Marine reserves and selective fishing shape mating behaviour, secondary sexual trait and growth in European lobster

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Preface

To my supervisors over the years, thank you Halvor Knutsen and Esben M. Olsen at the Institute of Marine Research (IMR) and University of Agder (UiA), for support, for believing in me and for giving me the freedom to pursue my own ideas, even though some did not turn out as expected. To Leif Asbjørn Vøllestad at the University of Oslo (UiO) for your time and patience, for encouragements and for regularly asking me how things are going. I also thank all the national and international co-authors for all your invaluable help. I have been fortunate to build my work on the unique lobster survey, for which I am very grateful to Even Moland and Esben M. Olsen. Thank you also to the fishermen in Arendal for helping me sample egg-bearing females for my first paper when I didn't think I would get hold of any more.

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Little did I know how this thesis would turn out when I first started on this journey. After failing with experiments and almost succumbed under the weight of laboratory work, I found inspiration in the work of Jeffrey A. Hutchings and Sherrylynn Rowe, who sparked my interest in the topic of the interaction between fishery selection and matings system. These perspectives have undoubtedly shaped the focus of my work.

My deepest gratitude goes first and foremost to Kim, first as my colleague then also as my best friend and father of our son. Thank you for bringing me so much inspiration, love and happiness, and for encouraging me to do my very best even when the days are long, and the energy is low. Countless hours have been spend discussing what exactly it is that drives us to do what we do, imagining a better world and then contemplating new ideas and projects to do. I'm grateful and proud to have you as my partner and I doubt I would have made it here without you and your help. I am also very thankful for the support from my family and friends for believing in what I do, even though I know you find my choice of profession a bit strange.

Lastly, I dedicate this thesis to my son, Julian and all other children who are the future stewards of the ocean. I sincerely believe you will do a better job than us.

Arendal, February 2019
Tonje Knutsen Sørdalen

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Paper I – IV and appendices

Summary

Well-functioning mating systems are perceived as vital for population growth rate and resilience to environmental change, but we know surprisingly little about the interplay between human-induced mortality and the mating systems of exploited marine species. Fishing and hunting can reduce densities, shift sex ratios and often targets individuals with the largest body size or with the most conspicuous characters (e.g. horns and claw). These traits tend to be sexually selected traits important for the outcome of competitive interactions and mate attraction. Thus, human harvest probably has profound, but not straightforward, effects on mating patterns and the strength and dynamics of sexual selection in many species. Marine protected areas (MPAs) are implemented worldwide with the aim of restoring exploited species and ecosystem functioning and they should also have the ability to conserve species' mating patterns and secondary sexual traits. In this thesis, I have empirically examined several aspects of the mating system in wild European lobster (*Homarus gammarus*) and how it responds to intensive fisheries selection, but also whether marine protected areas (MPAs) have the ability to rescue a species' natural mating patterns and secondary sexual traits targeted by the fishery. I have used both genetic analysis methods and morphological data from three lobster reserves on the Norwegian Skagerrak coastline and adjacent area open to fishing as control, and also explored the typical female fertilization pattern in United Kingdom (UK). In **paper I**, I sampled DNA from males and egg-bearing females in one of the lobster reserves and fished area across multiple years and compared paternity data for any differences in mating behaviour. The results confirmed size-assortative mating, with females' preference for males with a body size larger than their own, however, the size difference within each pair were much larger in the reserve than in the fished area (22.5% compared to 6.4% in the fished area). Two cases of multiple paternity were also found in the fished area. Male size (body and claws) strongly influenced male mating success, but only in the reserve as selection differentials on these traits were not significant in the fished area. Lastly, estimation of sexual selection gradients on male traits found the selection to be acting strongest on relative claw size (claw size relative to body size), rather than on absolute claw and body size. In **paper II**, I joined a paternity study in a fished region of the coast of UK where we found no incidence of multiple paternity on egg-bearing females and concluded single paternity to be the common fertilization pattern. In **paper III**, I show that legal-sized male lobsters have larger relative claw sizes inside MPAs compared to same sized in fished areas (up to 8.4% larger). There were no differences between areas for

females, which have smaller claws than males. This study is possibly the first to document the usefulness of MPAs in preserving a trait under strong sexual selection and under ongoing harvest selection in the same study system. In **paper IV**, I also found support for a positive MPA effect on body growth for legal-sized lobsters and most clearly for moult increment of females. It suggests that this may be caused by the catchability of lobsters in the trap fishery to be positively correlated with high growth rate and that lobster undergo intensive and selective fishing pressure against faster growing individuals. In sum, the findings in this thesis suggest that (1) selective fishing has the ability to weaken sexual selection with potential consequences for rates of fisheries induced evolution, (2) that MPAs can be highly effective in preserving sex-specific variation and phenotypic diversity and (3) that even small-scale MPAs can help maintaining the scope for sexual selection in a sedentary species with complex mating behaviour and life-histories such as the lobster.

List of papers

This dissertation is based on the following four research papers (published or manuscripts), which will be referred to in the following text by their Roman numerals.

I.   **Harvesting changes mating behavior in European lobster**
     Sørdalen, T.K., Halvorsen, K.T., Harrison, H.B., Ellis, C., Vøllestad, L.A., Knutsen, H., Moland, E. and Olsen, E.M. 2018.
     in *Evolutionary Applications* 11(6): 963-977 (doi:10.1111/eva.12611).

II. **Genotype reconstruction of paternity in European lobsters (*Homarus gammarus*)**
     Ellis, C.D., Hodgson, D.J., André, C., Sørdalen, T.K., Knutsen, H. and Griffiths, AG.F. 2015.
     in *PloS One* 10 (11): 1-14 (doi:10.1371/journal.pone.0139585).

III. **Marine reserves rescue an important secondary sexual trait in male European lobster**
     Sørdalen, T.K., Halvorsen, K.T., Vøllestad, L.A., Moland, E. and Olsen, E.M.
     Manuscript.

IV. **Improved body growth of lobster inside marine protected areas compared to intensively fished areas**
     Sørdalen, T.K., Halvorsen, K.T. and Olsen, E.M.
     Manuscript.

1. Introduction

1.1 The interplay between harvesting, marine protected areas and mating systems

Oceans and coastal ecosystems are dynamic systems, but human activities are causing unprecedented changes to the natural seascape at a pace much faster than species can keep up with (Halpern *et al.* 2008). The majority of commercially (Worm *et al.* 2009) and some recreational (Cooke and Cowx 2004) fished species are now regarded as fully- or overexploited with many examples of declining and collapsed stocks (Jackson 2001; Myers and Worm 2003; Hutchings and Reynolds 2004). Fishing can be a strong selective force and have been shown to shift phenotypic distributions and drive evolutionary change on contemporary timescales (Heino *et al.* 2015 and references therein). Fisheries selection for smaller body size and earlier maturity has been extensively studied, but fishing may also be selective on behaviour, morphological and physiological traits. For example, on elongated bodies and swimming speed (Hamon and Foote 2005; Alós *et al.* 2014), slower growth rate in trap fishery (Biro and Post 2008; Biro and Sampson 2015) and behaviour along the boldness/shyness axis (Biro and Sampson 2015; Diaz Pauli *et al.* 2015; Twardek *et al.* 2017). There is also an increasing awareness that harvesting may interfere with sexual selection and mating patterns when densities, size structure and sex ratio is altered (Parker 1992; Rowe and Hutchings 2003), which is typical for many fisheries (Zhou *et al.* 2010). When population densities are reduced, individuals may use more energy and time finding mates, which in turn can increase risk of predation and starvation or limit the opportunity to mate at the optimal time, habitat, environmental conditions, or simply with the preferred mate (Kokko and Rankin 2006). This may reduce populations productivity and their resilience to environmental stochasticity (Møller and Legendre 2001; Rowe and Hutchings 2003). Moreover, harvesting has been shown to select against sexually selected characters in males, such as large body size or the size of weaponry (e.g., horns, antlers and claws); traits which are important in mate choice and intraspecific competition (Wilber 1989; Swain *et al.* 2007; Woolmer *et al.* 2013). Sexually selected characters' positive relationship with reproductive success may be even stronger than for traits solely subjected to natural selection. This is because the slope of reproductive success on male body size is higher than that of females', since more females than males will have the opportunity to mate (Kingsolver *et al.* 2001).

In the context of fisheries-induced evolution, modelling has shown that size-selective fishing may erode the size variation needed for sexual selection to work properly, and that

fisheries-induced evolution would be accelerating faster compared to a scenario assuming random mating with respect to body size (Hutchings and Rowe 2008). Nevertheless, how the strength and direction of sexual selection is affected by fishing is not straightforward (Hutchings and Rowe 2008; Urbach and Cotton 2008; Lane *et al.* 2011).

As a response to the increasing pressures on our marine ecosystems, a growing number of marine protected areas[1] (MPAs) are implemented around the globe and have become an important tool for conservation and fisheries management (Hastings and Botsford 2003; Lester *et al.* 2009). MPAs may prohibit all fishing activity (no-take area) or they can be partially protected, banning landing of specific species and/or types of fishing gear to be used. In addition, how fishers comply by these rules and how well the areas are enforced are naturally affecting the effectiveness of MPAs. If well enforced and designed in terms of quality of habitat and size, MPAs can be a valuable aid in protecting biodiversity and fragile habitats, species and populations. It is now well documented that MPAs generally have positive effects on the number, biomass, size and age structures of harvested species (Halpern 2003; Russ *et al.* 2006; Claudet *et al.* 2008; Lester *et al.* 2009; Baskett and Barnett 2015). MPAs can also provide benefit to local fisheries yield through spill-over of juveniles, adults and export of pelagic eggs and larvae to surrounding areas (Goñi *et al.* 2006, 2010; Harrison *et al.* 2012; Lorenzo *et al.* 2016; Port *et al.* 2017). Through these mechanisms, MPAs may act as a buffer against fisheries-induced evolutionary changes and help preserve genetic diversity (Berkeley *et al.* 2004; Baskett and Barnett 2015). Thus, in addition to its utility in conservation and management, MPAs can be particularly valuable as reference systems for studying natural ecological processes and population dynamics. Contrasted against similar areas open to fishing, we may also gain insights in how harvesting interfere with ecology and evolutionary trajectories (Gell and Roberts 2003). When a no-take MPA is established, the upheaval of selective fishing is expected to restore trait distributions towards the direction of pre-fishing condition inside the area, provided that enough genotypic variation remains. Beyond the many examples of improved size and age structure (e.g. Claudet *et al.* 2008; Moland *et al.* 2013; Fidler *et al.* 2018) aquatic protected areas have been shown to house more naïve fish (Januchowski-Hartley *et al.* 2013; Goetze *et al.* 2017), fish with slower flight response (Kennedy Rhoades *et al.* 2018) and more attentive male fish with better parental care (Sutter *et al.* 2012). Lastly, since traits are a product of genotypes and the environment, the trait distribution in both fished and unfished populations will be shaped by the interaction between natural and human-induced selection

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[1] Hereafter I will use the terms marine protected areas (MPAs), protected areas and reserves interchangeably.

and phenotypic plasticity. Protection from fishing may therefore also affect traits indirectly if the environment is altered, for example through changes to inter -and intraspecific competition and interactions, mortality and habitat quality.

Even though the concept and challenges associated with harvesting effects on mating systems have been recognised long ago, the interaction between sexual selection and selective fishing is poorly studied empirically in the marine environment. Reasons for this lies partly in the difficulties in designing a study that have the means and the power to obtain direct or indirect observations of cryptic mating events. Therefore, elucidating mating patterns in an open ocean system would need refined methods. For instance, pairs of MPAs and fished areas may be highly valuable as field laboratories for understanding how fishing affects mating behaviour and traits under sexual selection, or perhaps equally important, for assessing whether MPAs can play a significant role in preserving functional mating systems and diversity in sexually selected traits. Furthermore, the rapid development in DNA sequencing technology and analytical methods have alleviated some of these challenges by allowing us to study individual mating success though parentage assignments techniques. Some species may be particularly good models for such studies. For example, many decapod crustaceans show strong sexual dimorphism (e.g. body size, claw size) and support fisheries worldwide. They also come with the advantage of long periods of maternal care that allow us to simultaneous collect DNA from mother and offspring, which makes large-scale parental studies in open systems a lot more achievable.

The overarching goal of my doctoral thesis was to elucidate potential effects of harvesting on the mating system of the of the highly valued and overexploited European lobster (*Homarus gammarus*) by characterizing mating patterns and to identify morphological traits under sexual selection and fishery selection. Most of the work is done in a framework of protected areas (hereafter, MPAs) particularly designed for lobster and in control areas open to fishing on the Skagerrak coast. I address how selective pressure caused by human harvest (size-selective fishing) can exert maladaptive changes to these patterns and potentially drive evolutionary trait-changes, but also how management options can mitigate such unintended consequences. In the next part of the introductory of the thesis I provide a description of the study species, including mating behaviour and the fishery in Norway, with the intend to contextualize the studies presented in each paper. In the last part of the introduction I present the objectives of my work, and briefly how I address them in each paper. In section 2, I describe the study area and main methods used. Lastly, in section 3, I summarize the main results and discuss the implications of the findings in light of fisheries and conservation management with

perspectives on the role of MPAs in preserving traits under pressure by human-induced selection.

1.2 The biology of European lobster

The European lobster (Figure 1) is a large marine decapod crustacean of the family Nephropidae (clawed lobsters), which also includes the American lobster, *H. americanus* (Milne Edwards, 1837). The distribution range of European lobster cover much of the coastal shelf seas of the eastern North Atlantic from Morocco in North Africa to arctic Norway, only bound by the Black sea and the Baltic Sea (Triantafyllidis *et al.* 2005). Unlike other species of lobsters, adult European lobster do not move great distances. Instead they are stationary once they settle into a suitable habitat and typically live within limited home ranges (~0.02 km^2) (Moland *et al.* 2011; Skerritt *et al.* 2015). The larvae, on the other hand, have a pelagic phase of 1-2 months before settlement with potential to travel 10 - 100s of kilometres with currents, suggesting considerable dispersal capacity and connectivity among populations (Huserbråten *et al.* 2013; Wahle *et al.* 2013). However, a recent population study found no spatial genetic structure throughout the species' range, but only a weak differentiation between lobsters from larger regions of the Swedish Skagerrak and the Atlantic areas to the west, with the population in Norway being a mix of these two (Ellis *et al.* 2017).

The European lobster is solitary and nocturnal and usually spend daylight hours hiding in shelters under rocks, boulders or borrows in sediments down to 60 meters of depth but may be found much deeper. They have highly developed sensory organs on their legs to detect food in the absence of light. Juvenile lobsters are mostly suspension feeders as they live completely hidden during juvenile years, whereas adults are mostly scavengers and predators on fish and a variety of ground dwelling invertebrates like molluscs, crabs, bivalves and worms (Wahle *et al.* 2013). Lobster can also cannibalise on injured or newly moulted animals at all stages in their life cycle and will eat their old shell after moulting to reabsorb much needed calcium.

Growth. Like all crustaceans, the lobster needs to shed the outer shell (exoskeleton) and replace it with a new one in order to grow; a no-linear growth process called moulting. The growth rate is influenced by two elements: how much the animal grows from one moult to the next (moult increment) and the time interval between moults. Generally, younger adults increase more in size than older lobster, and males more than females. Juveniles can moult several times a year, whereas adults usually moult once or twice every year or once every two-three years, especially when females are carrying eggs because the egg-period inhibit moulting. Water temperature and food supply are some other known determinants that

can influence the moulting schedule and growth rate (Waddy and Aiken 1995). After the old is replaced with a new soft shell, the it must remain in hiding for a couple of weeks to avoid predation until the shell is hard enough to yet again function as body armour.

Figure 1. Study species, the European lobster (*Homarus gammarus*). Photo by Tonje K. Sørdalen.

Males and females can live to become 40 - 70 years or older, respectively, although age determination is difficult to assess with certainty in many crustaceans (Sheehy *et al.* 1999). Because of the variable growth rate, lobsters recruiting to the fishery may consists of as many as seven year classes (Sheehy *et al.* 1999). The longevity and the indeterminate growth allow them to reach impressive with only negligible senescence (Elmore *et al.* 2008). The largest specimen ever recorded (from a recovered crusher claw of 360-370 mm in Skagen, Denmark) was estimated to be a male of 650 mm total length, corresponding to a weight of 8.4-9 kilogram (Wolff 1978). Large lobsters have very few enemies other than a few big fishes, octopuses, otters and humans. A recent study has found that the lobster can produce a low-frequent buzzing sound of narrow band width, a range that corresponds with sound sensitivity in octopuses. Sound production may be used as warning signal but perhaps also be a means of communication between lobsters since they have receptors for low-frequent vibrations (Jézéquel *et al.* 2018).

Sexual dimorphism and maturation. Estimates of size at the onset of sexual maturity varies from differences in morphological, physiological and functional indices of maturation (Wahle *et al.* 2013). The timing of maturation may also depend on summer temperature and would most likely differ throughout the geographic range (Wahle *et al.* 2013). On the east coast

of Scotland, the size at maturity has been estimated to be 79- and 80-millimetres carapace length for females and male respectively, based on morphologic change in the relative growth between the body size and claw/abdomen (Lizárraga-Cubedo *et al.* 2003). In Ireland, female physiological maturity by examination of ovaries has been estimated to be 92.5-96 mm carapace length (Tully *et al.* 2001). Neither female nor male maturity schedules have been investigated in wild populations in Norway.

Relative growth in crustaceans, that is the rate of development of one part of the body relative to another, or the whole body, is useful in studies of the development of primary or secondary sexual characters. It can also inform about the emergence of physiological (i.e., ability to produce gametes), morphometric (i.e., full expression of secondary sexual characters), and functional (i.e., ability to mate and spawn) maturity when the size relationship of a body part changes relative to a reference variable (i.e. the whole body) (Émond *et al.* 2010). Adult lobster has dimorphic claws; one is a major molar-toothed (crusher) claw and the other is a minor incisor-toothed (cutter) claw. The claws have dual functionality being both tools used in foraging, and as weapons in male-male conflicts (armaments) and a signal of attractiveness towards females (ornaments) (Elner and Campbell 1981; Atema 1986). When approaching maturation, males begin to grow larger and heavier claws than females whereas the abdomen of females becomes proportionally broader to accommodate more eggs (Templeman 1935b; Mariappan, P., Balasundaram and Schmitz 2000; Émond *et al.* 2010). In females, the first pair of swimmerets (pleopods), called gonopods, are soft and feathery whereas in males they become enlarged and rigid and are used for transferring spermatophores during intercourse. Thus, the difference between males and females in allometric enlargements of claws and abdomen, and the modified swimmerets, represent sex-specific investment in secondary sexual characters that results in a clearly visible sexual dimorphism. A recent study on antenna morphology have also discovered sexual differences in size and distribution of the aesthetascs on antennas, a specialized organ used to determine concentration and direction of smell (Skog 2009a).

1.3 Mating system of clawed lobster

Lobster are renowned for their complicated sex life. Some 100 million years of evolution have provided ample time to refine techniques for finding mates, coerce male aggression and to court (Bracken-Grissom *et al.* 2014). Much of what we know about lobster mating system and mating behaviour derives from studies on the American lobster, but because of the strong similarity between the two species, I will use references from both species.

Female mate choice and courting. Females usually mate in a males' shelter in summer just after molting and all observations both in field and laboratory show that females, not males, make the initial mate choice (Karnofsky *et al.* 1989b; Debuse *et al.* 2003). In the weeks before moulting, a female American lobster will evaluate potential mates by making frequent visits around the neighbourhood and approach shelters of a male of interest. She is looking for a dominant male that has acquired a high-quality shelter and she is attracted by the scent of his urine-borne chemical cues which he broadcast by fanning his swimmerets from inside the shelter (Atema and Cowan 1986). The urine plays an important role as chemical communication in clawed lobster. It contains pheromones that likely convey information about level of aggressiveness or fighting abilities, sexual receptivity, sex and moult state of the signaller, although the actual molecules have not been described (Atema and Cowan 1986; Bushmann and Atema 1997; Breithaupt and Atema 2000). The urine-pheromone mix may advertise at least some important aspects of the males' quality. The urine is also critical for the establishment and maintenance of social dominance status and sexual behavior of both sexes (Karavanich and Atema 1998; Skog *et al.* 2009). The higher the dominance order of males, the more often their shelters are checked by courting females (Cowan and Atema 1985). Lobsters are solitary by nature and highly aggressive towards one another. Males are even threatening the safety of female during mating if the male aggression is not 'disarmed' prior to and during mating. The trick to reduce this dangerous aggression lies in female sex pheromones in the urine and is critical in ensuring successful courtship and normal mating behavior (Atema and Cobb 1980; Skog 2009b). If the female finds the male and his shelter to be suitable, both as a father of her offspring and as post-moult protector, she will make regular visits over the next days or weeks to deposit her urine scent until he invites her in (Atema *et al.* 1979; Bushmann and Atema 1997). She moults in his shelter, followed by one ritualized mating act (see Atema and Cobb 1980 for spicy details). Over the next week the bonded-pair continue to cohabitate, a strategy believed to increase successful pre- and post-copulatory guarding of the soft-shelled female (Atema *et al.* 1979; Karnofsky *et al.* 1989b,a; Karnofsky and Price 1989b; Cowan and Atema 1990). She will stay in the shelter until her new and soft exoskeleton has hardened and she can fend for herself.

Mating and spawning events are separated in time and space as the spermatophore are stored in a seminal receptacle (sperm storage) before fertilizing the eggs (Aiken *et al.* 2004). The sperm remains viable in the storage of very large females for as long as three years and can, if enough sperm, fertilize two clutches of eggs (Waddy and Aiken 1986). Until quite recently, one of the greatest mysteries of lobster reproductive biology, puzzling scientists more

than hundred years, was understanding whether the fertilization happened internally or externally and how sperm escape from the storage of the female. The fact that the stored, immotile spermatophore is located farthest away from the opening of the storage under an impermeable sperm plug that do not change before, during and after spawning (and is only removed by moulting), have made the ejection of the stored sperm difficult to explain. At spawning, which usually occur the following spring, sperm leaves the storage via two grooves located at the side of the main opening, bypassing the sperm plug and externally fertilize the eggs as they are extruded onto the tale (Aiken *et al.* 2004). Females stores the inseminated eggs on the ventral side of her body until they hatch 9-11 months later when temperature are more favourable (Agnalt *et al.* 2007). Without a sperm supply, eggs are still extruded but are lost within a few weeks.

Although the description of the mating cycle above is the general pattern, the mating habits of clawed lobster are flexible and it is not uncommon that larger females are able to spawn in consecutive years, either by fertilizing two egg-batches with same sperm supply, or through intermoult mating (Waddy and Aiken 1986; Comeau and Savoie 2002). Intermoult mating is a beneficial strategy when a large female can skip a moulting but has used up the sperm storage and need to receive new sperm to fertilize her eggs. It is also thought to be useful for females living in areas where males are more difficult to find (Waddy *et al.* 2017).

Male mating capacity and sperm limitation. Males of clawed lobsters are known to mate with several females in a mating season (polygyny) and there is little evidence to suggest that males are particularly selective with whom they mate with. Multiple females of American lobster have been seen regularly checking in on a dominant males' shelter when he is cohabiting with a female and as soon as she leaves, a new female move in (Cowan and Atema 1985). For lobsters, bigger bodies translate into higher fecundity in both sexes. In females, egg production increases exponentially with increasing female size and large male decapods have greater sperm storages, are capable of tailoring ejaculate load to the size of the female, and replenish depleted sperm faster than smaller males (Agnalt 2008; Jivoff 1997; MacDiarmid *et al.* 1999; Kendall *et al.* 2001; Gosselin *et al.* 2003). Contrary to eggs, however, sperm are produced all-year-round. A recent study has demonstrated impressive mating capacity in mature males of American lobster, where some males were able to inseminate 30 to 54 females in one mating season and neither sex showed indication of being sperm depleted. Almost all females spawned and carried full clutches of fertilized eggs (Waddy *et al.* 2017).

Despite this recent finding there is a growing concern that the population productivity of many crustaceans, including clawed lobster, can be constrained by sperm limitation; a

scenario where a population in sum has too little sperm to fertilize all the eggs (Fogarty and Gendron 2004; MacDiarmid and Sainte-Marie 2006; Pugh *et al.* 2013; Wahle *et al.* 2013). Fisheries susceptible to sperm limitation are those managed by male-biased or male-only strategies, which is common for most crabs and for many lobster fisheries where the focus is to protect mature or egg-bearing females from harvesting (Montgomery and Liggins 2013; Smith and Jamieson 1991; Orensanz *et al.* 1998). If the fishery reduces the density and remove large males and creates a sex ratio imbalance, the mating behavior may change (Fogarty and Gendron 2004). It has been suggested that large and popular males may exhaust their sperm reservoirs after multiple copulations in a mating season with the result that females receive inadequate amount of sperm (Gosselin *et al.* 2003, 2005). Alternatively, or concurrently to the above scenario, females may turn to smaller males of lower quality if large males are not available. Multiple paternal fertilizations have been documented among individual egg-bearing females in heavily fished population of American lobster and though to be the result of individual females mating with several smaller males in attempts to avoid sperm limitation (Gosselin *et al.* 2003).

Competition and dominance. Clawed lobster of both sexes establish and maintain dominance hierarchies. Aggressive males need to pursue victories to achieve reproductive success because it is dominance and access to good shelter that are the determining factors for male attractiveness towards females (Karnofsky and Price 1989a). Male dominance is also directly correlated with mating success in aquariums (Atema *et al.* 1979; Cowan and Atema 1990). This results in strong male-male competition in lobster. Both in field and aquariums the highest ranking and preferred ("Alpha") male have been seen regularly patrol and evict other males from their shelters (Atema 1986). Observations also show that dominance in lobsters is almost entirely size dependent but that males have a higher dominant order, even if females are slightly larger (Atema and Cobb 1980; Atema 1986). The strategies in maintaining dominance order differ between the sexes and also here urine-borne chemicals are the underlying mechanisms for signalling and recognition of dominance (Karavanich and Atema 1998). Males that lose a fight will remember and try to avoid the winners in future encounters (for a couple of weeks) but aggressively fight with new unfamiliar opponents, even if they are dominant by size (Karavanich and Atema 1998; Skog 2009a). Females that lose a fight, on the other hand, will avoid encounters with a new dominant regardless whether they are familiar or not (Skog 2009a). Both sexes will know its place, but females identify, and abide by, dominance status more so than males.

Species with strong male competition invest in ornaments or weapons with the purpose

to ensure a winner in contests or display. In lobster, larger claws increase male competitive abilities and are a better predictor of victories than body size (Atema and Cobb 1980; Elner and Campbell 1981; Van Der Meeren and Uksnøy 2000). Thus, individual claw size is likely important when establishing dominance. The sexual dimorphism in claw size with the onset of maturation support this argument.

1.4 The European lobster fishery

The European lobster is one of the most valuable and sought-after species in Northern Europe's commercial and recreational fisheries. In Norway, the fishery has a long history as one of the most popular recreational fishing activities in coastal communities and used to be an important source of income for many fishermen. However, the lobster catches in Norway declined by 65 % from the 1950s to 2000s, and is today at the lowest record in history with no sign of recovery (Pettersen *et al.* 2009). Although the reason for the collapse is not known for certain, there is a consensus that it is due to increasing fishing pressure and highly ineffective regulations (Agnalt *et al.* 1999; Pettersen *et al.* 2009). The catches today have little economic value. The fishery is unreported and unregulated, and the total yearly catch is estimated to be 14 times higher than official landings (Kleiven *et al.* 2012).

In response to declining catches, a variety of management measures have been adopted and particularly in recent years. The fishery is regulated by closed season and a prohibition on fishing with exception from 1 October to 30 November on the Skagerrak coast and to 31 December in northwest. All participants must be registered prior to opening of the season (from 2017). Lobster can only be caught by one type of gear (pots) which are usually baited with mackerel (salted and rotten) and Ballan wrasse. After 2008, commercial fishers are allowed to fish with a maximum number of 100 pots, whereas recreational fishers are limited to 10 pots per person and boat. It is required that pots must be fitted with two circular escape vents (60 mm in diameter) to reduce capture of undersized individuals and a cotton tread must be installed in agreement with specifications (from 2017) to prevent ghost-fishing if lost. The minimum legal-size limit was raised to 250 mm total length (*TL*) in 2008, corresponding to 88.6- and 86.9-mm carapace length (*CL*) for males and females respectively (Paper III). In 2017, a maximum size limit at 320 mm *TL* (~116 mm *CL*) was introduced for lobster caught along the Skagerrak coastline (Kleiven *et al.* 2017). A ban on the harvest of egg-bearing females was implemented in 2008, which is a common regulation in heavily exploited crustacean populations. The scientific rationale for such a ban is to directly increase egg production and increase the population productivity by allowing females to release their larvae

before being harvested. Approximately 50% of the legal sized female lobster are protected by the ban (Figure 2).

Being one of the most popular recreational fishing activities in coastal communities, the declining stock has sparked great concern and interest (and debate) from both fisheries' management and conservationists to understand what prevents a population recovery and how small-scale MPAs can help restore lobster populations.
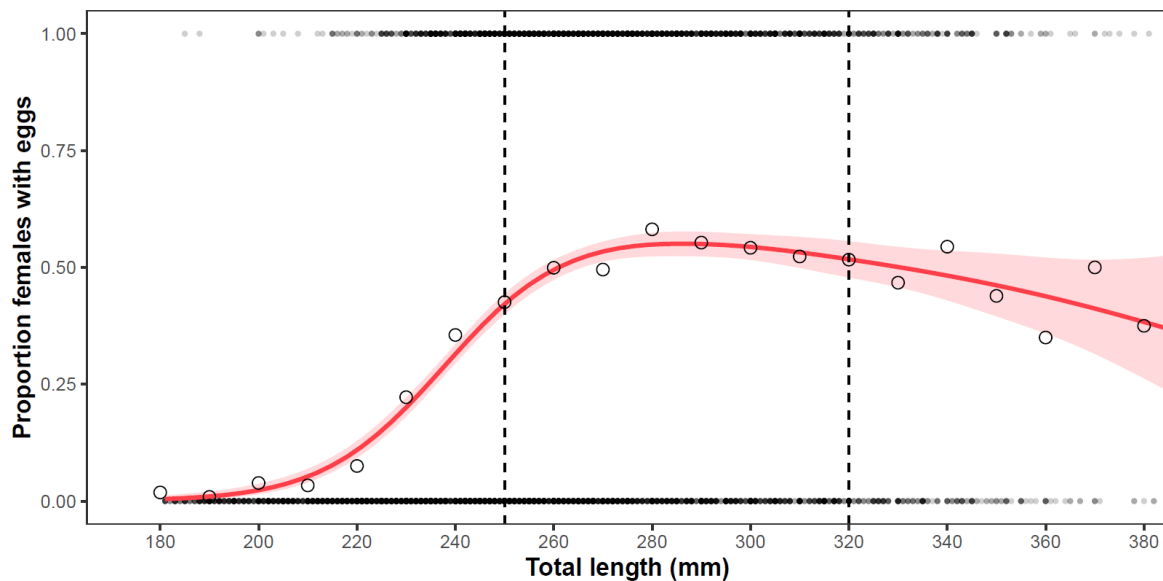

Figure 2. The proportion of females bearing eggs as a function of total length. Data is from the lobster survey in the three regions 2006 – 2018, all areas combined (n = 5577 females). A binomial gam smoother with P-splines is fitted to the data, with shaded area showing the 95 % confidence interval around the estimate. The circles show the observed proportion of egg-bearing females per 10 mm length classes, starting at 175 mm – 185 mm. The dashed vertical lines illustrate the harvest slot; minimum size limit of 250 mm (~87 mm *CL*) and the newly implemented maximum size limit of 320 mm (~116 mm *CL*), respectively.

1.5 Outline of the research

The research topics and specific objectives addressed are as follows:

1. **Female mate choice and determinants of male mating success (paper I).** In laboratory studies, it has been documented that female clawed lobsters preferentially choose a large male as mate and that large claw size is important when establishing dominance status. Inside MPAs on the Skagerrak coast of Norway, lobsters have rapidly become more numerous and larger (Moland *et al.* 2012), which increases the scope for mate choice. In the areas with

high fishing pressure, larger males can be few and far between. Thus, my first objective was to compare mate choice and mating patterns in and outside an MPA. I employed a parentage assignment with four years of data sampled inside both areas in order to explore to what extent there is a consistent size difference between mated pairs (size-assortative mating pattern), and if the mating pattern differ between the contrasting areas. I also compared the strength of sexual selection on body size, absolute claw size and relative claw size (adjusted for body size).

2.   Female fertilization pattern in a fished population (paper II). Female fecundity increases with increasing body size and studies on other crustacean species have found the ejaculate load to be size-specific. In an intense size-selective, or male-biased fishery, populations may become sperm limited when the total production of male gametes are not able to fertilize the maximum egg capacity produced by females. Multiple female mating with several smaller males could be indicative of a sperm limited population. The objective of this study was to obtain information of paternity in lobster by estimate the frequency of multiple paternity and thus clarify the typical fertilization pattern in lobsters from an important regional fishery in the United Kingdom subjected to hatchery stocking.

3.   The effect of protection on a sexually selected trait under harvesting selection (paper III). Secondary sexual characteristics such as horns, antlers and claws are the results of strong sexual selection and known to be important for the outcome of competitive interactions between males, and for female attraction. A recent study (Moland et al. *in press*) shows fisheries selection to be strongest on claw size (adjusted for body size). Since this trait was identified to be under the strongest sexual selection in males (Paper I), my objective was to investigate whether MPAs could rescue this trait from fishery selection, which should be evident as relatively larger claws in side MPAs vs. fished areas. To this end, I analysed two years of claw and body size measurements of lobsters caught in three lobster MPAs and their respective fished control areas on the Skagerrak coast of Norway.

4.   Growth of lobsters in fished and protected areas (paper IV). Growth rate is a key trait for lobster reproduction since large size is correlated with better mating opportunities and fecundity. Recent experimental studies report evidence for that crustacean and fish with high growth rates and/or aggressiveness are more prone to be captured with passive gears. As such, the intensive fisheries for lobsters on the Skagerrak coast could be depleting fast growing individuals, while MPAs may serve as refuge for all phenotypes, including fast growth. My objective was to test this prediction by analysing 12 years of capture and recapture data from

the three pairs of MPA-fished areas on the Skagerrak coast (same sites as in 3), specifically by comparing annual moulting probability and moult increments adjusted for body size.

2. Methodological approaches

2.1 Study areas and sampling

In September 2006, three small-scale MPAs were established along the Norwegian Skagerrak coast to investigate if they could be used to rebuild the local lobster population and to assess the effects of lobster fishing. The three MPAs in Aust-Agder, Vestfold and Østfold county (Figure 3), have regulations that prohibit capture of lobster and use of fishing gears such as fyke nets and pots/traps. Fishing with hook and line is permitted. To monitor the effects of protection, all MPAs have one nearby area open for fishing as a control.

Lobster was caught with pots as part of the annual standardized capture–mark–recapture sampling programme conducted by the Institute of Marine Research (IMR). All individuals where tagged with T-bar tags, sexed and carapace length and total body length measured (see papers for more details on study areas and sampling protocol). In Aust-Agder county, lobster where fished more extensively throughout 2010–2013 to sample DNA (tissue) from as many males as possible for the parentage assignment. Females and offspring were sampled summer and autumn 2011 and 2012 (see paper I for details on sampling protocol). Prior to 2017, claw measurement had only been sampled in Aust-Agder county, but extended to all counties in 2017 and 2018 (see paper I and II).

The Celtic Sea and the western English Channel where chosen as study areas for genotyping of egg-bearing females in United Kingdom. Females where sampled for eggs and tissue in 2013 with similar procedure as for the parentage analysis in Norway, although the lobster were obtained with help from local fishermen (see paper II for detailed description of the study sites and sampling protocol).
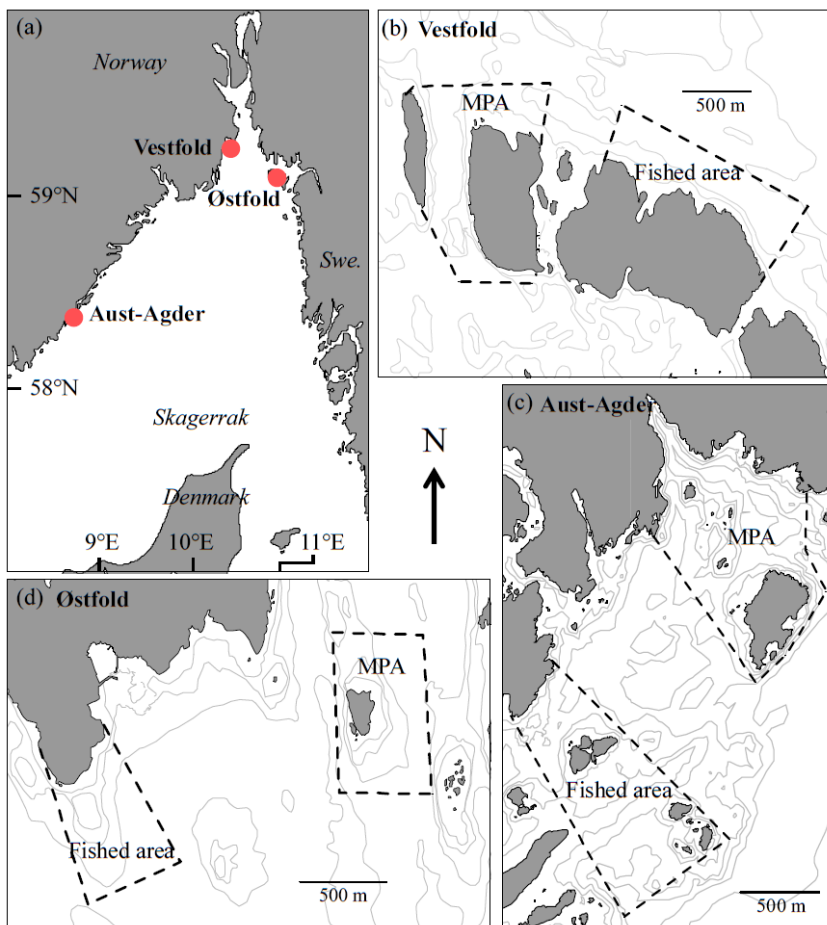
Figure 3. Study area of main focus. From top, (a) red circles shows the location of the lobster MPAs and fished control area in pairs on the Norwegian Skagerrak coast and in each of the three counties; (b) Vestfold, (c) Aust-Agder and (d) Østfold, respectively.

2.2 Genetic analysis and mark-recapture data

DNA was extracted from adult tissue and individual egg samples following protocols as described in paper I and II. Genotyping of DNA was done using 10 and 13 microsatellite loci for paper I and II, respectively. Polymerase chain reaction (PCR) was used to amplify DNA fragments before they were analysed using capillary sequencers, see paper I and II for further details of primer and PCR conditions. In paper I, I manually scored genotypes for each individual based on characteristic peaks in each locus, but because two different sequencers were used, I had to calibrate the results, so the alleles would end up being compatible (alleles with same length). Furthermore, due to allelic drop-out (i.e. null alleles), false alleles and random laboratory and genotyping errors, I calculated locus specific error rates in a series of steps which was then incorporated into the parentage analysis. This ensured the best possible

family configuration between siblings (offspring), their known mothers and the assignment of parentage among fathers. In cases where the true fathers of offspring had not been sampled, genotypes were reconstructed. Full details on descriptive population genetics, approach and estimation of error rates, and parameters and runtime in the paternity analysis can be found in main text and appendix in paper I.

When determining whether a female had been sired by more than one male in paper I, I inspected both the results that were flagged as cases of multiple paternity in the paternity analysis together with the original genotype data to not overestimate the number of multiple sired females. In paper II, all parental genotypes had to be reconstructed prior to inferring if females had mated multiple times or not (see paper II for details). In both paper I and II, we only sampled 10 offspring per female, which is a very small fraction of the total egg-mass females produces. Since males may contribute fertilization unevenly, skewed parentage (i.e. 1:9 or 2:8) among multiple males could go undetected when analysing such small number of offspring. We therefore calculated the power to detect multiple paternity under various scenarios of skewed contributions.

In paper I, I established a size relationship between mated pairs in order to analyse size-assortative mating patterns. I then calculated standardized selection differentials and standardized selection gradients on male body size and claw size (including residual claw size in the latter) to discern sexual selection on the male traits.

In paper III, a linear model was used to test whether legal sizes lobster in the three MPAs had larger claws (relative to body size) than conspecifics in the contrasted fished areas. I chose to only analyse claws that was not unusual small in size, compared to body size, because they were most likely regenerated claws and thus expected to be unrelated to selective fishing mortality.

In paper IV, I estimated individual body growth of lobster from mark-recapturing data (2006-2018) over consecutive seasons by calculating the probability of moulting and the moult increment. Moulting probability was analysed with generalized linear mixed effects models and the effect of protection on moult increment was analysed with linear mixed effects models.

3. Results and discussion

3.1 Summary of main results

Up until now, there have been few studies and examples of fisheries inducing changes in sexually selected traits in marine systems. In this thesis, I have empirically examined several aspects of the mating system and sexual selection in wild European lobster (*Homarus gammarus*) and demonstrated different patterns of assortative mating in and outside a marine reserve. Furthermore, I present evidence that lobster reserves (or MPAs) can rescue key sexually selected (claws) and life history (growth) traits, which are likely to be under strong harvest selection outside of MPAs. Combined, these results are important for marine conservation biology as they demonstrate that fishing can strongly alter mating behaviour, but at the same time, MPAs can be highly effective in preserving sex-specific variation and phenotypic diversity important for reproduction and productivity (Figure 4).
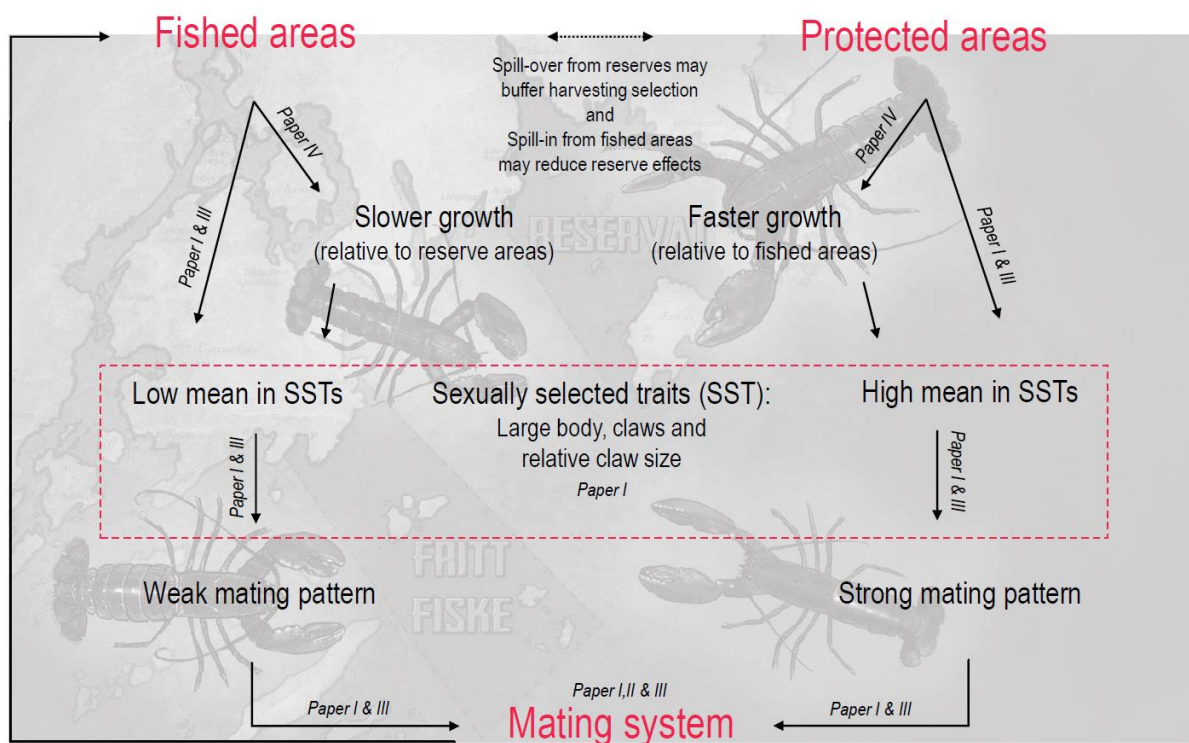

Figure 4. General overview of the main differences in growth and sexually selected traits (SST) between harvested and protected areas (MPAs) and how they interplay with the mating system of lobster. Text in italics refers to the papers from this thesis that address these topics; Female mate choice and determinants of male mating success (paper I), female fertilization pattern in a fished population (paper II), the effect of protection on a secondary selected trait under harvesting selection (paper III) and growth of lobsters in fished and protected areas (paper IV).

In **paper I**, "Harvesting changes mating behaviour in European lobster", paternity data from genotyped males and egg-bearing females confirmed females' preference for males with a body size larger than their own (the 43 known males assigned would almost exclusively be larger). However, the size difference between mated females and males were significantly larger in the reserve (22.5% compared to 6.4% in the fished area). We also found positive selection differentials on male body and claw size inside the reserve, but not in the fished area. These results suggest that when females have the opportunity to choose among a greater diversity of male traits, they mate with large males with large claws. Contrary, the mating pattern is weakened if the population is subjected to selective fishing pressure. When estimating sexual selection gradients on male traits, we found the selection to be acting strongest on relative claw size (claw size relative to body size), rather than on absolute claw and body size. Single paternity on female egg-batches was the prevalent fertilization pattern in both the reserve and fished area, however, two females from the fished area showed evidence of being sired by two different males (2 out of 97 broods analysed). Of males with known identity, eight had mated with more than one sampled female and seven of these males were from the reserve, but they did not differ in size from those with a single mating. Thus, this study present novel empirical support for how fishing affects mating behaviour in wild lobster. The study in **paper II**, "Genotype reconstruction of paternity in European lobsters" was conducted at the same time as the study in paper I, but the results were presented prior to the paternity estimates in paper I. The study was undertaken in a fished region of the coast of United Kingdom (UK) and found no incidence of multiple paternity in any of the 34 egg-bearing females genotyped and concluded single paternity to be the common fertilization pattern in European lobster (at least in this region). However, because only a limited sample of offspring were used in both paper I and II, none of the studies had statistical power to detect contribution from a secondary male with high confidence if the contribution was highly skewed in favour of one male (9:1). Thus, besides the two cases that were discovered by chance in paper I, it is possible that additional cases of multiple paternity were present among the samples in both our studies but went undetected. After large relative claw size was found to be under strong sexual section in paper I, the same trait was later linked to increased risk of being captured in the fishery (Moland et al. *in press*). In **Paper III**, "Marine reserves rescue an important secondary sexual trait in male European lobster", we show that legal-sized male lobsters have larger relative claw sizes inside MPAs compared to equal sized lobster in fished areas (up to 8.4% larger). We did not find any difference in female claw size between MPAs and fished areas, most likely because claws are male-only sexually selected trait. This study is

possibly the first to document the usefulness of MPAs in preserving a trait under strong sexual selection and under ongoing harvest selection in the same study system. In **Paper IV**, "Improved body growth of lobster inside marine protected areas compared to intensively fished areas", we also found substantial support for a positive MPA effect on body growth for legal-sized lobsters. The differences in growth, a combination of moulting probability and moult increment per year, between MPAs and fished areas, increased as lobster became larger in size. The MPA effect was most clear for moult increment of females. Even though MPAs have higher densities, which should increase competition over resources that would expectedly limit individual growth rate, lobster in the protected areas still grow substantially faster than in fished areas. It suggests that catchability of lobsters in the trap fishery may correlate with high growth rate and that lobster undergo intensive and selective fishing pressure against faster growing individuals.
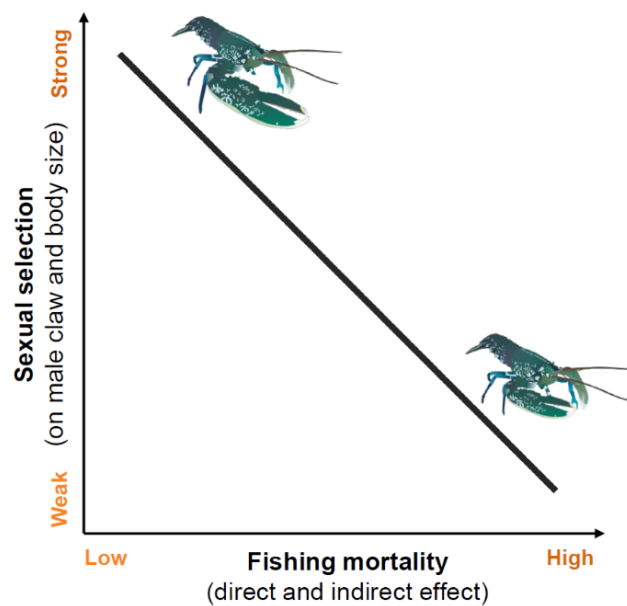

Figure 5. A simplified illustration describing the inverse relationship between fishing mortality and sexual selection and the gradual expression of male claw and body size in European lobster. Fishery driven trait changes are likely to operate under two processes; directly by selective removal of legal sized (larger and faster growing) males with larger claws and indirectly by lower the population density, thus weakening sexual selection on male traits. As fishery selection increases (towards high pressure), sexual selection for larger traits diminishes (towards weak selection). Protected from fishing mortality, MPAs can serve as hot spots for high variance in phenotypic traits and ensure stronger sexual selection (towards strong selection).

This thesis discloses a pattern of two opposing selective pressures that can be described as an inverse relationship; the lobster fishery directly selects and remove large (above legal

size) and faster growing males with larger claws, traits which are sexually selected (Figure 5). In fished areas, the reduced mean and variability in male traits would then leave females with a reduced opportunity for mate choice which results in a weak mating pattern. Additionally, the fishery is also affecting the population indirectly by lowering the density of available mates. The more individuals are dispersed, the lesser the ability of males with desired phenotype to attract and mate with females (Shuster and Wade 2003; Kokko and Rankin 2006), which would further attribute to weaker mating pattern and subsequently diminish sexual selection on male traits. If the fishery continues to target lobster with a higher chance in gaining reproductive success and relaxes sexual selection, fisheries- induced evolution could accelerate even faster than one would expect from fishing pressure alone (Hutchings and Rowe 2008; Urbach and Cotton 2008). In our case, a result from such selection could be smaller and less productive lobster. However, as I also show in this thesis, even small-scale MPAs have positive effects on claw and growth, traits that plays a key role in the lobsters mating system. Allowing females to choose among a broader assortment of males, and males to establish dominance relationships, should strengthen the overall sexual selection and reduce the likelihood for sperm-limitation.

3.2 Future prospects

This thesis highlights the need for a better understanding of how fisheries affect the mating system of exploited species and how we can consider such effects. But there is still much we could investigate in using this study system. For instance, what are the long-term, even lifetime, fitness benefits and costs of having much larger claws, in such as energy expenditure, reproductive success and natural mortality? It would also be interesting to study behaviour around baited traps more closely to gain a better understanding of why some lobster are more prone to capture than others. Lastly, modelling studies could also be helpful to further explore what consequences the different management regulations and spatial protection has on trait distributions, productivity and evolutionary trajectories.

The vulnerability to exploitation differs between mating systems, yet we lack knowledge of mating patterns and mating behaviour, and how they respond the selectivity of fisheries, for most commercially important species (Rowe and Hutchings 2003). Part of the reasons is that studies of natural mating behaviour in marine animals can be a challenging task, especially for the most cryptic species. However, as shown in this thesis, the combination of parentage analysis and replicated MPAs with control sites could be an insightful tool and

should be applicable for many other species as well. For instance, many heavily exploited species have parental care, such as maternal brooding in crustaceans and paternal nest-guarding in fishes (e.g. salmonids, wrasses, sunfish), and thus are easy to sample for paternity analysis. It should be even possible to study the mating behaviour of broadcast spawners with these methods. For example, the coastal cod in Skagerrak have been found to have limited genetic connectivity between local cod populations and has high site fidelity (Olsen *et al.* 2008; Knutsen *et al.* 2011), but parentage studies have even succeeded on a much larger scale on coral reef fishes (Harrison *et al.* 2012).

Intra- and sex-specific variations are often ignored in stock assessments and fisheries research (Hanson *et al.* 2008), but we need to identify sexually selected traits (phenotypes) and measure them so we know if species are caught in a crossfire between sexual and fisheries selection. Many sexually selected traits manifest as morphological dimorphism and are easy to identify, such as body shape in salmon, claws in crustaceans or colours in wrasse and sunfish. Others may be more cryptic, such as mating calls in cod and differential quality in parental care behaviour in wrasses and largemouth bass. We must therefore look beyond body size and conduct in-depth studies when exploring sexually important traits.

Managing fisheries resources is complex and an evolving process. Alternative management regulations reducing or changing size selectivity are often encouraged (Froese 2004; Jørgensen *et al.* 2007; Zhou *et al.* 2010), such as restricting harvest of large individuals through gear modifications (e.g., reducing entrance diameter in traps) or maximum size limit (Zimmermann and Jørgensen 2017). A slot-size limit is now in effect for lobster on the Skagerrak coast when a maximum size limit was introduced as of the 2017 fishing season. Protecting both large and small individuals should increase variation in body size and a wide range of correlated life history traits. However, as other sexually selected traits may succumb to fisheries selection (i.e. relative claw size in lobster), slot size is no silver bullet. Another promising option that should be at the forefront in management and conservation is the establishment of interconnected networks of large and fully protected marine reserves that can function cooperatively by exchanging individuals (and genes). In particular, MPAs as "hot spots" should be able to work synergistically with slot size limits since spill-over of large individuals, likely to possess other attractive characters also, would be protected from fishing and contribute to population productivity outside of reserves. The positive MPA effect identified in this thesis are likely to show only a fraction of the many benefits of protection and I strongly encourage future studies into the depths of behavioural, ecological and fitness consequences of housing species in high densities and in all size and age classes.

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