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 my 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

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Contents

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 presuably 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 as 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., Sørdalen, 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., Sørdalen, 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., Sørdalen, 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-Heikkila 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).
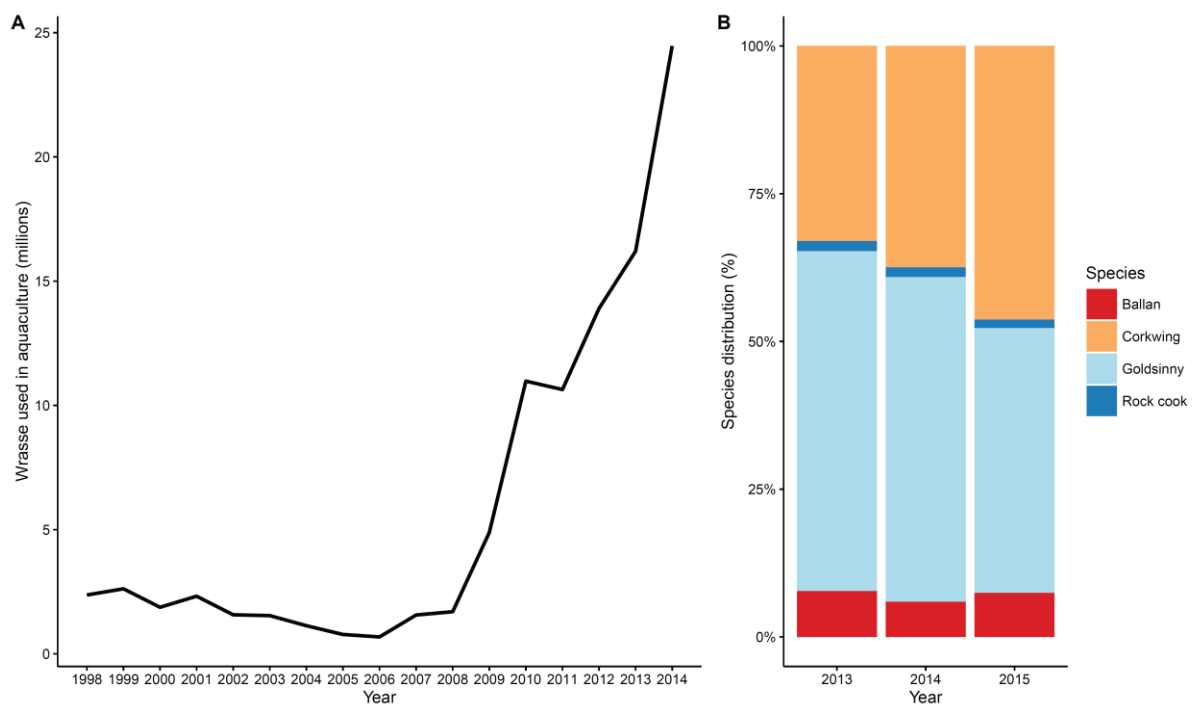
Figure 1:

A: The number of cleaner fish (including both wild caugth 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 caugth 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. Sørdalen. 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 Rijinsdorp 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 (Hillden 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).
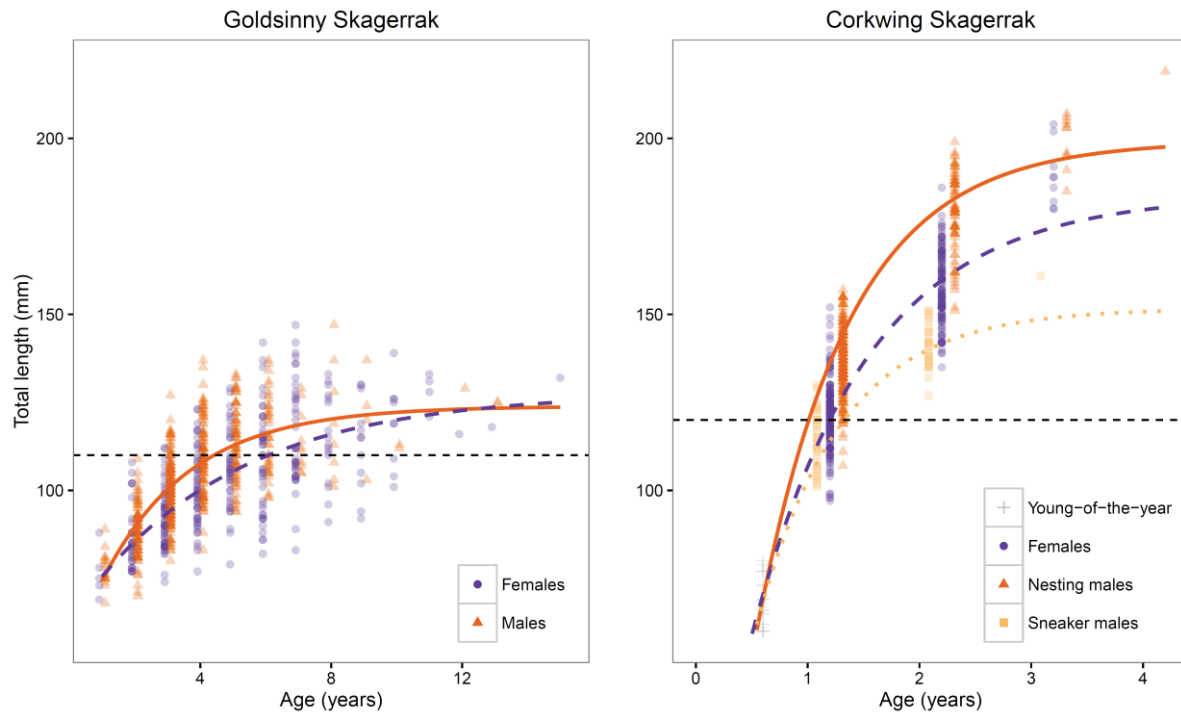
Figure 3: von Bertalanffy growth curves illustrating the different growth trajectories and lifespan between goldsinny (left) and corkwing (right) from Skagerrak populations (2013). The minimum size limit is indicated with the dashed horizontal line. The growth models are constructed using data presented 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.
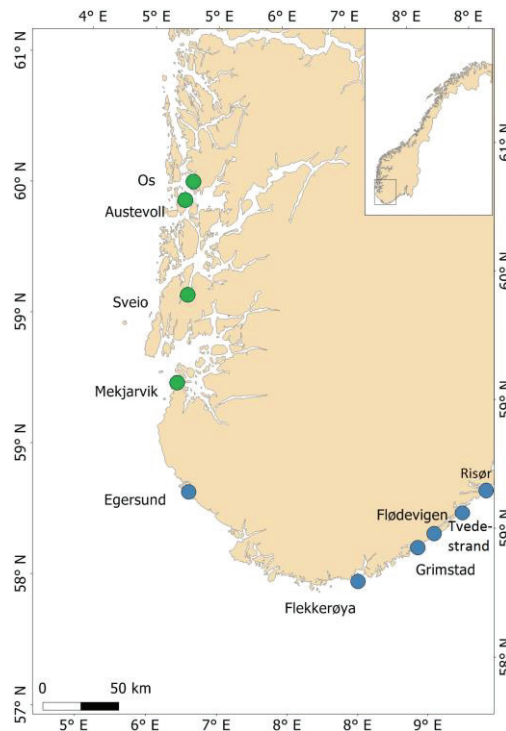
Figure 4: The study locations for this thesis. Circles with green fill represents the northern populations and blue the southern, as defined in paper I. Sampling for Paper I was conducted in all locations except for the two easternmost; Tvedestrand and Risør. The tagging experiment in Paper II was conducted 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.
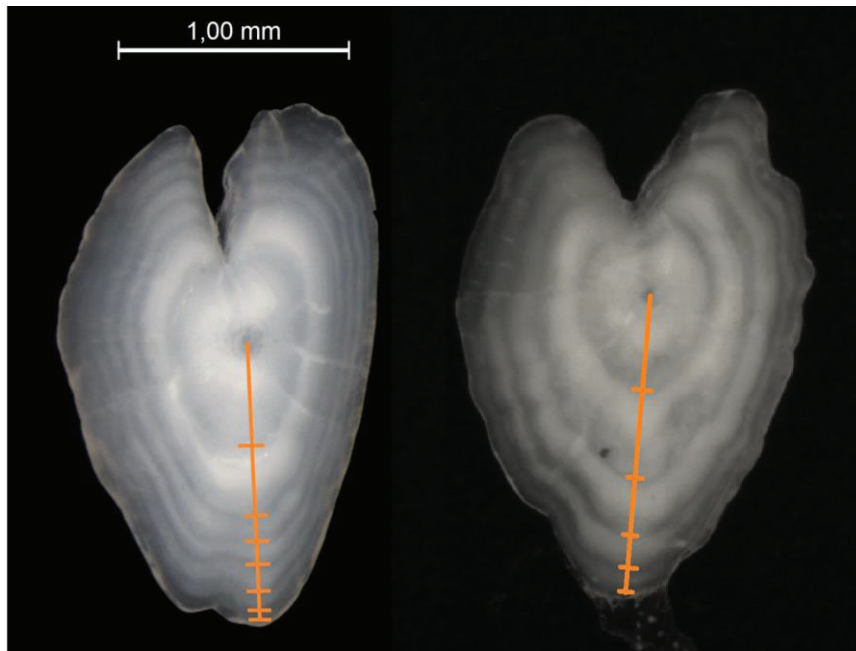
Figure 5: The sagittal otolith of a seven year old goldsinny (left) and a five year old corkwing (right). Summer growth increments (opaque zones) are interrupted by the shorter winter increments (darker bands).

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). Wrasses 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 base-line 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.
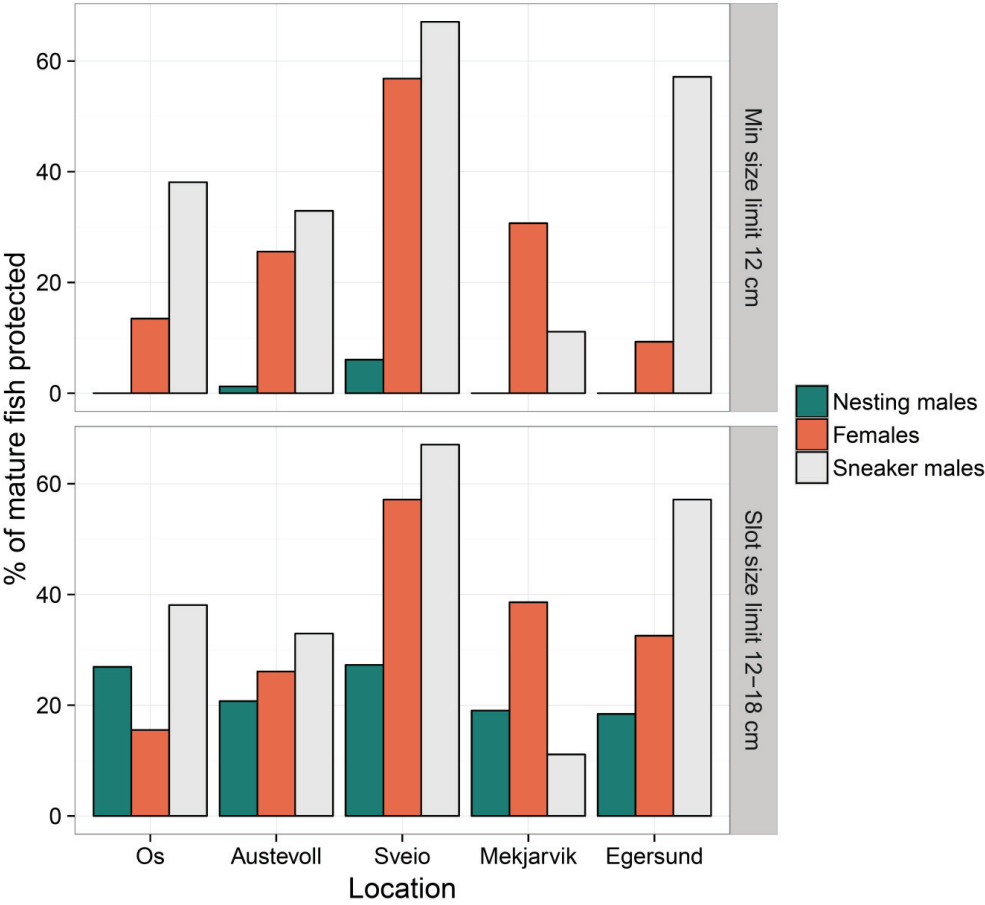

Figure 6: Comparison of the current size limit (12 cm; upper panel) with a slot-size limit (12-18 cm; lower panel) on the protection of mature nesting males, females and sneaker males. The data is size distribution from commercial and scientific fisheries (Austevoll) conducted in 2014 (Paper I).

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 resemblance 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 lumpsucker (*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-produsert-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 demonstrate 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.

Acknowledgements

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