males in the first period when the sneaker males could be distinguished from females (Logistic regression; Wald's test: $\beta=-0.18$, $z= -0.510$, $p=0.61$, **Table 1**).

For capture probability for fish tagged in the first period, the model with interaction between sex and length and an additive effect of site had marginally better AIC_c score as the model without interactions between the same factors. However, the latter model was considered the most parsimonious as fewer parameters were estimated (**Table 2**). Applying this model, nesting males had, adjusted of body size; higher capture probability than females but not sneaker males (**Table 3, Figure 2**). Regardless of sex, the capture probability decreased with increasing body size (**Table 3, Figure 2**). For those tagged in the second period, the model with interaction effect between sex and body size and additive effects of site was supported (**Table 2**). Female capture probability declined with body size as in the first period, while for nesting males, intermediate sized fish had the highest capture probability (**Table 3, Figure 2**).

When hauling the pots, the fishers sorted the catch on size consecutively by eye or sometimes (when in doubt) by using a length measures drawn on the sorting board. Two of the fishers occasionally used 130 mm as their size limit due to the demand from the salmon farms. In total, the fishers retained 87 % of the tagged corkwing and all fish larger than 123 mm at the time of tagging. Moreover, 43 % of the fish below the minimum size limit (110 mm) at the time of tagging ($n=79$) were retained. Model selection of retention probability favoured the model with only body size as predictor, although the more complex model with an interaction between sex and length had only

slightly lower AIC_c score (**Table 2**). The probability of being retained was strongly dependent on body size (**Table 3; Figure 3**).

Discussion

Our study has demonstrated male-selective harvesting of a commercially important species with male parental care, the corkwing wrasse. Independently of body size, nesting males had higher vulnerability to be captured in a baited pot fishery. Several possible factors could drive the higher capture probability of nesting males. First, their higher growth rates imply higher feed demand which can result in higher motivation for entering baited pots. Myers *et al.*, (2014) also proposed higher growth and feeding rates as an explanation for finding females (who grows faster) more prone to angling in a walleye (*Sander vitreus*) fishery. Second, higher growth rates can be correlated with more active and risk-taking behaviour which may increase the vulnerability to passive gears (Biro and Post, 2008; Biro and Sampson, 2015). Moreover, behavioural traits positively related to the intensity of parental care and the aggression of nest-tending males have been shown to be correlated with increasing vulnerability to angling in largemouth bass (*Micropterus salmoides*) (Sutter *et al.*, 2012). Sexual differences in life history traits, physiology and behaviour is widespread in fishes, but often ignored (Hanson *et al.*, 2008). Thus, the findings presented here underscore the need for more investigations of the extent, underlying mechanisms and implications of sex-selective harvesting in commercial and recreational fisheries.

In the light of the growth rate hypothesis, the similar pattern of size-dependent capture probability for sneaker males and nesting males was unexpected, given that sneaker males grow even slower than females (Halvorsen *et al.*, 2016). However, too few sneaker

males were tagged to draw any firm conclusion. Moreover, since we were unable to distinguish sneaker males from females outside the spawning season the differences in capture probability between nesting males and females in the second period must be interpreted with caution. Nevertheless, the main pattern was highest capture probability for intermediate-sized nesting males. Most of the commercial fishing happened after spawning, so the finding of higher capture probability of nesting males is most likely unrelated to reproductive behaviour.

There was a notable shift in body size towards smaller fish in the second period, which was most evident for nesting males. During the nesting period, the males are fiercely chasing away all conspecifics except for receptive females (Potts, 1974), and this activity may force immature fish away from the shallow depths where nesting occur (Potts, 1985). Both we and the commercial fishers targeted depths of 1-7 meters to avoid problems with inflated swim bladders when hauling the gear from deeper waters. A size-dependent shift in depth preference during and outside the spawning period could therefore lead to different selectivity on body size. This may also explain the negative correlation between body size and capture probability for those tagged in the first period. However, finding the same pattern for females and large nesting males tagged after spawning suggests that other factors may also be of importance. For instance, dietary preferences may change with body size and sex and therefore affect attraction to baited gear. In our study system, the commercial fishers used exclusively crustacean bait (prawn and crushed edible crab). The diet of smaller corkwing has been found to consist of predominately small crustaceans, while *bivalvia* is the main prey group for fish larger than 15 cm (Deady and Fives, 1995). Thus, crustacean bait may attract smaller corkwing wrasse more strongly. Alternatively, larger (and older) fish must have survived

previous years of selective fishing in the area, so those remaining may possess traits that are less vulnerable to capture. Lastly, despite the relatively short time between tagging and capture in the fisheries, there is a possibility that some large individuals die or move larger distances after the spawning period. During the first period, nesting males and sneaker males were often observed with flesh wounds and missing several scales, presumably caused by aggressive encounters with other males. The spawning behaviour and nest building and guarding may also increase the risk to predation. Natural mortality could also explain the finding of lower fishing mortality for those tagged in the first period relative to the second, since the time from tagging to fisheries capture was generally longer in the first period and therefore increasing the probability of dying from natural causes before being fished. Future tagging studies investigating spatial and depth behaviour and multi-year capture-recapture data for estimating natural mortality would be useful for understanding why the larger corkwing wrasse have low encounter rates after spawning.

Fishing mortality was similar to capture probability, since the fishers retained the majority (87 %) of the captured corkwing and even quite few of those that were below the size limit at the time of tagging. This does not necessarily reflect the fishers retaining under-sized fish, but is most likely caused by fish growing to reach harvestable size during the time between tagging and capture. The survival of discarded fish was probably high, as the fishers released the catch at shallow depths and the fish was kept in running water at any time. However, we occasionally observed some of the discarded fish being eaten by seagulls. Intermediate-sized nesting males (125-155 mm) had the highest fishing mortality (Fished site, period 1: 44 %; period 2: 76 %) and is comparable to annual fishing mortality (> 60 %) estimated for large (≥ 45 cm) coastal Atlantic cod

(*Gadus morhua*) in Southern Norway (Fernández-Chacón *et al.*, 2015). Increased adult mortality in general selects for maturing at younger ages and potentially smaller size (Stearns 1992). Thus, the corkwing fishery may induce selection for nesting males maturing at smaller size, as the size class experiencing the highest fishing mortality correspond to the size at maturation for nesting males ($L_{50} = 136.6$; Halvorsen *et al.*, 2016). On the other hand, since capture probability was found to decrease with body size, this may counter such selective pressures as those growing fast may be less prone to capture once a large body size is attained, under the premise that the low capture probability for large individuals we observed was not caused by higher natural mortality or effects of past fisheries selection.

Sex-selective fishing mortality has the potential to alter sex ratios and therefore have consequences for sexual selection and population productivity. If fishing reduces the density of nesting males, this may relax competition over nesting territories and consequently weaken sexual selection for large male body size. In a fisheries-induced evolution perspective, modelling has demonstrated that evolutionary rate of reduction in body size may accelerate if fishing erodes phenotypic variation in traits under sexual selection (e.g. body size) (Hutchings and Rowe, 2008). Fishing can also affect the relative fitness between nesting males and sneaker males (Darwall *et al.*, 1992). Although we did not detect differences in fishing mortality between nesting males and sneaker males, sneaker males mature 1-2 years earlier than nesting males and grow slower, so the ratio of male types on the spawning ground can be expected to be altered by fishing (Halvorsen *et al.*, 2016). In turn, a higher proportion of sneaker males could have consequences for mating system dynamics as studies of the closely-related *Symphodus ocellatus* has shown that the number of sneaker males affects the nesting males and

females willingness to spawn and the probability of the male deserting the nest (Alonzo and Warner, 1999, 2000; Alonzo and Heckman, 2010).

The horizontal movements of corkwing wrasse appears to be limited, as only one individual was found to have moved between the two sites and the number of recaptures was substantially lower in pot chains set further away from the tagging sites. Managing species with high site-fidelity is challenging, since fishing may deplete populations with limited potential of being replenished from nearby areas with lower exploitation rates (Gunderson *et al.*, 2008; Wilson *et al.*, 2010). It is also difficult to set catch quotas and monitor trends in the fishery based on landing statistics, as fishers may constantly move from depleted areas to lesser exploited sites and therefore maintain high catch per unit effort. We have shown that fish tagged in the no-take site had significantly lower fishing mortality despite the small size of the MPA, but sex-selectivity was similar to the open site. Thus, to ensure equal protection for sexes, an MPA size should be larger than the home range of both sexes and male types, and studies on spatial behaviour are therefore needed. As a measure to protect a declining European lobster (*Homarus gammarus*) population, a network of nine MPAs has been established in the Hardangerfjord in Western Norway, effective from October 2016. These are fully protecting wrasse from commercial fishing since passive gear such as fyke nets, pots and gillnets are prohibited. However, five of these MPAs are only protecting 1-4 km of a coastline with little complexity in terms of islands, reefs and skerries. Thus, a comparable sex-bias in protection as found for the MPA in this study may be anticipated in the smaller MPAs. On the Skagerrak coast further south, a total of ten MPAs with similar gear regulations have been established from 2006 to 2016. The effects of

protection on sex-ratio, age and size structure of wrasses are currently being investigated in four MPA and control pairs in Skagerrak.

Another possibility for reducing sex- and size selectivity is to change the length-based management regulations. Sex-specific minimum size limit reflecting the differences in growth and size at maturation, or a slot limit, protecting both small and large fish of both sexes has previously been proposed (Halvorsen *et al.*, 2016). One may argue, as we have shown that capture probability appears to decrease with body size, that large fish are “naturally” protected with less need for a maximum limit. However, as already pointed out, we do not know whether the absence of observations of larger fish in the fishery is due to effects of past harvest selection, natural mortality or size-dependent behaviour changes. Furthermore, protecting the larger fish will have small economic consequences, as the fish is sold per individual regardless of body size (Halvorsen *et al.*, 2016).

To conclude, we show that trap fisheries can be sex-selective, in this case harvesting corkwing wrasse males at higher rates than females. This selectivity was primarily caused by nesting males having higher capture probability, but not due to larger body size. The present study highlights the importance of investigating and recognizing sexual differences in life history traits and behaviour to better understand how populations may respond to fishing. MPAs, in combination with sex-specific size limits or slot-size limit, appear to be a promising solution of reducing the risk associated with sex-selective harvesting.

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Tables

Table 1: Summary of the number of tagged corkwing wrasse, the mean body size, number of fish captured and fishing mortality in the Storebø bay summer 2014.

Site	Sex	Sampling period 1 (20.5-26.6)				Sampling period 2 (18.7-22.7)			
		n	Total length mm (SD)	Captured (retained)	Fishing mortality (%)	n	Total length mm (SD)	Captured (retained)	Fishing mortality (%)
Fished	Nesting males	74	140.9 (24.8)	28 (27)	36	63	118.7 (22.2)	40 (31)	49
	Females	308	135.9 (20.1)	94 (89)	29	78	126.2 (19.2)	33 (28)	36
	Sneaker males	41	122.8 (14.7)	17 (16)	39	1	99.0	1 (0)	0
	Total	423	135.5 (21.0)	139 (132)	31	142	122.7 (20.9)	74 (58)	41
No-take	Nesting males	105	141.0 (26.6)	12 (12)	11	62	124.0 (22.1)	11 (9)	15
	Females	189	130.9 (18.7)	6 (5)	3	108	125.5 (18.5)	9 (5)	5
	Sneaker males	26	129.0 (15.2)	1 (1)	4	2	115.5 (12.0)	1 (1)	50
	Total	320	134.1 (21.9)	19 (18)	6	172	124.8 (19.8)	21 (15)	9
	Grand total	743	134.9 (21.4)	158 (150)	20	314	123.9 (20.3)	95 (73)	24

Table 2: Model selection of logistic regression on capture probability (fish captured in the fishery) and retention probability once captured. For capture probability models were fitted separately for the two sampling periods. The table gives model structure, the number of estimated parameters (P) the ΔAIC_c score and the difference between the specified model and the model with the lowest AIC_c score. The model with the lowest AIC_c score is used for statistical inferences (in bold), or in the case when ΔAIC_c is less than two units between two models, the model with fewer parameters is considered the most parsimonious.

Capture probability

Model structure	Period 1			Model structure	Period 2		
	P	AIC_c	ΔAIC_c		P	AIC_c	ΔAIC_c
Sex x Length x Site	12	659.5	4.67	Sex x Length x Site	8	314.39	5.18
Sex x Length + Site	7	654.83	0	Sex x Length + Site	5	309.21	0
Sex + Length x Site	6	655.52	0.69	Sex + Length x Site	5	314.7	5.49
Sex x Site	6	681.19	26.36	Sex x Site	4	317.02	7.81
Sex + Length + Site	5	654.84	0.01	Sex + Length + Site	4	312.64	3.43
Length x Site	4	659.79	4.96	Length x Site	4	320.44	11.23
Sex + Site	4	681.11	26.28	Sex + Site	3	314.97	5.76
Length + Site	3	659.48	4.65	Length + Site	3	318.39	9.18

Retention probability

Model structure	P	AIC_c	ΔAIC_c
Sex x Length	6	180.5	0
Sex + Length	4	184.51	4.01
Sex	3	283.96	103.46
Length	2	180.63	0.13

Table 3: Summary of the selected logistic regression models on capture probability and retention probability once captured. Nesting males and the fished site are considered as reference levels. The *Length* variable is scaled and centered in both analyses.

Capture probability

Variable	<u>Period 1</u>					Variable	<u>Period 2</u>				
	β	SE	Odds ratio	z-value	p		β	SE	Odds ratio	z-value	p
<i>Intercept</i>	-0.09	0.22	0.91	-0.42	0.67	<i>Intercept</i>	0.57	0.26	1.77	2.19	0.03
Sex (<i>Females</i>)	-0.72	0.24	0.49	-2.97	0.003	Sex (<i>Females</i>)	-1.15	0.33	0.32	-3.46	0.0005
Sex (<i>Sneaker males</i>)	-0.54	0.37	0.58	-1.45	0.15	Length	-0.01	0.20	0.99	-0.05	0.96
Length	-0.56	0.11	0.97	-5.07	<0.0001	Site (<i>No-take</i>)	-2.15	0.30	0.12	-7.11	<0.0001
Site (<i>No-take</i>)	-2.28	0.27	0.10	-8.45	<0.0001	Sex (<i>Females</i>) x Length	-0.77	0.34	0.46	-2.26	0.02

Retention probability

Variable	β	SE	Odds ratio	z-value	p
<i>Intercept</i>	2.96	0.41	19.25	7.21	<0.0001
Length	2.82	0.43	16.83	6.60	<0.0001

Figures

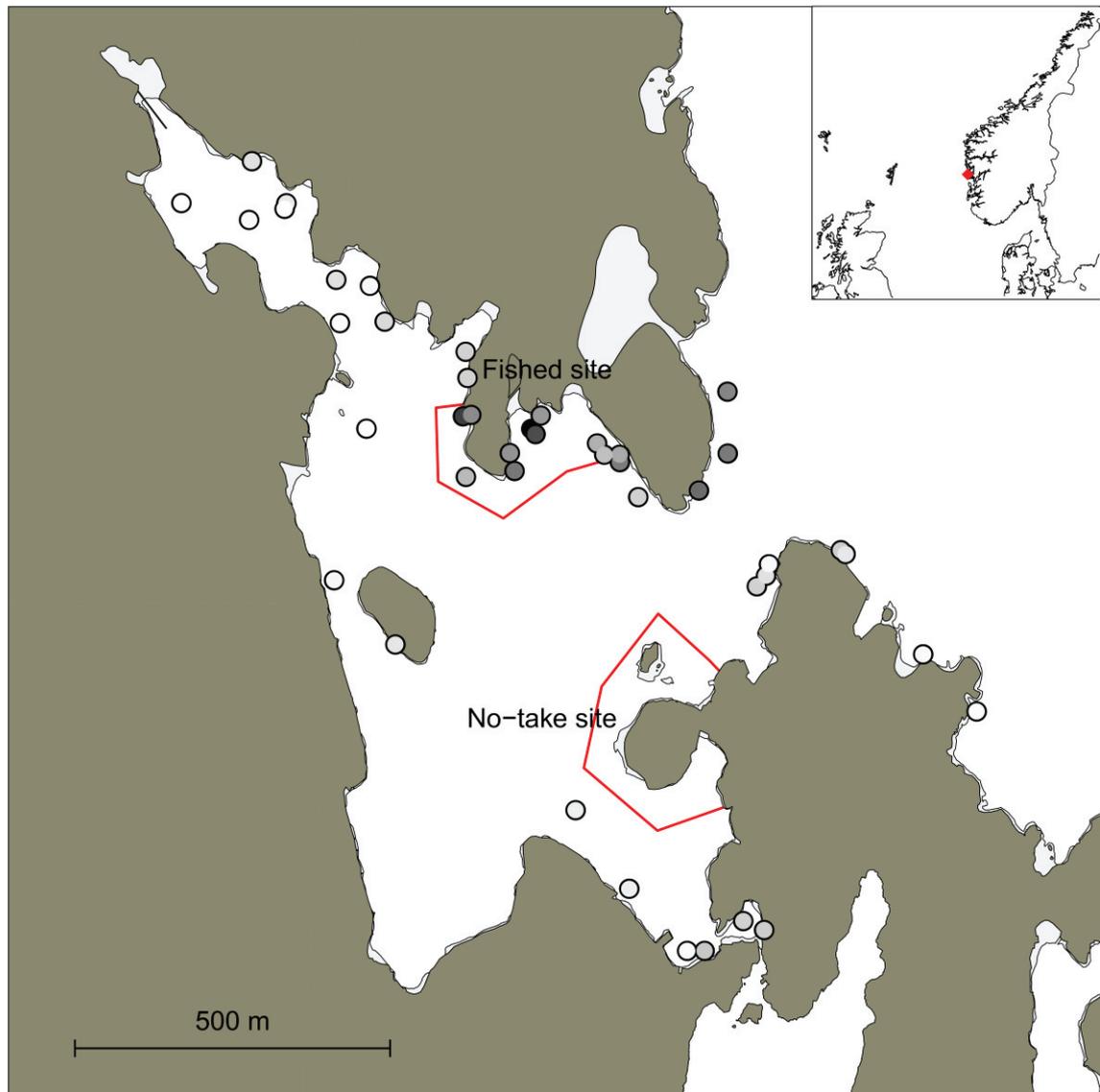


Figure 1. Study area, tagging sites (within red lines) and distribution of commercial fishing activity in the Storebø bay July-August 2014. The circles represent the approximate centre position of each pot chain (7-22 pots linked) hauled by fishermen during the commercial fishery. The number of tagged corkwing captured per pot in the fishery is indicated by the white-black gradient fill in the circles (black= 1.5 recaptures per pot, white=0 recaptures). A total of 820 pots of 43 pot chains were set and 280 recaptures of tagged fish were recorded.

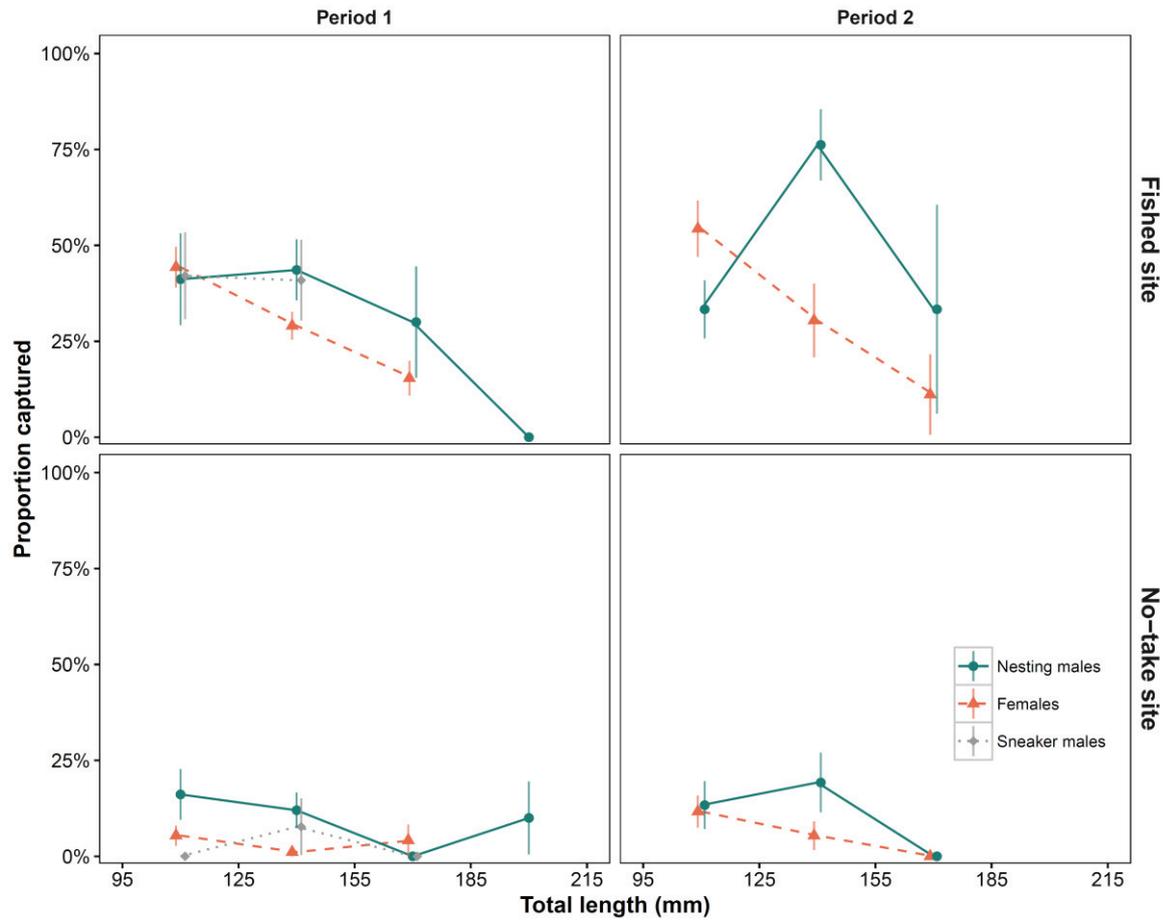


Figure 2. The proportion of corkwing wrasse captured in the corkwing wrasse fisheries in Austevoll 2013 in four size categories (95-124,125-154,155-184,185-214 mm). The data is aggregated in to tagging period and site. Error bars show standard error around the observed proportions.

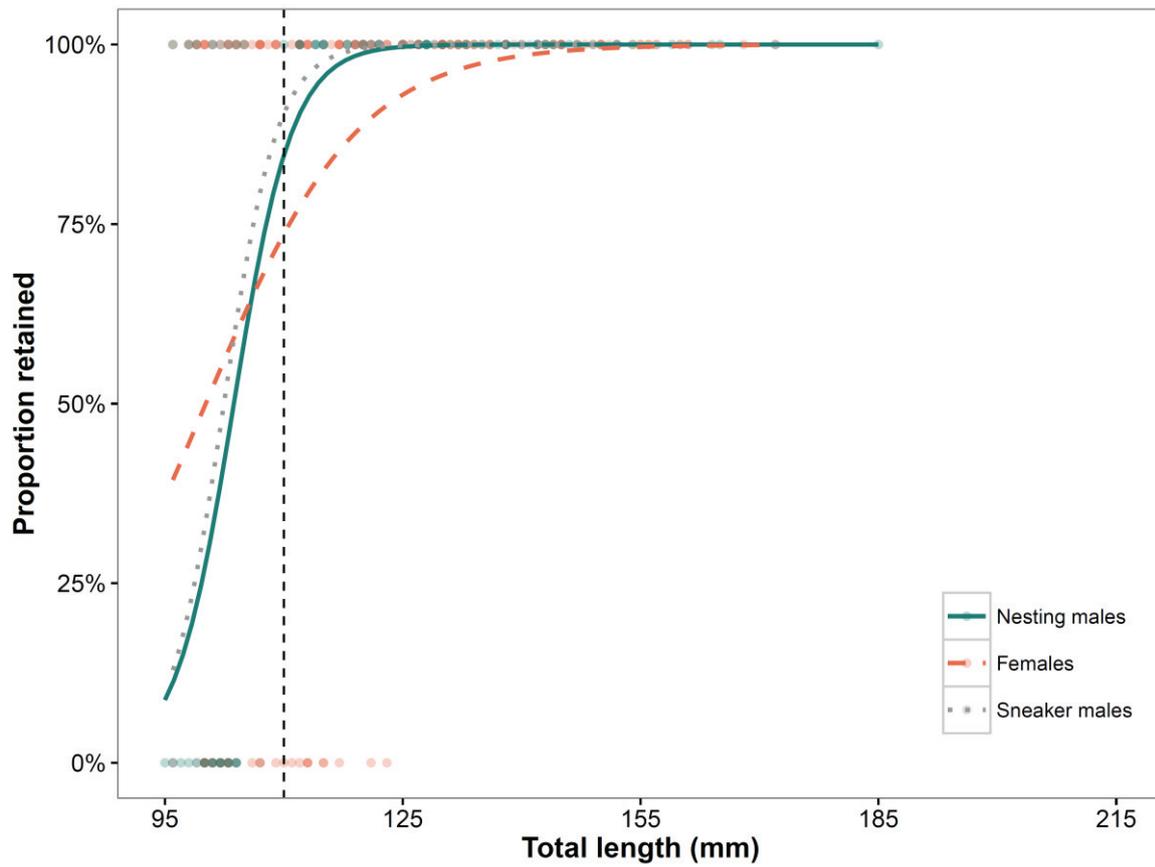


Figure 3. The probability of being retained once captured in the corkwing wrasse fishery as a function of total length at tagging. The vertical dashed line refers to the official minimum size limit (110 mm).

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Paper III

Impact of harvesting cleaner fish for salmonid aquaculture assessed from replicated coastal marine protected areas

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Running head

Impact of harvesting cleaner wrasse for salmonid aquaculture

Abstract

Wrasse (*Labridae*) fisheries have increased markedly in Norway since 2010. Wrasse are being used as cleaner fish in salmonid aquaculture to control sea-lice infestations. However, fundamental knowledge on demography and abundance of the targeted wrasse populations in Norwegian waters is lacking, and the consequences of harvesting at the current intensity have not been assessed. Here, we compared catch per unit effort (CPUE), size, age and sex ratio of goldsinny wrasse (*Ctenolabrus rupestris*) and corkwing wrasse (*Symphodus melops*) between marine protected areas (MPAs) and control areas open for fishing in four localities on the Skagerrak coast in Southern Norway. The CPUE of goldsinny larger than the minimum size limit was 33-65 % higher within MPAs, while for corkwing three out of four MPAs had higher CPUE with the relative difference between MPAs and control areas ranging from -16 % to 92 %. Moreover, corkwing, but not goldsinny, was significantly older and larger within MPAs than in control areas. Sex ratios did not differ between MPAs and control areas for either species. Our study suggest that despite its short history, the wrasse fisheries have considerable impacts on the target populations and further, that small MPAs hold promise as a management tool for maintaining natural population sizes and size structure. Goldsinny, being a smaller sized species also seems to benefit from the traditional minimum size limit management tool, which applies outside MPAs.

Key words

Marine protected areas, aquaculture–environment interactions, wrasse, fisheries management, fishing impacts, Skagerrak

Introduction

Different species of wrasse (*Labridae*) are among the most numerous fish species on shallow rocky reefs and coastlines in Northern Europe, but their commercial value as food fish is low due to their relatively small body size. However since the late 1980's, wild caught goldsinny wrasse (*Ctenolabrus rupestris* (Linnaeus, 1758)), corkwing wrasse (*Symphodus melops* (Linnaeus, 1758)), ballan wrasse (*Labrus bergylta* Ascanius, 1767) and rock cook (*Centrolabrus exoletus* (Linnaeus, 1758)), has been used as cleaner fish in open-pen farming of Atlantic Salmon (*Salmo salar* Linnaeus, 1758) to reduce infestations of salmon lice (*Lepeophtheirus salmonis* Krøyer, 1837) in Norway and the British Isles (Bjordal 1988; Darwall et al. 1992; Treasurer 1996). The Norwegian demand of wild caught wrasse increased

sharply after 2009 when the lice problem intensified as the lice had evolved resistance to most of the available pesticides (Costello 2009; Besnier et al. 2014; Skiftesvik et al. 2014a). In 2014 and 2015, wrasse landings surpassed 20 million individuals, with corkwing and goldsinny wrasse as the dominating species (The Norwegian Directorate of Fisheries). Wrasses are caught by small boats operating inshore using fyke nets and pots and are transported with boats or trucks to the salmon farms. The fishery is regulated with minimum size limits, gear modifications for escapement of undersized fish and a fishing closure from January to July. From 2015, minimum size limits are species-specific (goldsinny 11 cm, corkwing 12 cm and ballan 14 cm), after previously being the same for all wrasse (11 cm) (Skiftesvik et al. 2014a). In addition, a total landing cap of 18 million individuals has been set in 2016, divided among three regions (South: 4 million, West: 10 million and North: 4 million individuals).

Whether and how the wrasse fishery affects the natural populations in Norway has not been investigated and the increasing exploitation has attracted concerns from the scientific community (Espeland et al. 2010; Skiftesvik et al. 2014b,a; Halvorsen et al. 2016). The sedentary behaviour of wrasses poses a challenge for management and fisheries assessments; they hold territories and have small home ranges (Hilddén 1981; Potts 1985; Sayer 1999; Villegas-Ríos et al. 2013). Also, large differences in species composition, abundance and life history traits have been observed at small spatial scales (Sayer et al. 1996a; Varian et al. 1996; Skiftesvik et al. 2014b). Goldsinny and corkwing populations are also genetically structured in Norway (Sundt & Jørstad. 1998; Gonzalez et al. 2016). During the wrasse fisheries on the British Isles in the 1990's, harvested populations of corkwing and goldsinny showed signs of reductions in abundance and changes in size structure (Darwall et al. 1992; Sayer et al. 1996b; Varian et al. 1996). Probably, around 150 000 wrasses were caught and used in Scotland in 1994 (Treasurer 1996), while the total catch in Norway in 2015 reached 21 million individuals. The higher intensity of the current Norwegian fishery raises concerns about its long-term sustainability. However, fishery impacts on the wild wrasse populations in Norway remain unclear, partly due to data deficiency.

Marine protected areas (MPAs) represent a tool for management and conservation where selected areas are partially or completely closed for harvesting. Depending on the MPA design (size, location, distance to nearby MPAs and fishing pressure) and the behaviour and ecology of the protected species, this may preserve natural densities and demography and in some cases increase fisheries yield through spill-over of adults or increased overall

recruitment (Gaines et al. 2010; Goñi et al. 2010; Babcock et al. 2010). MPA's has specifically been highlighted as useful for managing protecting and managing sedentary reef fishes (Roberts and Polunin 1991; Carr & Reed 1993; Gunderson et al. 2008). On the Skagerrak coastline in Southern Norway, six smaller partial protected areas were established in 2006 (four) and 2012 (two), and have been demonstrated to yield positive effect on biomass, size structure and mortality rates of European lobster (*Homarus gammarus* (Linnaeus, 1758)) and Atlantic cod (*Gadus morhua* Linnaeus, 1758) (Moland et al. 2013; Fernández-Chacón et al. 2015). These are partially protected areas where passive standing gears are prohibited (gillnets, pots and fyke nets). Wrasse are effectively fully protected in all these MPA's since they are normally not targeted in recreational hook-and-line fisheries.

Here, we studied catch per unit effort (CPUE), age, size and sex ratio of goldsinny and corkwing wrasse on the Skagerrak coastline, where harvested wrasse is exported to the salmon farming region in Western and Northern Norway (Taranger et al. 2013, Skiftesvik et al. 2014a). Coastal MPAs in Skagerrak provide the opportunity to assess whether the increase in exploitation have affected important population parameters. Wrasse were sampled with passive gears in four of the MPAs and compared with corresponding control areas of similar habitat, open to commercial fisheries. We predicted MPAs to have relatively higher CPUE and the wrasse to be older and larger than in the control areas. As males have been found to be the larger sex in both species (Dipper & Pullin 1979; Sayer et al. 1996a; Halvorsen et al. 2016), we also predicted the sex ratio to be more female-skewed in fished areas. A secondary objective was to compare the by-catch, size, age and sex composition of wrasse caught in fyke nets and baited pots, which are the two types of gear used in the commercial wrasse fishery and therefore potentially valuable for evaluating gear based management regulations.

Material and Methods

Study area

The four MPAs and control areas are situated on the Norwegian Skagerrak coast outside the town of Arendal, Tvedestrand (two MPAs) and Risør (**Table I, Figure 1**). The coastline is characterized with many small islands and skerries with rocky and sandy bottom substrate. The two youngest MPAs (Tvedestrand) are larger than the older ones (**Table I, Figure 1**). The control areas were selected on the basis of habitat similarity to sites in the corresponding MPA (exposure, kelp coverage and rocky bottom substrate). MPA and control pairs were separated by a depth barrier (>20 meters), or by having at least 900 meter coastline between

them (**Figure 1**). The region under study (Aust-Agder county, Southern Norway), has sustained a moderate wrasse fishery since the early 1990-s. Gjøsæter (2002) reported that 15 fishers operated within the county, catching typically 50-100 000 wrasse per year. Consulting with the current fishers, the number of fishers is likely to be slightly higher at the time of study. Detailed knowledge on previous fishing effort in the control areas was not available, but local wrasse fishers confirmed that the control areas had been fished in the year of study (2013) or in earlier seasons. Seasonal catch data from the last three years was obtained from a fisher operating near the Flødevigen MPA and control area. Wrasse fishers in this region use small open boats and fishes at all suitable inshore sites with rocky bottom (< 7 meters depths) covered with *Laminaria* sp. and other macroalgae species (Gjøsæter 2002). Both pots and fyke nets are in use and several fishers may operate within the same area.

Sampling

Sampling was conducted from August - September 2013 (**Table II**). Wrasse were captured with un-baited fyke nets (5 meter single leader, 55 cm diameter entrance ring and leader mesh size of 30 mm) and wrasse pots (rectangular prism shaped, 70 x 40 x 29 cm, circular entrances (75 mm diameter), two chambers and 15 mm mesh-size) baited with 2-3 raw prawns (*Pandalus borealis* Krøyer, 1838). As in the commercial fishery, the gear was deployed at rocky, kelp covered substrate at one to seven meters depth and hauled the following day (19-26 hours soak time). In each site (MPA or control), goldsinny and corkwing wrasse were randomly collected for ageing and euthanized with an overdose of clove oil. An arbitrary minimum sample size of 50 individuals per site was decided upon. Sampling was conducted for 2-5 days, the duration depending on weather conditions and catch rate. Only the first goldsinny captured in each area (n=61-153) were collected for ageing since this species was more abundant than the corkwing. Goldsinny captured later were measured for total length and released at site. All other fish species were identified, counted and released.

Ageing and sex determination

The total length of the fish was measured to the nearest mm and sex was determined by examining external coloration and gonad morphology. Corkwing wrasse males are found in two distinct morphs, *nesting males* and *sneaker males* (Uglem et al. 2000). Nesting males are readily distinguished from females and sneaker males by having distinct patterns of blue, green and red. The coloration of females and sneaker males is brown-green and they have a distinct blue urogenital papillae. Sneaker males and females are visually indistinguishable in

the field, but could readily be sexed by inspecting their gonads. The female gonad is pale or yellow and has clearly visible egg structures, whereas male gonads are opaque, thin and white. For goldsinny, the sexes are similar in appearance, but males have orange or red spots on the lower part of their abdomen behind the pectoral fins (Hilldén 1981). Sagittal otoliths were dissected out, cleaned and stored dry. For aging, the otoliths were placed in black multi-celled trays containing 96 % ethanol and photographed under a stereo microscope (20 x; Leica MZ 16 A). The otoliths of both species have broad, opaque (summer) and narrow, translucent (winter) growth increments, which allowed age to be determined without further processing (Sayer et al. 1996a; Uglem et al. 2000). Age was determined by counting winter zones. Two trained people read the otoliths independently and agreed about the age of those yielding disparate estimates. Non readable goldsinny otoliths were excluded ($n = 40$).

Data analysis

Differences in body size (total length, TL) between sexes were assessed with two-sided t-tests assuming unequal variances. We used generalized linear models (GLMs) to test for differences between the sampling localities, effects of MPAs and influence of sampling gear on the following response variables: **catch per unit effort** (CPUE; the number of wrasse in each fyke net or pot haul), **age**, **total length** and **sex ratio** (proportion of males). The models were fitted separately for each species with the appropriate distribution of errors. A likelihood ratio test was used to compare the goodness of fit of models with and without an interaction effect between protection and locality for each response variable:

$$1) \text{ response} = \text{Protection} + \text{Locality} + \text{Gear} + (\text{Protection} \times \text{Locality})$$

$$2) \text{ response} = \text{Protection} + \text{Locality} + \text{Gear}$$

This provided a framework for testing whether the responses to protection differed among the four localities. Including the *Gear* covariate accommodates for any variance arising from the differences in selective properties of the two gear types, as the proportion of the two gear types differed slightly (121 pots and 180 fyke nets in total; **table II**). Since we compared models chosen a priori, all explanatory variables were kept in the final model (as determined by the likelihood ratio test) regardless of their statistical significance. CPUE was estimated for fish larger or equal to the minimum size limit (110 mm for both species at the time of study - 2013), and modeled by a negative binomial error distribution using the MASS-package in R (Venables and Ripley 2002). The length data was modeled with a Gaussian error distribution with normality assumptions of the residuals checked by diagnostics plots from the fitted

model object. For modeling age, the goldsinny data best conformed to a Poisson distribution, checked for over-dispersion by comparing degrees of freedom with residual variance of the model. For corkwing, 65 % of the individuals were either one year old or young-of-the-year. Therefore, corkwing age was transformed to a binary response variable (age 0-1 = 0, age 2-4 =1) before modeling. A binary response was also used to model sex ratio (the proportion of males). For corkwing, sneaker males were omitted from this analysis. Lastly, we compared the proportion of by-catch species in the two gear types with a proportion test. When reporting the observed relative difference in means between MPA and control areas, data from both gear types were pooled, since the relative proportion of the two gear types were similar in MPA-control pairs (**Table II**). All statistical analyses were performed using the R software version 3.2.2; (R Core Team 2015).

Results

In total, 3906 goldsinny and 709 corkwing were captured and measured for total length in the eight study sites from 24 August – 12 September 2013, of these 846 goldsinny and 705 corkwing were aged (**Table II**). Mean length of goldsinny was 105 mm (range 56-164), while the mean length of corkwing was 140 mm (range 60-219). Thus, only 36.6 % of the goldsinny were larger than the legal size limit at the time of the study (110 mm), compared to 93.2 % for corkwing. Goldsinny mean age was 4.2 years and attained maximum age of 15 years, while the average corkwing was 1.4 years and with only one individual reaching four years. Nesting males of corkwing were larger (mean = 150 mm) than females (mean = 137 mm; $t = 7.00$, $df = 617.93$, $P < 0.0001$) and sneaker males (mean = 127 mm, $t = 9.35$, $df = 106.70$, $P < 0.0001$), but no sex-related difference was evident for goldsinny ($t = -0.54011$, $df = 1494.6$, $P = 0.589$). Pooling all sampling sites, the goldsinny sex ratio was male-biased (62.7 % males, $SE=1.7$), while for corkwing, the sex ratio (nesting males to females) was slightly female-biased (47.2 % nesting males, $SE = 2.0$). Nesting males were more common than sneaker males (79.3 % of all males, $SE=2.1$).

There were considerable differences in catch per unit effort (CPUE), length and age for both species between localities and MPA-control pairs (**Figure 2**). The CPUE of legal-sized goldsinny was significantly (33-65 %) higher within MPAs relative to harvested control areas (**Table III**, **Figure 3(a)**). For corkwing, a model with locality x protection interaction effect was supported (**Table III**, **Figure 3(e)**). Three localities had higher abundance (61-91 % observed difference in means) within MPAs (largest effect in the MPA in inner

Tvedestrand), whereas the Flødevigen MPA had 16.4 % lower mean CPUE relative to the control area (**Figure 3b**). For length and age, the model with locality x protection interaction was supported for both species (**Table III**). All MPA's had relatively larger and older corkwing (**Figure 3(f), Figure 3(g)**), with a notably higher difference between the MPA and control area in Risør (age: 39 %, length 16 %). On the other hand, there was no clear effect of protection on goldsinny body size and age, where the model with interaction between locality and protection was supported (**Table III**). Goldsinny was smaller in the MPA's with the exception of Flødevigen (**Figure 3(b)**). Goldsinny in Tvedestrand inner MPA was 21 % older than in the control area, while the differences in means between MPA and control areas were less than 3 % in the other three localities (**Figure 3(c)**). The sex ratio in MPA and control areas did not differ for either species (goldsinny: $\chi^2 = 1.7827$, $P = 0.18$, corkwing $\chi^2 = 0.0076$, $P = 0.93$), but there were significant differences between localities for goldsinny, with more male-biased sex ratios in Risør (**Table III, Figure 3(d)**).

There were significant effects of sampling gear on CPUE for both species (**Table III**). For goldsinny the observed mean CPUE was 32 % higher in pots relative to fyke nets whereas for corkwing fyke nets had 72 % higher relative mean observed CPUE. Moreover, pots caught smaller and younger goldsinny but no differences were detected for corkwing (**Table III**). There were close to significant differences in sex ratio between fyke nets and pots, with pots capturing more males of both species (**Table III**). Other species than wrasse constituted 28 % of the total catch in fyke nets compared to 15 % in pots (**Figure 4**, proportion test $\chi^2 = 149.72$, $P < 0.0001$). Of specifically interest was by-catch of the protected eel (*Anguilla anguilla* (Linnaeus, 1758)), which constituted 6 % of the catch in fyke nets, but less than 0.1 % in pots (**Figure 4**, proportion test $\chi^2 = 213.41$, $P < 0.0001$). Catch data from a fisher in operating in the Flødevigen area shows goldsinny to dominate the catch in all three years (**Figure 5**). Ballan and corkwing are captured in similar proportions, but with different seasonal trends, with catches of ballan is highest in June and July and in August and September for corkwing. A total of 47101 goldsinny, 3992 corkwing and 6172 ballan wrasse were caught and sold by this fisher in 2013.

Discussion

This study applied a field-experimental approach to assess effects of harvesting wrasse to be used as cleaner fish in salmonid aquaculture on wild wrasse populations. Using four replicated MPA-control areas, we found that targeted species tended to have higher catch per

unit effort (CPUE) in MPAs. For the corkwing wrasse, MPAs had consistently larger and older fish, while these life history effects for goldsinny were less clear. We also found that the two gear types can be selective on species composition and for goldsinny, size and age. Admittedly, this study and its design have some limitations. Information of the intensity and distribution of the commercial fisheries would facilitate a clearer interpretation of the findings, but unfortunately this was not available. The fishers did not have records of when and where they had been fishing, which they reported to depend on the day to day weather conditions, season and competition from other fishers in the same area. Moreover, the size, age and physical features of the MPAs varied, so in the strictest sense, the four MPA-control pairs are not true replicates. Nevertheless, the consistent MPA-effects evident for some of the measured parameters falls in line with our predictions based on the development and intensity of the fishery in this region during the last 20 years. From a conservation perspective, this study adds to the growing amount of evidence of positive effects of MPAs on abundance and demographic structure of harvested fish species (Lester et al. 2009; Baskett & Barnett 2015). In particular, both goldsinny and corkwing wrasse are sedentary, territorial reef fish with limited adult dispersal capacity, so even small protected areas like those studied here should be efficient conservation tools (Gunderson et al. 2008; Wilson et al. 2010). Both species showed positive effects of MPAs on CPUE, although in Flødevigen, CPUE was slightly lower in the MPA. The abundance, mean body size and survival of coastal Atlantic cod (*Gadus morhua*), a potentially important wrasse predator, has increased substantially in the Flødevigen MPA after its implementation (Moland et al. 2013; Fernández-Chacón et al. 2015), so while fishing mortality may have declined, it is possible that this has been accompanied by an increase in natural mortality through increased predator densities (Babcock et al. 2010; Frank et al. 2011). The rate of such indirect effects has been shown to be slower than direct effects of protection of target species (Babcock *et al.*, 2010), which may explain the similar or better effect on CPUE in two youngest MPAs in Tvedestrand. However, other factors could explain this as well, such as the larger size of the Tvedestrand MPAs, or it is possible that fishing intensity in the control areas have been higher there.

The MPA-effect on size and age differed between the two species; the MPAs had larger and older corkwing than control areas, but no clear pattern was evident for goldsinny. A possible explanation could be related to the finding of higher spatial variation between the different MPAs for goldsinny age and body size, so other local factors (e.g. density, predation and habitat) than fishing may have stronger effects on goldsinny life history traits. For

example, the observation that the CPUE of goldsinny was generally higher than the CPUE for corkwing could imply stronger density-effects on the goldsinny. In that context, the reduced abundance of goldsinny we observed in control areas may have increased growth rates for the remaining fish. Moreover, as these two species have overlapping habitat requirements and diets (Costello 1991; Sayer et al. 1996a), a reduction in abundance of the larger corkwing wrasse could benefit the goldsinny. The considerable variation in goldsinny size and age structure over distances less than 30 km as found in this study implies a mismatch between the unit of management and the spatial variation in life histories, as seen on larger scales for corkwing (Halvorsen et al. 2016). The same minimum size regulations are enforced throughout Norway, and populations with faster growth would reach the size limit at a younger age and be more prone for overexploitation. If a size-selective fishery primarily target immature fish, this may induce selection for earlier maturation, slower growth and increased reproductive investment at younger age (Law 2000; Fenberg and Roy 2008; Heino et al. 2015). In a study conducted during the spawning season in 2014, corkwing examined in Flødevigen were found to mature in their first or second year, but few nesting males had reached maturation below the minimum size limit ($L_{50} = 139$ mm), while mature females were somewhat better protected ($L_{50} = 110$ mm) (Halvorsen et al. 2016). The maturation of goldsinny has not been investigated in Norway, but it has been found to mature in their second year on the British Isles (Darwall et al. 1992; Varian et al. 1996), and could spawn for two to three years before reaching harvestable size (10 cm in those studies) (Sayer et al. 1996b; Varian et al. 1996). In order to set appropriate size regulations for maintaining healthy breeding populations of goldsinny in Norwegian waters, a comprehensive spatial assessment of growth and maturation and the underlying factors causing variation should be conducted.

The sex ratio did not differ between MPAs and control areas for either species. This makes sense for goldsinny, since males and females was not found to differ in body size. Corkwing nesting males were larger than females, but since almost all corkwing wrasse were larger than the size limit at the time of study, the possibilities for the fisheries to be sex-selective were limited. Stronger male-biased size dimorphism has been demonstrated in populations further north on the western coast compared to those on the Skagerrak coast with consequently higher potential for sex-selective harvesting (Halvorsen et al. 2016).

Currently, both pots and fyke nets are used in the fishery. Many of the wrasse fishermen in Southern Norway were previously involved in a fyke-net fishery for eel, which was prohibited in 2010 with the eel now listed as vulnerable according to the International

Union for Conservation of Nature (IUCN). A special permit has to be obtained in order to use fyke nets for fishing wrasse, and we have shown that fyke nets have a significantly higher proportion of eel and by-catch species. To our knowledge, fishermen release all by-catch on shallow depths, so the survival of by-catch species may be expected to be relatively high. Moreover, pots caught smaller and younger goldsinny, but this is expected as the pots used had smaller mesh size than fyke nets. No gear differences in size and age was evident for corkwing, which is most likely related to their larger size and deeper body shape relative to goldsinny. The fisher in Flødevigen had higher catches of ballan than corkwing, as opposed to what we observed in our sampling. However, the fisher's catches of ballan were highest in June and July, whereas we sampled in late august and the beginning of September. In addition, ballan tend to prefer more exposed sites than corkwing (Skiftesvik et al. 2014b), and three of the MPAs in this study were relatively sheltered with low to moderate exposure.

Our study provides the first insights into the effects of harvesting of wild wrasse in Norway, but it should be noted that the wrasse landings are considerably higher in Western Norway than on the Skagerrak coastline (Espeland et al. 2010; The Norwegian Directorate of Fisheries). Salmonid aquaculture is virtually absent in Skagerrak, and harvested wrasse is transported to western and northern Norway where local wrasse population cannot sustain the demand for cleaner fish (Skiftesvik et al. 2014a). Thus, the modest, but significant differences between MPA and control areas we found here would likely have been larger if a similar study was conducted in the more intensively fished areas but which unfortunately do not have MPAs. In addition, the annual national landings have increased by 32 % since this study was conducted, so differences between fished and unexploited areas may have increased. The minimum size limit for corkwing was increased from 11 to 12 cm in 2015, but still 82 % of the corkwing would be harvestable using the size distribution in our data. Reduction of wrasse densities may lead to cascade effects in the coastal ecosystems where the different wrasse are important both as predators on molluscs and crustaceans (Deady & Fives 1995a,b; Sayer et al. 1995) and prey for larger species, such as gadoids, seabirds and otters (Steven 1933; Rui Beja 1995; Nedreaas et al. 2008). Moreover, the wrasse diet is size and sex dependent (Deady & Fives 1995a,b; Sayer et al. 1995), thus ecological consequences on prey species may be anticipated if fishing mortality is selective with regards to size and sex.

We have shown that MPAs in Skagerrak have higher abundance of wrasse and may sustain the natural size and age composition under increasing harvest pressure. Thus, MPAs appears to be useful management and conservation measure for the targeted wrasses. By

conserving a natural abundance, age and size structure, MPAs may have positive effects on recruitment and could buffer for eco-evolutionary effects of size selective harvesting. Our data from the MPA-control contrasts in Skagerrak provide a baseline for monitoring the development of the fisheries in this region, but we also suggest implementing networks of wrasse MPAs in the other harvested regions. There are still several knowledge gaps to be filled on the environmental consequences of using wild-caught wrasse as cleaner fish, specifically on the effect of selective harvesting on reproduction and recruitment (Darwall et al. 1992; Halvorsen et al. 2016), the indirect ecosystem effects and the consequences of the large scale translocations and escapement of wrasse to genetically distinct populations further north in Norway (Sundt & Jørstad 1998; Skiftesvik et al. 2014a).

Tables

Table I: The location, size, year of establishment and exposure to open sea of the MPAs surveyed in this study.

Locality	MPA location	MPA size (km ²)	MPA est.	Exposure
Flødevigen (F)	58° 24'-25'N, 8° 43'-46'E	1.1	2006	moderate
Tvedestrand inner (TI)	58° 34'-36'N, 8° 56'-9° 0'E	4.1	2012	low
Tvedestrand outer (TO)	58° 35'-37'N, 9° 4'-7'E	5.3	2012	high
Risør (R)	58° 42'-44'N, 9° 13'-15'E	0.6	2006	moderate

Table II: Number of gear used, number (*n*) of wrasse and goldsinny caught and aged (in parenthesis) at the control and MPA sites. Time of sampling during 2013 is also given for each locality. See Figure 1 for details about the localities.

Locality (date)	Treatment	Pots	Fyke nets	% pots	<i>n</i> goldsinny (aged)	<i>n</i> corkwing (aged)
Flødevigen	MPA	46	30	61	914(153)	90 (90)
(30.08 – 03.09)	Control	47	31	60	1249 (146)	112 (112)
Tvedestrand (inner)	MPA	8	14	36	400 (97)	80 (80)
(24.08 – 29.08)	Control	15	24	38	328 (79)	58 (54)
Tvedestrand (outer)	MPA	6	6	50	195 (112)	117 (117)
(24.08 – 29.08)	Control	7	9	44	153 (98)	86 (86)
Risør	MPA	12	16	43	473 (100)	108 (108)
(11.09 – 12.09)	Control	12	18	40	194 (61)	58 (58)
Total	MPA	56	82	41	1982 (462)	395 (395)
(24.08 – 12.09)	Control	65	98	40	1924 (384)	314 (310)

Table III: Summary of generalized linear models on the effects of Protection (MPA vs. control), Locality and gear on catch per unit effort (CPUE), total length, age and sex ratio (proportion males, sneaker males excluded for corkwing). Significant *P*-values in bold. A likelihood ratio test was applied to select the model for statistical inference between models with and without protection x locality interaction effects.

Response	Species	Likelihood ratio test Protection x locality	Predictors	χ^2	Df	<i>P</i>		
CPUE	Goldsinny	$\chi^2=1.30, P=0.72$	Protection	8.66	1	0.003		
			Locality	8.81	3	0.003		
			Gear	7.08	1	0.008		
	Corkwing	$\chi^2= 12.01, P=0.007$	Protection	6.18	1	0.013		
			Locality	53.40	3	<0.0001		
			Gear	19.10	1	<0.0001		
			Protection : Locality	12.30	3	0.006		
	Length	Goldsinny	$\chi^2= 98.99, P<0.0001$	Protection	27.58	1	<0.0001	
				Locality	100.19	3	<0.0001	
Gear				448.68	1	<0.0001		
Protection : Locality				100.03	3	<0.0001		
Corkwing		$\chi^2= 12.37, P=0.006$	Protection	18.00	1	<0.0001		
			Locality	10.74	3	0.013		
			Gear	0.03	1	0.85		
			Protection : Locality	12.32	3	0.006		
Age	Goldsinny	$\chi^2= 22.23, P<0.0001$	Protection	6.62	1	0.010		
			Locality	56.69	3	<0.0001		
			Gear	57.24	1	<0.0001		
			Protection : Locality	22.23	3	<0.0001		
	Corkwing	$\chi^2= 7.12, P=0.07$	Protection	13.30	1	<0.001		
			Locality	6.55	3	0.088		
			Gear	0.55	1	0.46		
Sex	Goldsinny	$\chi^2= 0.76, P=0.86$	Protection	1.78	1	0.18		
			Locality	20.08	3	0.0001		
			Gear	3.30	1	0.069		
	Corkwing	$\chi^2= 4.96, P=0.18$	Protection	0.10	1	0.75		
			Locality	5.93	3	0.12		
			Gear	3.83	1	0.050		

Figures

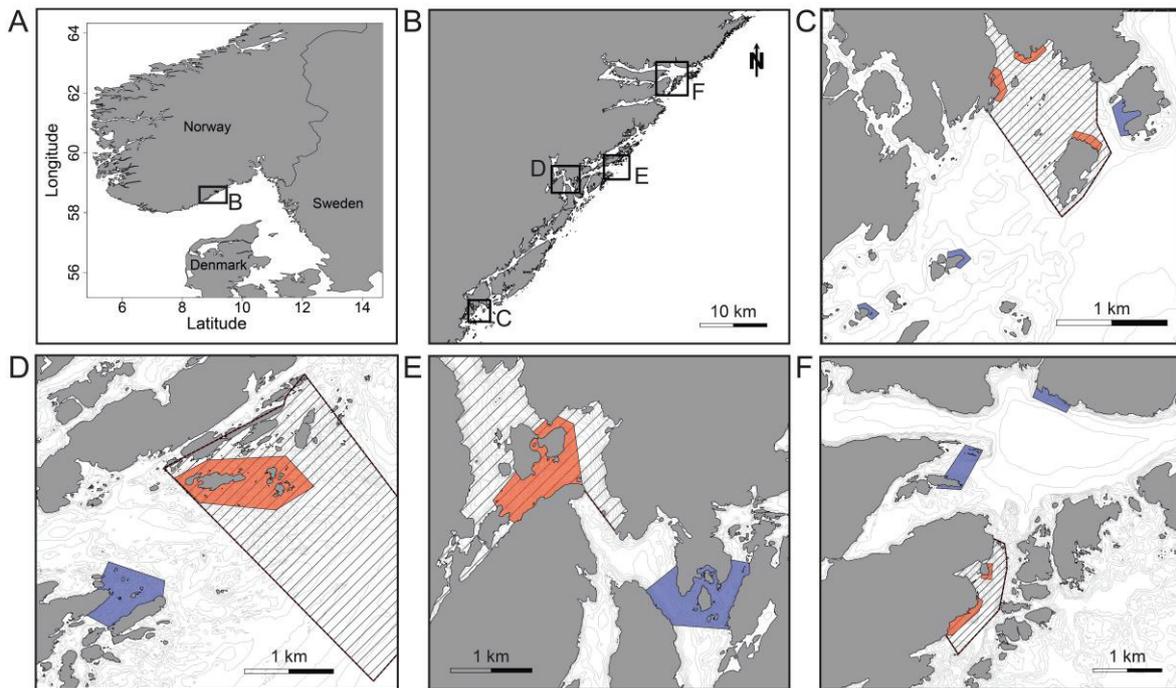


Figure 1: Map showing the study area in Southern Norway (A) with the four localities along the Norwegian Skagerrak coast used in this study (B). C-F shows the four MPAs (boxed areas with lines) with the sampling sites (solid fill). C: Flødevigen, D: Tvedestrand Outer, E: Tvedestrand Inner and F: Risør.

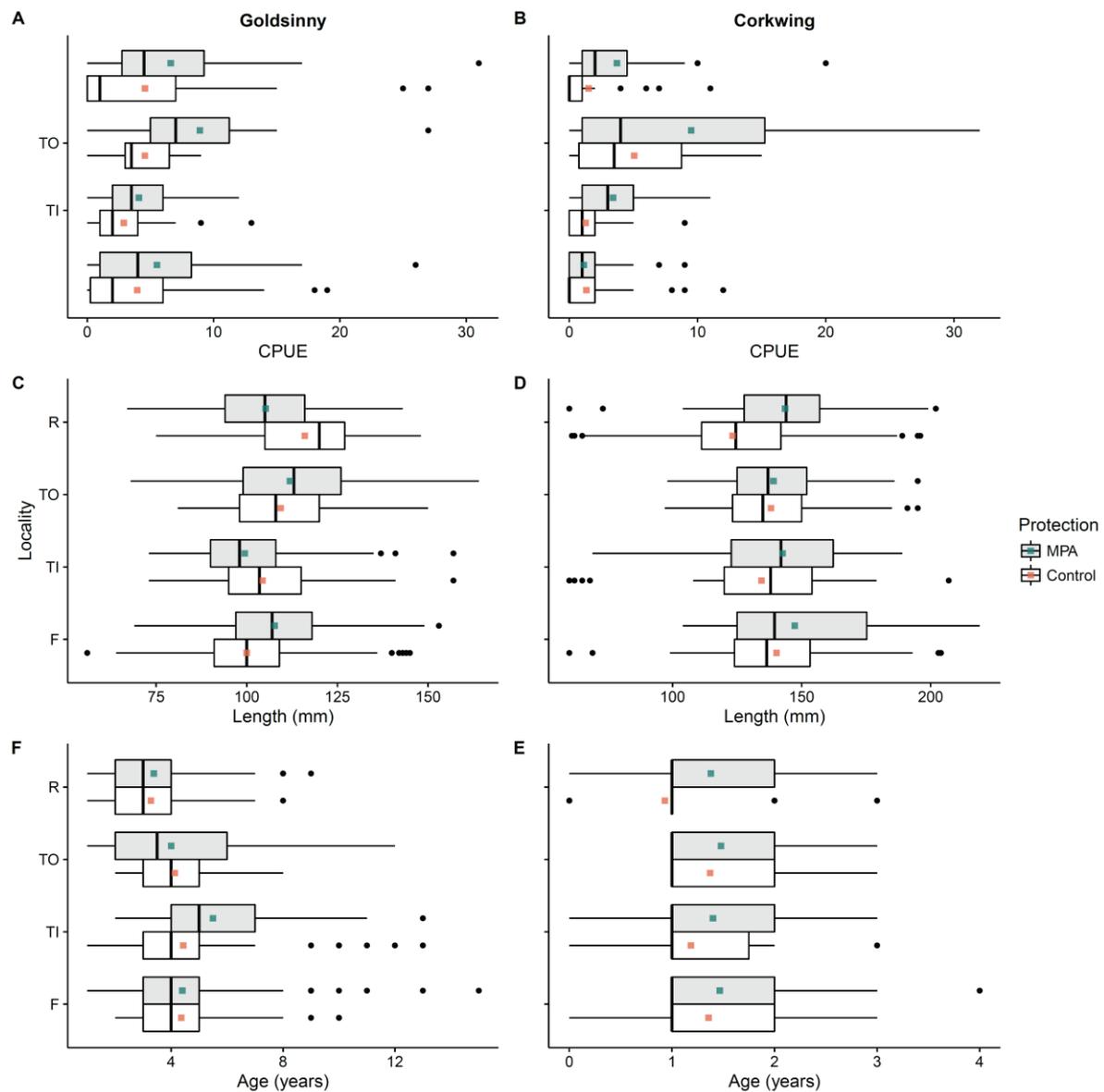


Figure 2: Boxplots showing the median (thick vertical line) and mean (solid squares) of catch per unit effort (CPUE: pooled for both gear types), total length (mm) and age of goldsinny and corkwing in the four sampling localities (F=Flødevigen, TI=Tvedestrand Inner, TO=Tvedestrand Outer and R=Risør). Shaded boxes are MPAs, open control sites. The upper and lower edge of box represents the 25th and 75th percentiles, respectively. The whiskers extend to the highest value maximum 1.5 times the distance between the 25th and 75th percentiles and filled dots represents outliers.

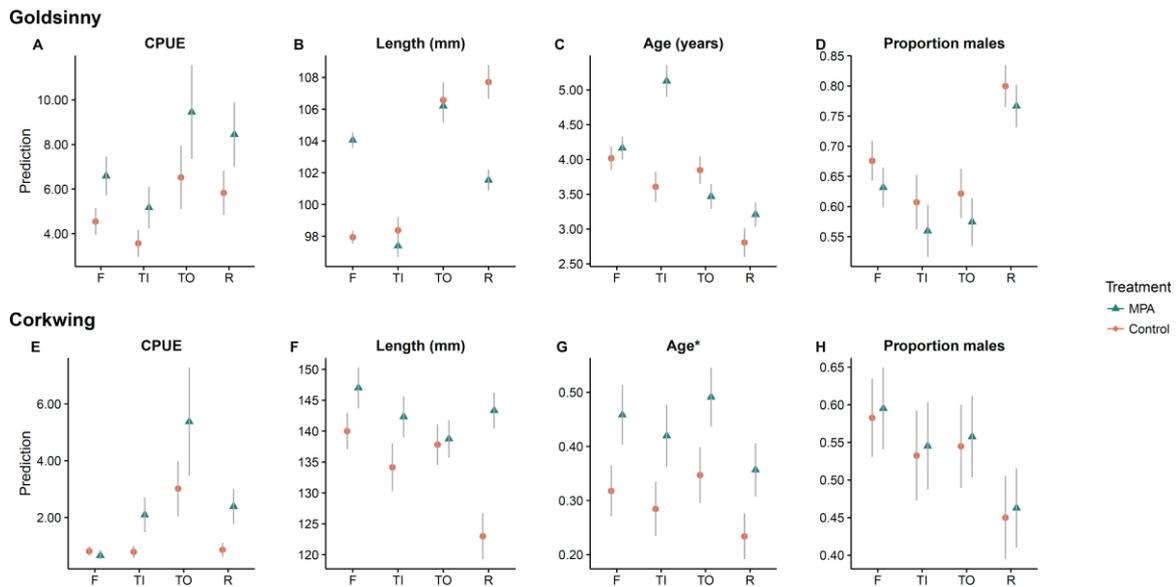


Figure 3: The predicted effect of protection (MPA or control site) on catch per unit effort (CPUE), body length, age and the proportion males as estimated by generalized linear models for goldsinny and corkwing wrasse captured in pots in the four localities (F=Flødevigen, TI=Tvedestrand Inner, TO=Tvedestrand Outer and R=Risør). Error bars show standard error around the predicted means. * Corkwing age was modeled with a binominal age distribution (0: 0-1 and 1: 2-4 years).

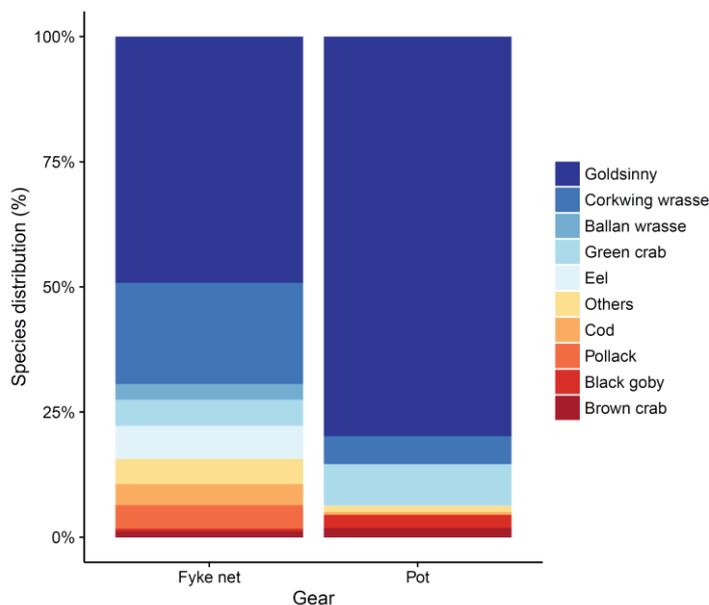


Figure 4: The relative species distribution in the two gear types used for sampling wrasse in Skagerrak 2013. The data is pooled for all sampling sites.

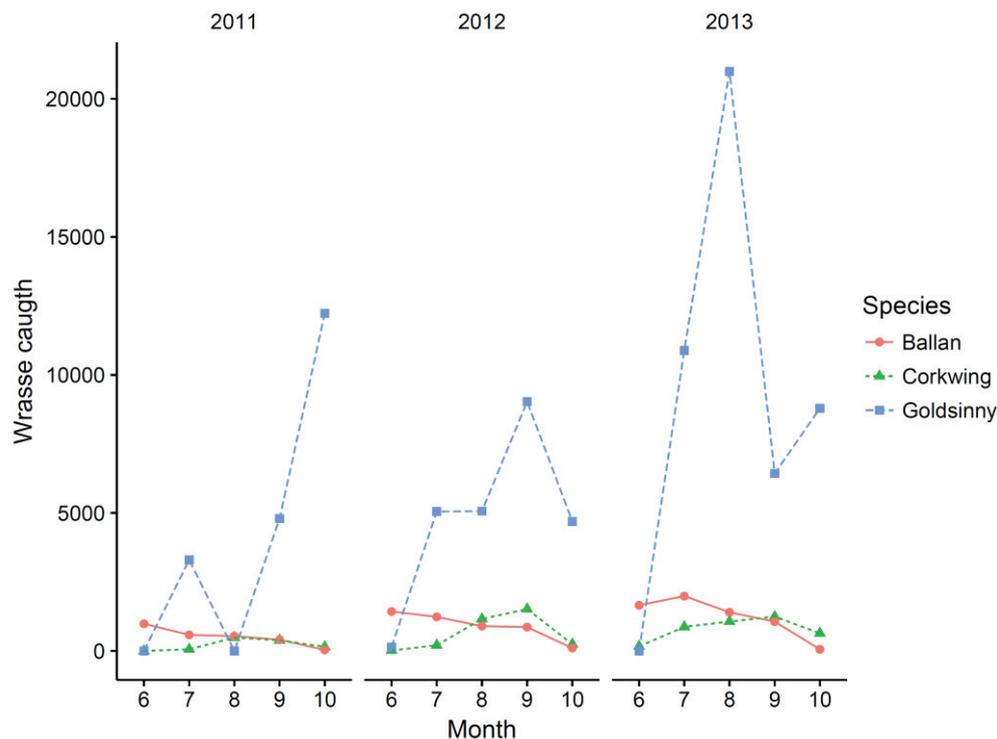


Figure 5: Seasonal variations in landings of the three target species of a fisher operating in the Flødevigen area.

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Paper IV

Life history variability of an intermediate predator (*Ctenolabrus rupestris*) in northern European marine protected areas and harvested areas

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Abstract

Understanding the drivers behind spatial variation in fish life histories is important for management. Small-bodied wrasse species are increasingly harvested for the aquaculture industry, since their natural behaviour as parasite cleaners on other fish could help to reduce sea-lice infestations on salmonids. However, there is limited knowledge on the spatial ecology and life history traits influencing population productivity of these intermediate predators. We studied individual growth of goldsinny wrasse (*Ctenolabrus rupestris*) across replicated marine protected areas (MPAs) and areas open to commercial harvesting along the Norwegian Skagerrak coast. Growth varied among localities separated by 5 km or less without any clear effect of MPAs. However, the data did support negative effects of local wrasse abundance and abundance of the Atlantic cod apex predator on growth. Furthermore, males tended to reach bigger asymptotic sizes than females. Our study highlights the role of biotic interactions as potential drivers behind fine-scale spatial variation in fish life histories, and the challenges associated with selective harvesting of species with sex-differentiated growth.

Introduction

Intermediate predators play a key role in structuring marine ecosystems, as prey for apex carnivores and predators on planktivorous and benthic herbivores (Eriksson *et al.*, 2009; Frank *et al.*, 2011). In oceanic systems, typical intermediate predators include small-bodied fish such as sprat (*Sprattus sprattus*), capelin (*Mallotus villosus*) and herring (*Clupea harengus*) (Hjermann *et al.*, 2004; Olsen *et al.*, 2007; Casini *et al.*, 2009) while in coastal systems various species of gobies, wrasses, sticklebacks, pipefish and crabs can take this ecological role (Moksnes *et al.*, 2008; Baden *et al.*, 2010; Hughes *et al.*, 2013). For instance, in northern European coastal systems, intense harvesting and depletion of Atlantic cod (*Gadus morhua*) apex predator populations (Fernández-Chacón *et al.*, 2015) could potentially

drive changes in nearshore seagrass (*Zostera marina*) ecosystems through a trophic cascade involving more abundant intermediate predators on mesograzers (Östman *et al.*, 2016). Fishing down marine food webs have also exposed many smaller species to commercial harvesting (Pauly *et al.*, 1998). For management and conservation purposes, there is a need for more knowledge on population dynamics, life history variability and spatial ecology of these intermediate predators.

Marine protected areas (MPAs) are clearly defined locations managed for a specific conservation purpose, with some level of restriction to human activities. MPAs are increasingly used as a management tool in coastal systems. In Europe, however, the implementation of MPAs has often been somewhat ad hoc, while developing, monitoring and surveilling coherent networks of MPAs spanning larger geographical distances remains a challenge (Fenberg *et al.*, 2012). In addition to their primary conservation- and fisheries management goals, MPAs also hold promise as large-scale field experiments where ecological and evolutionary processes can be studied in absence of human impacts such as harvesting (Dale *et al.*, 2011; Freitas *et al.*, 2016). Interestingly, MPAs could protect old-growth age structure in fish populations against selective harvesting, but may also set up new and unanticipated protection-induced selection pressures on, for instance, fish behaviour (Berkeley *et al.*, 2004; Baskett and Barnett, 2015; Villegas-Ríos *et al.*, 2016). Further, MPAs could drive reductions in individual growth rates because of potential crowding effects when population densities of protected species are increasing (Gårdmark *et al.*, 2006). However, intermediate predators may also suffer from increased predation when species at higher trophic levels recover within MPAs (Babcock *et al.*, 2010).

Different species of wrasse are abundant intermediate predators in shallow rocky shore ecosystems in Northern Europe (Sayer *et al.*, 1996, Skiftesvik *et al.*, 2014). Wrasses are increasingly being harvested as cleaner fish for the aquaculture industry in Norway and on the

British Isles (Darwall *et al.*, 1992, Skiftesvik *et al.*, 2014). Commercial exploitation of these smaller-bodied coastal fishes began in 1988 when it was discovered that their natural behaviour as parasite cleaners on other fish (Potts, 1973) could be used to reduce sea-lice (*Lepeophtheirus salmonis* and *Caligus elongatus*) infestation on farmed salmon (Bjordal, 1988). The wrasse catches remained relatively low throughout the 1990's and 2000's, when wrasses were only complementary to chemical treatments. However, more recently, the lice infestation problem in salmonid aquaculture worsened considerably and the annual landings of wild-caught wrasse in Norway have surpassed 20 million individuals (Skiftesvik *et al.*, 2014, The Norwegian Directorate of Fisheries). Wrasse are caught with small vessels using fyke nets and baited pots at shallow depths on rocky, kelp covered habitat (Skiftesvik *et al.*, 2014). Four different species are being harvested in Norway, with corkwing wrasse (*Symphodus melops*) and goldsinny wrasse (*Ctenolabrus rupestris*) holding the larger share of the landings. Since 2011, goldsinny in Norway has been managed with a minimum size limit of 11 cm and a spring closure to limit fishing during the spawning period. Moreover, 12 mm selective grids in the fishing gear to reduce the catch of juveniles has been compulsory from 2015. The long-term sustainability of a size selective wrasse fishery has been questioned, since reductions in abundance of larger and older goldsinny and corkwing wrasse coincided with the emergence of the fishery in Scotland and Ireland (Darwall *et al.*, 1992; Sayer *et al.*, 1996; Varian *et al.*, 1996). In Norway, a lack of information on life history variability of these wrasses has impeded knowledge-based management (Skiftesvik *et al.* 2014, Halvorsen *et al.*, 2016).

Here, we explore fine scale spatial variation in life histories of goldsinny wrasse along the southern coast of Norway. Specifically, we model individual growth trajectories based on otoliths from samples collected within a network of replicated coastal MPAs closed to commercial wrasse harvesting, as well as neighbouring control areas open to wrasse

harvesting, allowing us to study life-history diversity in absence of selective harvest mortality and also to test for potential effects of harvesting on life histories of this intermediate predator.

Material and methods

Sampling and age determinations

Goldsinny was sampled within four MPAs and neighbouring control areas open to harvesting along the Norwegian Skagerrak coast from 24 August to 12 September 2013 (Figure 1). Two of these MPAs, Flødevigen and Risør, were established in 2006 specifically to protect the European lobster (*Homarus gammarus*). The reserves are managed through gear restrictions allowing only hook and line fishing (Pettersen *et al.*, 2009). Wrasse fishing for the aquaculture industry is conducted with fixed gear types (fyke nets and baited traps) and is therefore excluded from the MPAs. The two other MPAs included in this study, inner and outer Tvedestrand fjord, were established in 2012 and are managed with the same gear restrictions as the Flødevigen and Risør MPAs. Wrasse were sampled using un-baited fyke nets (diameter: 55 cm, leader: 5 m, mesh size: 30 mm) and two-chamber pots (size: 70 × 40 × 29 cm, entrance diameter 75 mm, mesh size: 15 mm) baited with shrimp (*Pandalus borealis*). The gear was set over night at 0-7 m depth on vegetated or rocky substrate. These are preferred habitats of goldsinny, where the fish has access to refuges such as spaces between rocks, crevices or caves (Costello, 1991; Sayer *et al.*, 1999; Gjøsæter, 2002). A total of 935 goldsinny was sampled and measured for length and weight. Sex was determined by examining morphology and gonads, while age was determined from otoliths (Richter and McDermott, 1990; Gordo *et al.*, 2000). For this purpose, the otoliths were placed in a 96% ethanol bath on a black background, and digital pictures were taken using a Leica microscope (MZ 16 A) and camera (DFC425 C) with 20 x magnification. A total of 109 fish were

excluded from further analyses because the otoliths were of poor quality and could not be reliably interpreted. For the remaining 826 fish (Table 1), interannual distances (growth zones) were measured along a transect through the horizontal plane of the otolith as the distance from the centre (nucleus) to the outer margin of each opaque annulus, using the open-source image analysis program ImageJ (Abràmhoff *et al.*, 2004). A simple Dahl-Lea equation was used for back- calculation of lengths-at-age based on the distances measured on the otoliths (Francis, 1990):

$$L_a = (O_a / O_c) L_c,$$

where L_a is the estimated length-at-age a , L_c the length at capture, O_a the distance from the centre of the otolith to the outer edge of the annulus defining age a , and O_c the distance from the centre to the outer margin of the otolith.

Growth analyses

Growth trajectories were back-calculated using von Bertalanffy growth (VB) curves:

$$L(t) = L_\infty - (L_\infty - L_0)e^{-kt},$$

where $L(t)$ is fish length at age t , L_∞ the asymptotic length, L_0 the average length at $t = 0$, and k the intrinsic growth rate (von Bertalanffy, 1938). Non-linear least squared regression, with L_0 , L_∞ and k as free model parameters, was used to fit VB curves to the individual back-calculated growth trajectories (Pardo *et al.*, 2013). Only fish with an otolith age of four years or older were included in these analyses ($n = 413$), since VB curves could not be reliably fit to only three data points (back-calculated lengths at age) or less. Linear mixed-effects models

were used to test for the effects of MPAs and sex (as factors) on VB parameters. We focussed the analyses on L_{∞} as the key growth parameter capturing growth differences; k and L_{∞} are known to be strongly and negatively correlated (Charnov 1993) and L_0 is mostly relevant for growth curve statistical fit. Locality was included as a random effect in the models. To further explore potential mechanisms underlying any MPA effects, the abundance (mean catch per trap) of goldsinny wrasse was considered as a fixed effect to test for effects of intraspecific competition (density-dependence). Similarly, the abundance of cod (mean catch per trap), an apex predator in this coastal system, was considered as a fixed effect to test for effects of selective predation on goldsinny wrasse growth trajectories.

Results

The otoliths revealed considerable variation in back-calculated growth trajectories of goldsinny wrasse (Figure 2). In fact, the fastest growing fish were approximately 100% larger at age compared to the slowest growing fish (Figure 2). VB curves were successfully fitted to the back-calculated growth trajectories (R^2 ranged between 97.9 and 100%). One outlier with an estimated asymptotic length of 710 mm was excluded from further analyses. Linear mixed effects models did not support an effect of the MPA treatment on von Bertalanffy asymptotic lengths ($p = 0.92$), but did support fixed effects of sex and gear type (Table 2). Overall, male goldsinny wrasse had larger asymptotic lengths compared to female goldsinny wrasse, while the baited pots captured goldsinny wrasse with smaller asymptotic lengths than the fyke nets (Table 2). Furthermore, there was support for negative effects of goldsinny wrasse abundance and Atlantic cod abundance on goldsinny wrasse asymptotic length (Table 2). A total of 5.8% of the total variance in asymptotic length was associated with the random *Locality* effect (Figure 3).

Discussion

This study on life history variation of goldsinny wrasse from the Norwegian Skagerrak coast revealed that growth trajectories of this species can vary on a fine spatial scale of 5 km or less. Contrary to our expectation, growth trajectories apparently did not vary consistently between protected MPA sites and control sites open to harvesting. Interestingly, we found that males tended to grow faster than females, and that fyke nets captured faster-growing individuals compared to baited pots. Also, the local population densities of conspecifics and predators (Atlantic cod) appeared to have a negative influence on the average growth trajectories. Below, we discuss these main findings from a life history perspective, as well as management and conservation.

The lack of clear statistical support for an MPA effect on goldsinny wrasse growth could in theory mean that the wrasse fishery in this coastal region is not strongly selective and of sufficient scale to cause major impacts on the targeted populations. It seems highly unlikely though, that the fishery is unselective with regard to body size since current management regulations includes a minimum size limit of 11 cm. Furthermore, our study suggests that baited pots tend to capture slower growing goldsinny wrasse, reaching smaller maximum sizes, compared to fyke nets. These are the two gear types commonly used in commercial wrasse fisheries in Norway (Skiftesvik *et al.*, 2014). The abundance of goldsinny wrasse tends to be higher inside MPAs than in harvested areas suggesting that the fishery indeed has a significant impact on the populations (Larsen, 2015; see also Table 1). Thus, it is possible that the impact of selective harvesting on goldsinny wrasse life histories is neutralised, or at least modified, by other ecological effects linked to the fishery, such as increased intraspecific competition associated with higher population densities.

This study detected a negative effect of goldsinny wrasse abundance on asymptotic size, indicating that growth trajectories are regulated by local population density. A similar pattern

of low population density and higher growth was also found for goldsinny compared in three localities differing by a degree or less in latitude or longitude in Western Scotland (Sayer *et al.*, 1995). Goldsinny wrasse typically defend territories on rocky shores, and there is some evidence suggesting that territory size decrease at higher population densities (Sayer, 1999). Density-dependent growth is likely a widespread phenomenon in marine fish (Lorenzen and Enberg 2002) and is also seen for juvenile Atlantic cod in our study region (Rogers *et al.*, 2011). As pointed out by Gårdmark *et al.* (2006), such crowding effects might impact the conservation and fishery benefits that are expected from MPAs, and thus MPA design programmes could benefit from linking individual traits such as growth to population responses.

We found that goldsinny wrasse growth curves differed between the sexes, with males reaching a larger asymptotic size than females. Under the current management regime relying on a 11 cm minimum size limit, goldsinny wrasse fisheries are therefore likely to be sex-selective. A similar pattern has recently been documented for the corkwing wrasse, which is often captured together with goldsinny wrasse (Skiftesvik *et al.*, 2014; Halvorsen *et al.*, 2016). Sex-selective fisheries could impact the matings system of targeted populations via effects on sex-ratios and size-structure, with potential negative consequences for population productivity and conservation (Rowe and Hutchings 2003; Zhou *et al.*, 2010).

The Atlantic cod has suffered major declines in Skagerrak, but could still play a role as an apex predator in this coastal ecosystem (Hop *et al.*, 1992; Olsen *et al.*, 2009; Roney *et al.*, 2016). Specifically, the negative effect of Atlantic cod local abundance on goldsinny wrasse life histories suggested here means that this intermediate predator could be regulated by natural top-down effects in addition to fisheries. Alternatively, other environmental factors not measured by us (and correlated with cod abundance), could have been the underlying drivers. Life-history changes could also result from correlated selection on, for instance,

behavioural traits, where bold individuals may feed more and grow faster at the cost of increased predation risk (Biro and Post, 2008; Biro *et al.*, 2015).

The fine-scaled life history variability found here has implications for translocation of goldsinny to the salmon farming areas. Salmon farms located in northern regions depend on live wrasses being imported from southern populations (Taranger *et al.*, 2013). Goldsinny from Skagerrak is genetically different from the recipient areas in mid and northern-Norway, and genetic structure between neighbouring fjords has been detected in Western Norway (Sundt and Jørstad 1998). Thus, considering the high life history variability among nearby populations in the present study, it is likely that southern goldsinny escaping and interbreeding can affect fitness and life history traits in the northern populations. For corkwing, populations in Skagerrak have been found to grow faster and mature earlier than populations further north, which are also genetically different (Gonzalez *et al.*, 2016; Halvorsen *et al.*, 2016).

In summary, this study shows how life-histories of an intermediate predator fish can vary on fine spatial scales and also between sexes. Space selection as well as sex selection by fisheries may impact population diversity and mating systems (Zhou *et al.*, 2010). Life history traits are key determinants of population productivity, and identifying the spatial scales of life-history variability is therefore important from a management and conservation perspective (Kuparinen *et al.*, 2016).

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Tables

Table 1. Summary statistics of goldsinny wrasse sampled from four MPAs and neighbouring control areas along the Norwegian Skagerrak coast in August and September 2013, showing their mean body length (range) and age (range), and also the mean number of goldsinny wrasse (GW) and Atlantic cod (AC) caught per trap.

Locality	Treatment	<i>n</i>	Length (mm)	Age (years)	GW	AC
Flødevigen	MPA	141	104 (75–147)	4.1 (1–13)	12.0	0.5
	control	136	98 (70–129)	4.3 (2–10)	16.0	0.4
Tvedestrand inner	MPA	85	98 (76–133)	5.3 (2–13)	18.2	0.2
	control	74	106 (78–139)	4.2 (1–13)	8.4	0.4
Tvedestrand outer	MPA	106	107 (68–147)	3.9 (1–12)	16.3	0.3
	control	94	105 (81–142)	4.0 (2–8)	9.6	1.1
Risør	MPA	133	99 (67–128)	3.3 (1–9)	16.9	0.2
	control	57	107 (75–137)	3.2 (1–8)	6.5	0.3

Table 2. Parameter estimates (standard error, SE) from a linear mixed effects model explaining variation in goldsinny wrasse asymptotic length, including fixed effects of sex, gear type, goldsinny wrasse abundance (GW) and Atlantic cod abundance (AC). Females and fyke nets were set as reference levels in the model. Locality (Figure 1, Table 1) was included as a random effect.

Model term	Parameter estimate	SE	p-value
Intercept	155.89	6.41	<0.0001
Male	11.58	1.58	<0.0001
Pot	-8.45	1.75	<0.0001
GW	-1.87	0.31	<0.0001
AC	-17.12	5.24	0.0012

Figures

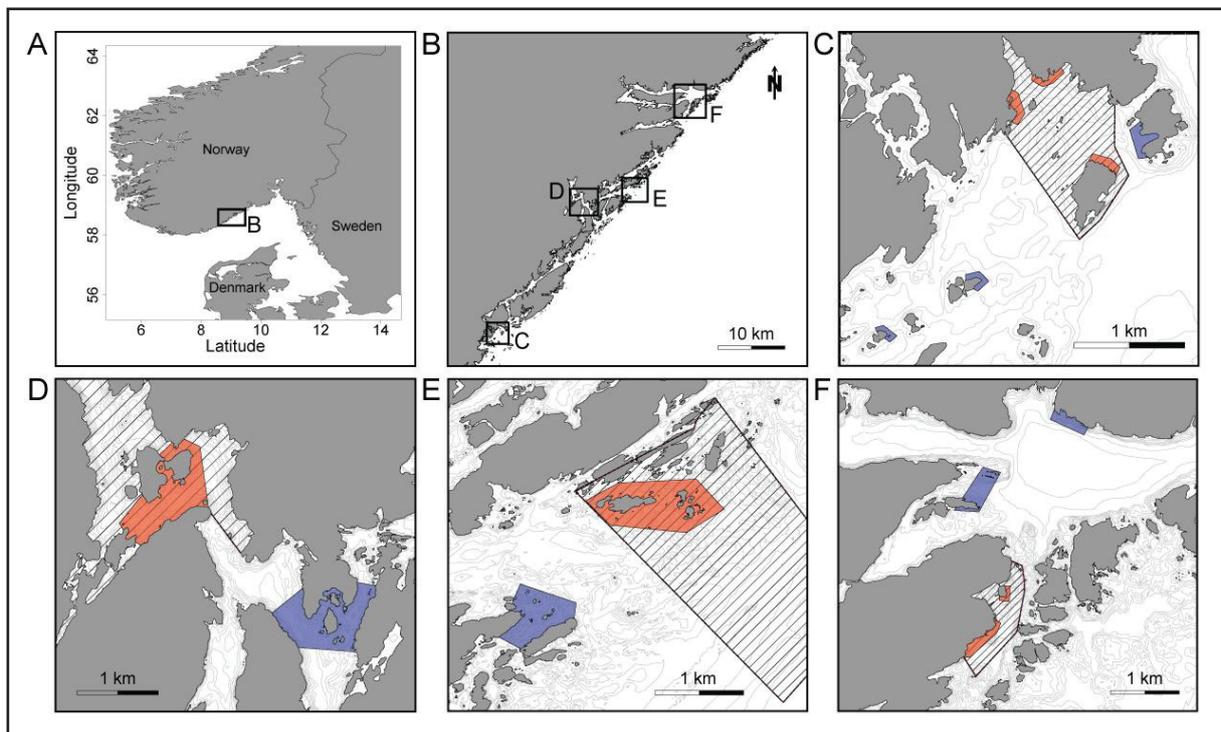


Figure 1: Study area. A: map of Scandinavia with map B outlined. B: All four areas outlined. C: Flødevigen. D: Tvedestrand inner. E: Tvedestrand outer. F: Risør. Dashed areas are the MPAs. Red areas are the areas of the MPAs used in the study. Blue areas are the control areas used in the study.

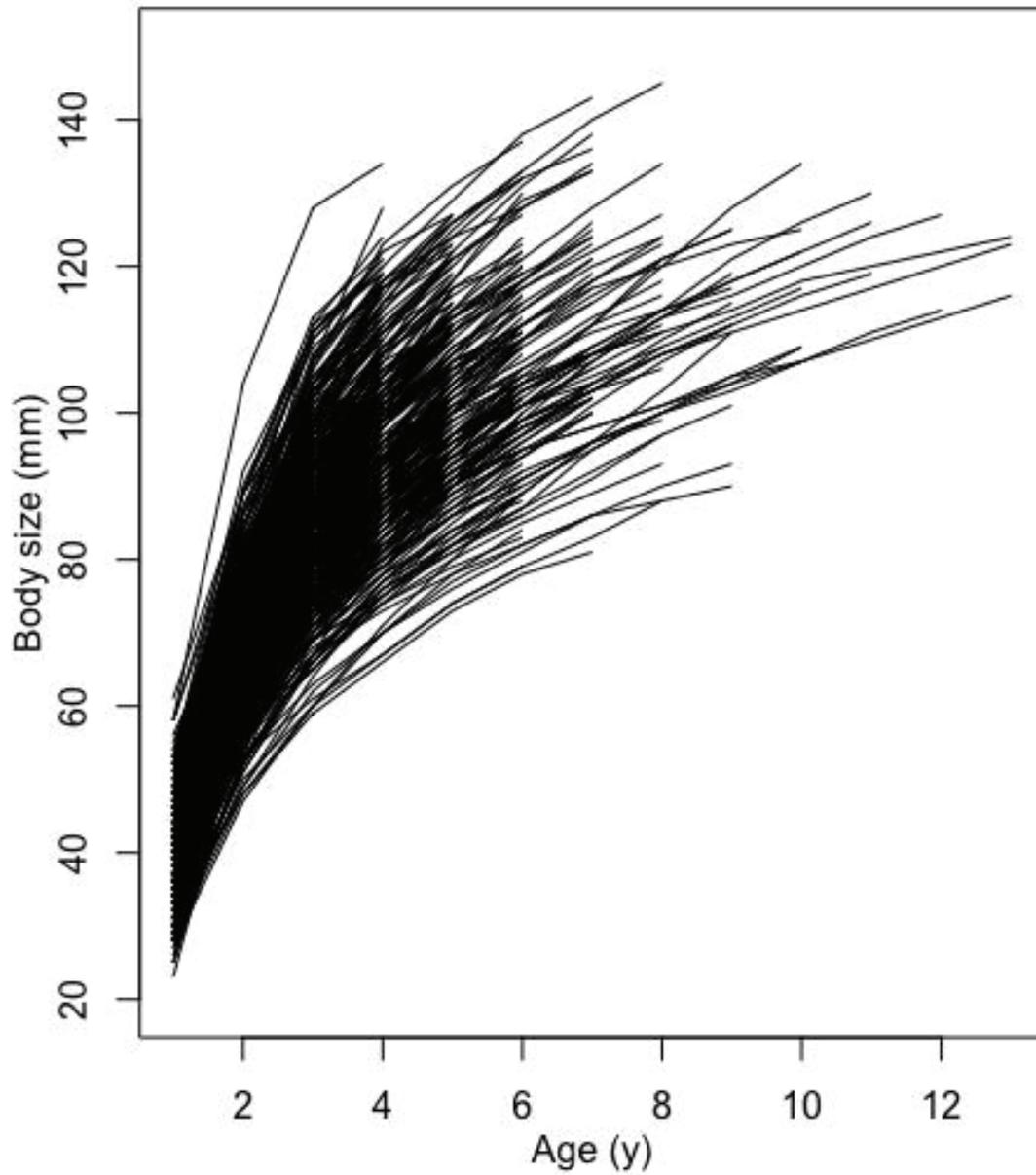


Figure 2: Individual goldsinny wrasse growth trajectories back-calculated from distances measured on otoliths.

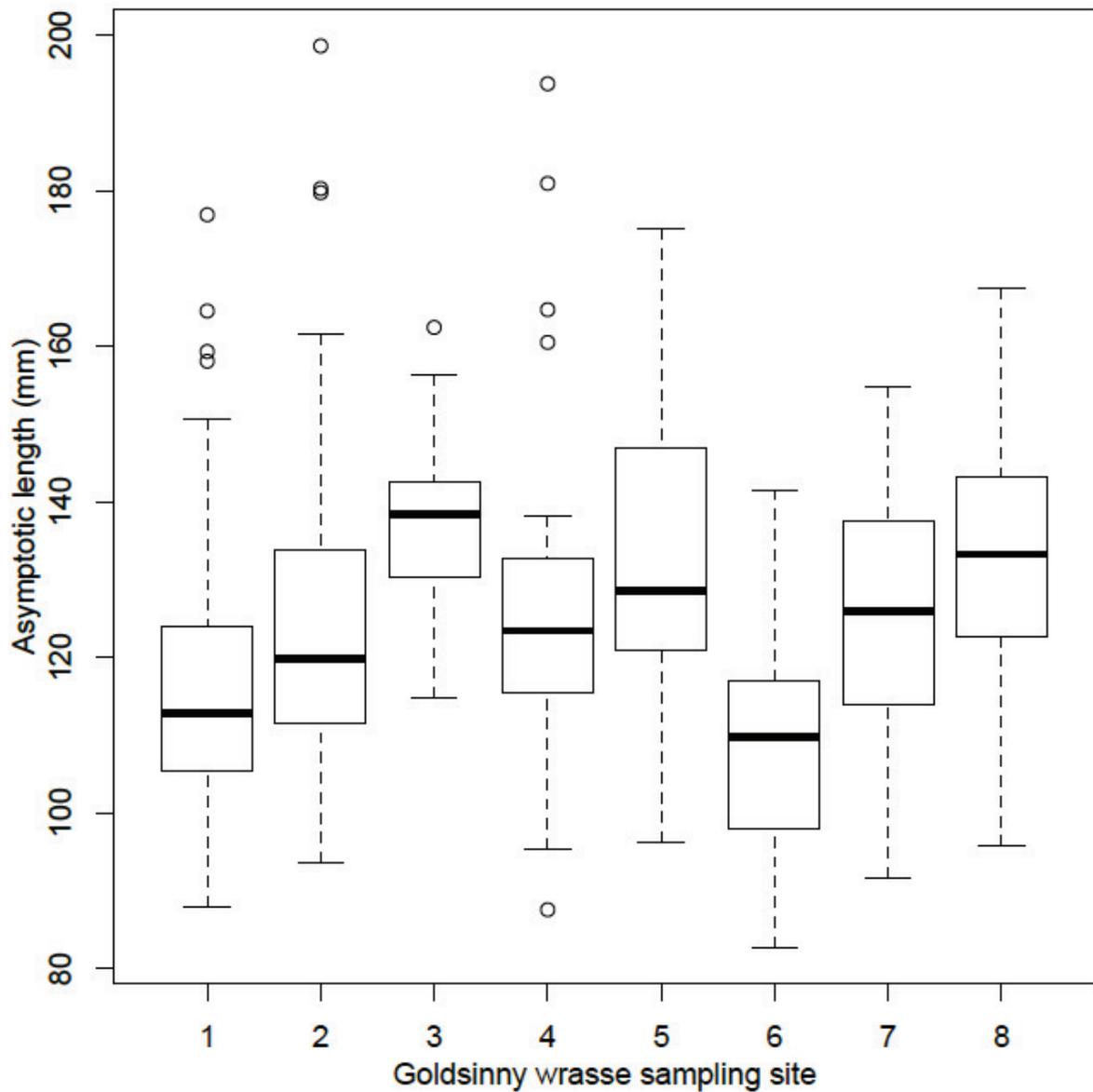


Figure 3: Goldsinny wrasse asymptotic lengths estimated by fitting von Bertalanffy growth curves to individual back-calculated lengths at age of fish sampled from four MPAs and neighbouring control areas along the Norwegian Skagerrak coast (Flødevigen control (1), Flødevigen MPA (2), Risør control (3), Risør MPA (4), Tvedestrand inner control (5), Tvedestrand inner MPA (6), Tvedestrand outer control (7) and Tvedestrand outer MPA (8)).

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