Modelling the Interaction of Fishing with Size Structure, Dimorphism, and Egg Production of Clawed Lobsters

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ABSTRACT

Many management strategies are available to fishery managers to improve the sustainability of a fishery; however, it is not always clear how implemented strategies interact with the demographics of the exploited species. Management decisions are often made in order to maximize egg production and recruitment or to preserve specific size classes to increase reproductive output. Consequences of these strategies could include variation from a natural size structure of the population, exaggerated sexual dimorphism, skewed sex ratios, and suboptimal mating conditions. To examine the possibility of these consequences, I ran a series of deterministic models to simulate the fished and unfished population dynamics of two clawed lobster species, American lobster (*Homarus americanus*) and European lobster (*Homarus gammarus*), under a variety of management strategies. Protection of ovigerous females takes two forms in this model. The American fishery in the Gulf of Maine requires fishers to v-notch ovigerous females for up to four years of protection from fishing. The European fishery in southern Norway bans the harvest of ovigerous females, which translates to one year of protection. I compared the relative impact of the two levels of ovigerous female protections on factors that may be important for reproductive success: size structure, dimorphism, sex ratio, and egg production for both species. I then considered a case study on European lobster to evaluate the interaction of a no-take marine protected area with a slot limit to compare relative impacts to egg production, overall size structure and dimorphism. Results showed that American lobster females benefited greatly from strict protections such as v-notching in terms of mean size increase and egg production, but mean size dimorphism and the overall proportion of females also increased with higher fishing pressure. European lobster females also benefitted from protections, but less dramatically than American lobsters, and with lower size dimorphism. In the case study, European lobsters benefitted most from the implementation of a no-take marine protected area in combination with a slot limit to preserve the largest individuals of both sexes which improved overall egg production. By taking a simulation approach to evaluate these different management strategies on two closely related species of lobster, this thesis provides a basis for understanding how fishery decisions can achieve their sustainability goals in addition to quantifying some of the unintended impacts of management on parameters that may be important to overall reproductive success.

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GENERAL AUDIENCE ABSTRACT

Fishery managers make decisions about a fishery based on the species' biology to optimize catch while also ensuring that enough individuals remain to keep the population alive for years to come. However, it is not always clear what types of unintended consequences these decisions may have. Management decisions are often made in order to maximize egg production, to keep small individuals alive until they can reproduce, or to preserve the large individuals that have high reproductive potential. Some consequences of these strategies could include a reduction in the number of large individuals with high fishing pressure, increased female body size compared to males, unequal numbers of females and males, and less optimal conditions for mating. To examine the possibility of these consequences, I ran a series of models to simulate the fished and unfished populations of two clawed lobster species, American lobster (*Homarus americanus*) and European lobster (*Homarus gammarus*), under a variety of management strategies. The American lobster fishery in the Gulf of Maine requires a practice known as v-notching, which protects egg-bearing females for up to four years. The Norwegian fishery for European lobster bans the harvest of egg-bearing females, which is protection that lasts for one year. I compared the impact of the two types of egg-bearing female protections on factors that may be important for reproductive success: abundance of large lobsters, unequal numbers of females and males, difference in size between females and males, and overall production of eggs for both species. I then considered a case study on European lobster to test how a no-take marine protected area and a slot limit (minimum and maximum harvest size limits) affected those same factors. Results showed that American lobster females benefited greatly from longer lasting protections by growing to larger sizes and producing more eggs, but the average size difference between females and males and the overall proportion of females also increased as fishing became more intense. European lobster females also benefitted from protections, but less dramatically than American lobsters, and with lower mean differences in size between females and males. In the case study, European lobsters benefitted most from the no-take marine protected area in combination with a slot limit to preserve the largest individuals of both sexes which improved overall egg production. Using a simulation makes it easier to tease apart the effects of these different management strategies on two closely related species of lobster. This thesis helps managers see how fishery decisions affect lobsters in both desired and unintended ways. With this information, managers can better improve the sustainability of the fishery through considering what a specific species needs to improve reproductive success.

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Introduction

Fishery managers have many tools available to them to meet their sustainability goals, however there may be unintentional effects of these tools on the demography of the exploited species. Limiting access to the fishery, fishing seasons, regulating gear, mesh sizes, escape vents, quotas, size limits, protecting ovigerous females, and spatial regulation are some of the commonly used methods of conservation management in fisheries (King 2007). Generally speaking, these methods are intended to prevent overfishing, maximize catch of market-sized individuals, and optimize total egg production to continue fishing long term. Despite the many tools in fishery management, population-level changes in traits such as length and size at maturity of exploited species are known to occur in some fisheries, especially those that are size- and/or sex-selective (Hutchings and Rowe 2008). It is not known what the consequences of these demographic shifts are on the reproductive potential of a species. Because this subject can be difficult to study in nature, this thesis uses population dynamics models to simulate how an experimental series of management choices for clawed lobster fisheries alter population-level traits such as size structure, size dimorphism, sex ratio, and egg production. These variables were chosen because they are quantifiable traits that are important for reproductive success but are not frequently explicitly targeted by management.

Clawed lobster fisheries around the world use a variety of different management techniques. This is in part due to the facts that clawed lobsters can be sexed without invasive techniques and that they carry their eggs externally unlike most species of fish. For these reasons, fisheries for American lobster (*Homarus americanus*) and European lobster (*Homarus gammarus*), two species of clawed lobsters, provide an interesting case study to examine how management choices impact size structure, sex ratio, and egg production. Past work on clawed lobsters suggests that differential fishing selectivity for males and females could generate suboptimal mating conditions that could impact sex ratios (Daniel

et al. 1989; Pugh et al. 2013; Jury et al. 2019), mating success (Pugh 2014; Goldstein et al. 2014), and prevalence of sexually-selected traits (Sørdalen 2019; Fernández-Chacón et al. 2020). Current harvest management practices focus on preserving the female population to maximize egg production, and do not explicitly manage for changes in sex ratio or harvest-induced size dimorphism. In addition to female protections, slot limits and spatial protections such as marine protected areas are also used. This thesis identifies the consequences of these size- and sex- based fishing practices that could lead to skewed sex ratios, sexual dimorphism in size, and variation in egg production in terms of the number of spawning females.

Growth, Maturity, Mating, & Reproduction

Lobsters and other crustaceans have a discontinuous growth pattern where they undergo ecdysis, or molting, to grow. Most of their weight and length gain takes place during this process, where lobsters molt more frequently when they are smaller and growing fast, and less frequently as they are larger and growing more slowly (Phillips et al. 1980; Huntsberger et al. 2020). As lobsters molt, they lose the body parts that may be able to track age, making it difficult to age them with accuracy, although efforts have been made to study accumulation of cuticle layers in the gastric mill and eye stalks and accumulation of lipofuscin in cells (Kilada et al. 2012; Wahle et al. 2013; Huntsberger et al. 2020), as well as quantifying methylation of ribosomal DNA (Fairfield et al. 2021). Historically, American lobsters as large as 217 mm carapace length or that weigh as much as 19 kg have been seen, suggesting they may live to be more than 30 years old (Lawton and Lavalli 1995). Describing crustacean growth rate accurately requires knowledge of the molting increment (MI) and the intermolt period (IP), where MI refers to the difference between the post-molt size and the pre-molt size, and the IP refers to the time duration between two molts (Chang et al. 2012). These data are typically collected from mark-recapture

studies or laboratory growth experiments since lobsters cannot be reliably aged (Ennis 1978; Krouse 1981; Campbell 1983; Lawton et al. 1984; ASMFC 2020; Sørdalen et al. 2022).

Females usually maintain a cycle of molting and mating one year, and spawning the next year until they reach a large enough size where they can spawn multiple times in between molts, sometimes skipping molting for several years, while their male counterparts may molt more frequently under a different reproductive cycle (Talbot and Helluy 1995; Wahle et al. 2013; Waller et al. 2019). Larger males tend to molt on two to four year cycles, giving them the opportunity to mate over multiple seasons during their intermolt period (Waddy and Aiken 1991a; Waddy et al. 2017). Smaller males that molt on annual cycles are therefore unable to mate as frequently as the larger ones (Waddy et al. 2017). Size is therefore an important component to male reproductive cycles and mating frequency.

Size at maturity and growth rate are dependent on sex. Males mature at a smaller size than females, and females also grow slower after maturation to balance reproductive costs (Cobb 1995; Lawton and Lavalli 1995). While maturing at a smaller size may allow females to increase their reproductive output, their eggs may not be as high quality (Plante and Ouellet 2004) and they may be more likely to carry abnormal clutches than larger females (Tang et al. 2018; Waller et al. 2019). Studies have reported a decrease in length where 50% of females are mature over the last 20-50 years, which could be due to increasing temperatures or selective fishing protecting reproductive females (Le Bris et al. 2017; Waller et al. 2019, 2021). Although males mature at smaller sizes than females, they may not be as likely or capable of mating with the relatively larger females (Krouse 1973).

In female lobsters, mating and spawning occur independently. After molting, females will mate and incubate their eggs for 9-11 months and then spawn, releasing the eggs from the abdomen (Phillips et al. 1980). The eggs will hatch after several months depending on water temperature, but prior to females molting that year (Waddy and Aiken 1991b). Even if females did not mate, they will still spawn infertile eggs the following summer (Waddy et al. 2013). Females usually maintain this cycle of molting,

mating, and spawning until they reach a large enough size where they can spawn multiple times in between molts, sometimes skipping molting for several years, while their male counterparts may molt more frequently under a different reproductive cycle (Talbot and Helluy 1995; Wahle et al. 2013; Waller et al. 2019). Females become more fecund and can make larger eggs as they grow larger (Estrella and Cadrin 1995), making large females 10-20 times more fecund than smaller females (Waddy and Aiken 1991b). For this reason, protecting females so that they can grow to larger sizes is a management target for clawed lobster fisheries.

Fisheries for Clawed Lobsters

American lobsters are widely distributed in the northwestern Atlantic Ocean where they can be found as far north as Newfoundland and Labrador, Canada and occasionally as far south as North Carolina, USA; however most are found north of Rhode Island (Lawton and Lavalli 1995). The European lobster is the northeastern Atlantic counterpart to the American lobster found (Figure 1.1). European lobsters are found as far north as the Norwegian Arctic Circle and as far south as Morocco and parts of the Mediterranean (Wahle et al. 2013).

Figure 1.1. Distribution of American lobster and European lobster boxed in red in the north Atlantic Ocean.

American and European lobsters have a pelagic larval stage followed by time spent as a benthic juvenile in sheltered areas (Wahle et al. 2013). As they enter adulthood and become sexually mature, they are more mobile and engage in seasonal migrations to track optimal temperatures (Lawton et al. 1984; Campbell 1986; Waddy and Aiken 1991b). As temperatures in the Guld of Maine rise due to climate change, it is predicted that overall productivity will shift northward, leading to a 42%-62% decline in American lobster abundance in the Gulf of Maine (Pershing et al. 2021). Another concern is recruitment success, as juvenile American lobsters have declined in recent years (Oppenheim et al. 2019; Pershing et al. 2021). Recruitment declines are thought to be correlated with larval and post larval survival and food availability (the copepod *C. finmarchius*) at these stages, but there may be other factors as well (Carloni et al. 2018). For this reason, understanding how fishing and management efforts influence lobster populations in terms of individual growth, size at maturity, size structure, and sex ratio could clarify how management can more effectively achieve their conservation goals.

In the US and Canada, commercial lobster fisheries began in the early 1800s, although native populations began subsistence lobster fishing much earlier (Fogarty 1995). At this time, landings were

high, and captured individuals were on average larger than they are today. Overexploitation was a growing issue until the two World Wars, when pressure on the fishery lessened. With new technology, renewed interest in the fishery, and favorable environmental conditions, effort and landings increased dramatically after the wars (Fogarty 1995). In the 1990s, the American lobster fishery experienced heavy fishing, with the estimated annual removal of 70-90% of legal-sized individuals (Cobb 1995). The fishery today predominantly occurs in nearshore waters using traps or pots (ASMFC 2020).

Current landings for the American lobster in the Gulf of Maine have been on the rise since the 1990s, likely due to changes in productivity; the depletion of one of their main predators, Atlantic cod (*Gadus morhua*); overfishing of the green sea urchin (*Strongylocentrotus droebachiensis*) which expanded macroalgae habitat for juvenile lobsters (Lawton and Lavalli 1995; Steneck et al. 2013); and the expansion of habitat within their preferred thermal range of 12 °C to 18 °C (Crossin et al. 1998; Goode et al. 2019). This increase also mirrors the global trend of crustacean fisheries growing rapidly compared with finfish fishery declines over the past 30 years (Boenish et al. 2021).

American lobster landings in the Gulf of Maine are currently some of the highest ever seen in this region (Le Bris et al. 2018; Goode et al. 2019). This fishery comprises 76% of all fishery landings in Maine (MCC STS 2020) with an estimated revenue of $631 million in 2018 (ASMFC 2020). Summer temperatures in the Gulf of Maine currently range from 11 to 18 °C in shallower waters, which fall within the preferred thermal niche for the American lobster (Crossin et al. 1998; Goode et al. 2019). It has also been suggested that because lobster walking rate increases above 20 °C, probability of encountering a lobster trap could be increased with higher temperatures (Cobb 1995). However, temperatures above 19°C have been linked to increased physiological stress and even mortality in lobsters (Dove et al. 2005). While slowing the rate of warming of the Gulf of Maine may not be possible, it is likely that management for population resilience via a healthy size/age structure could buffer expected changes in the fishery (Le Bris et al. 2018; Sørdalen et al. 2018).

Declines in American lobster abundance and a fishery collapse have already been seen in Southern New England, including Long Island Sound, due to rising temperatures, recruitment failure, and a prevalence of epizootic shell disease (Pearce and Balcom 2005; Bell 2010; Wahle et al. 2015; Le Bris et al. 2018). The upper stress threshold for temperature for American lobsters was exceeded in Long Island Sound during the summer of 1999, leading to a mass mortality event associated with infection by a parasitic amoeba (Pearce and Balcom 2005). Continued excessive warmth in coastal waters likely leads to lobsters moving offshore in search of cooler water. Model simulations suggest that had more restrictive harvestable size limitations been in place for southern New England lobsters, abundance would have decreased by about 20% less mainly due to preservation of large fecund females (Le Bris et al. 2018). Surveys in Narragansett Bay, Rhode Island have shown a clear decline in juveniles in coastal waters, while juveniles were often more numerous at the deepest survey site (Wahle et al. 2015). This reduction in nearshore juvenile abundance raises concerns for future growth of lobster populations in that region. Recruitment for American lobster is predicted to continue to decline in the future (Le Bris et al. 2018; Oppenheim et al. 2019).

The European lobster fishery in Norway was once highly valuable, but today the fishery is mainly recreational and limited to a season of two months in the fall. It has been estimated that catch per unit effort has declined by 92% over the past 90 years (Kleiven et al. 2022). The Norwegian lobster fishery began in the late 1600s when the Dutch would sail to Norway to acquire wood and coal (Knutsen et al. 2022). Current lobster populations have been at a historical low since 1970 and body size of lobsters is also smaller, requiring the implementation of restorative measures (Knutsen et al. 2022). These measures included restrictions on the allowable number of traps in 1993, a ban on the harvest of ovigerous females in 2008, and a minimum size that corresponded to size at maturity also in 2008. Ovigerous females within the harvest size limits were protected to preserve reproductive capacity beyond just protecting the smallest and largest classes with the slot limit, particularly because lobster is

heavily fished in this region (Sundelöf et al. 2015). While these measures were implemented only in the past 30 years, a summer closure was used starting in 1848 to protect spawning and address concerns for lobster meat quality during this time (Knutsen et al. 2022). Marine protected areas (MPAs) were proposed in the early 2000s as an attempt to rebuild the lobster population and fishery. Since then, studies have shown a number of positive effects on lobsters after the implementation of the MPAs such as increased local survival and abundance (Huserbråten et al. 2013; Fernández-Chacón et al. 2020), some spillover of lobsters into fished areas (Huserbråten et al. 2013; Thorbjørnsen et al. 2018), restoration of sexually-selected traits (Sørdalen et al. 2020), and benefits to lobster mating behaviors (Sørdalen et al. 2018; Sørdalen 2019).

The American lobster fishery in the Gulf of Maine uses slot limits—a minimum and maximum size for legal harvest. In addition, it is famous for the multi-year protection for proven female breeders through "v-notching" ovigerous, or egg-bearing, females. This practice has also been implemented by the Irish fishery for European lobster with positive results (Tully 2001). When fishers catch a female with eggs, they make a V-shaped cut (Figure 1.2) in the uropod to the right of the telson, ensuring protection for the lobster for several years (Code of Federal Regulations 2020). The European lobster fishery in Norway also uses size-specific slot limits, and bans the harvest of ovigerous females, but does not require v-notching. This practice provides a one-year protection for spawning females as any ovigerous females that are caught must be discarded. The idea behind both management choices is to maximize egg production by maximizing the number of spawning females in the population. This study compares both types of ovigerous female protections for both American and European lobsters in combination with their existing slot limit regulations.

Figure 1.2. An egg-bearing female American lobster with a v-notch (see yellow boxed area). Photo credit: National Oceanographic and Atmospheric Administration, Wikimedia.

The European Lobster Fishery and No-Take Reserves

The European lobster fishery in southern Norway is currently mainly recreational due to significant regionwide declines in abundance from overfishing. Estimates suggest that catch per unit effort has declined by 92% since the 1930s, although the fishery has existed since the late 1600s (Kleiven et al. 2022). A number of fishery regulations have been put in place as an attempt to rebuild the population of lobsters, but it remains at a historic low (Knutsen et al. 2022; Kleiven et al. 2022), and fishing pressure continues to be intense. Marine protected areas (MPAs) are the latest restorative measure for the fishery. Many studies have tracked the effects of these small reserves, showing that within 20 years, positive effects of the MPAs include higher survival (Huserbråten et al. 2013; Fernández-Chacón et al. 2020), limited movement of lobsters from the reserves to fished areas

(Huserbråten et al. 2013; Thorbjørnsen et al. 2018), and improved mating conditions in terms of more natural sexual dimorphism and selection (Sørdalen et al. 2018, 2020; Sørdalen 2019).

Lobster reserves, or MPAs, were implemented for the first time in southern Norway during the early 2000s. This was originally a difficult and controversial decision to make, but today they are widely supported, and studies have shown many positive benefits (Knutsen et al. 2022). It has also been shown that some large lobsters from protected areas move out of the protected areas, a behavior known as spillover, supplementing unprotected populations (Thorbjørnsen et al. 2018). These measures can help buffer exploited populations of lobsters that have high commercial and cultural value, while ensuring fishery sustainability. Previous work suggests that MPAs grant higher survival and diversity in sizes to lobsters due to the relationship between size and mortality in fished areas compared to size-independent mortality in the MPAs (Fernández-Chacón et al. 2020). Additional studies have shown that eliminating harvest can allow lobster populations to restore balanced size structures, preserve sexually-selected traits, and reduce mortality of the largest size classes (Sørdalen et al. 2018, 2020; Moland et al. 2019; Fernández-Chacón et al. 2020).

Chapter 1: Effects of Ovigerous Female Protections on Size Structure and Egg production of Clawed Lobsters

Abstract

While there is currently record high abundance of American lobsters (*Homarus americanus*) in the Gulf of Maine, we may see declines in lobster abundance in the future due in part to climate change. We need to study how fishing interacts with lobster size structure, mating, and reproduction to understand recent and future changes in lobster abundance. Better understanding of this relationship may also assist managers with decision-making for building resilience into the fishery to buffer the effects of climate change by maximizing egg production. The European lobster (*Homarus gammarus*) fishery in southern Norway is managed differently than the American lobster fishery and provides a good comparison to test the effects of different strategies of ovigerous female protections on both American and European lobsters. European lobsters are a close relative of American lobsters in the genus *Homarus*, and the two species are thought to share many biological traits. In this study, deterministic models are used to simulate relative changes in abundance, size structure, egg production, and sex ratio in response to ovigerous female protections. This simulation quantifies these relative changes without the noise of other variables to show the consequences of different management strategies. Results of this study show that while protecting reproductive females boosts egg production overall, it may also lead to greater sexual dimorphism in American lobsters as females survive to reach larger size classes than males. The proportion of females in the population of American lobster also increased with female protections. American and European lobsters also responded differently to these management strategies, likely due to differences in natural mortality, suggesting that decisions should be based on the biology of the specific species for best results.

Introduction

Identifying the demographic responses of species to fishing and other anthropogenic changes is essential to predict population dynamics and fishery sustainability. The effect of fishery selectivity on age and size structure, sex ratio, and mating systems can have consequences for population recruitment, which can support or undermine population productivity. This is especially true in size- and sex- selective fisheries such as those for clawed lobsters. This study examines how two levels of ovigerous female protections lead to changes in lobster size structure and reproductive success by modelling growth and annual egg production of two commercially exploited species of clawed lobsters, American lobster (*Homarus americanus*) in northeastern United States and European lobster (*Homarus gammarus*) in southern Norwegian waters. Despite the biological similarities between the two species, their fisheries are managed in different ways to account for fishery scale and cultural values. Because American and European lobsters have many similar traits, comparing the two species and their specific fishery management styles provides a unique opportunity to more closely examine the effects of fishing on size structure, sex ratio, and sexual dimorphism, as well as quantify the consequences of management for annual egg production.

Female-biased sex ratios in the catch of American lobsters have been noted as early as 1989 when researchers observed lobsters caught in traps near the coast had a sex ratio of 1.4 females for every male, of which, 0.3 were due to v-notched females (Daniel et al. 1989). A study sampled lobsters in Maine found that the sex ratio of sublegal lobsters hovered around 1:1 (Krouse 1973). More recently, one study found that while sex ratios were close to equal in smaller lobsters, samples ranged from 60-90% female once they surpassed the minimum harvestable size, with 100% female catch in some of the largest size classes – although sample sizes were small (Pugh et al. 2013). These results, taken together,

suggest that v-notching may be partly responsible for these skewed sex ratios—especially in larger size classes—in areas that are intensely fished, because the males are fished out.

The European lobster fishery in southern Norway uses a different method of ovigerous female protection. There, fishers are required to discard all egg-bearing females without the use of a v-notch. While both methods of protection meet immediate sustainability goals of preserving spawning stock biomass in the current year, v-notching lasts beyond the current fishing season to protect females for up to four years even if they do not have eggs (Mazur et al. 2019). It is not currently known exactly how this temporal difference in ovigerous female protections affects population-level demography and egg production of either species of clawed lobster.

Demographic models of population dynamics are useful tools that incorporate life history traits of species of interest to predict population-level trends. They may also be applied to species that are harvested to understand the consequences of different management choices. For crustaceans, including lobsters and crabs, the relationship between age and growth is often difficult to describe accurately, preventing the use of age in analyzing the impacts of size specific fecundity and mortality on population dynamics over time. To estimate this relationship for use in this study, the model predicted relative age given previously compiled data on annual size-based molt frequency and molt increments gained from mark-recapture studies of both American (ASMFC 2020) and European lobster (Sørdalen et al. 2022). This allowed for a projection of the mean probabilistic relationship between size and age for each species. With data on annual growth, the model integrates aspects of lobster biology and management that depend on size to function in an age-based model. This estimate of mean annual growth allows for the model to calculate egg production based on the mean size of spawning females. It also enables it to track mean changes in size for males and females across scenarios.

In Chapter 1, the dynamics of fishing are simulated to test for changes in annual egg production and in lobster population size structure for males and females under various management strategies.

This is done for both American and European lobster fisheries to assess how differences in life history may influence the results. More specifically, this chapter seeks to identify how fishing intensity and ovigerous female protections affect sex ratio, size structure, size dimorphism, and egg production for both American and European lobsters, while comparing the species-specific responses. I hypothesize that 1) management strategies that protect mainly females will lead to a female-skewed population with increased fishing effort, and that 2) increasing the level of female protection will also increase size dimorphism of females growing larger than males. In addition, I hypothesize that 3) if the population becomes female-skewed, egg production will change since it is typically calculated as a function of mature females. A final hypothesis is that 4) American and European lobsters will experience similar trends for each simulation.

Methods

For both American and European lobster, a deterministic sex-specific population dynamics model was constructed using the open-source statistical software R version 4.0.2 (R Core Team 2020). This model was based on the methods described in Mangel (2006) and Kindsvater et al. (2020), and extended to incorporate the specific biology of clawed lobsters and their unique fishing regulations. This model incorporates various types of protections for female lobsters in addition to the fisheries' slot limits on harvest. It is possible to simulate the potential consequences on relative trends and changes in size structure, sex ratio, and total egg production for each type of conservation measure for females in the American and European lobster fisheries. Because this model is not replicating a stock assessment model, it provides a unique opportunity to examine relative trends in egg production and size structure given different management decisions and the biology of both American and European lobsters without

the need for indices of abundance or landings data. Figure 1.3 is a visual representation of the assumed order of events that occur in the model where items with an asterisk (*) were varied in the simulation.

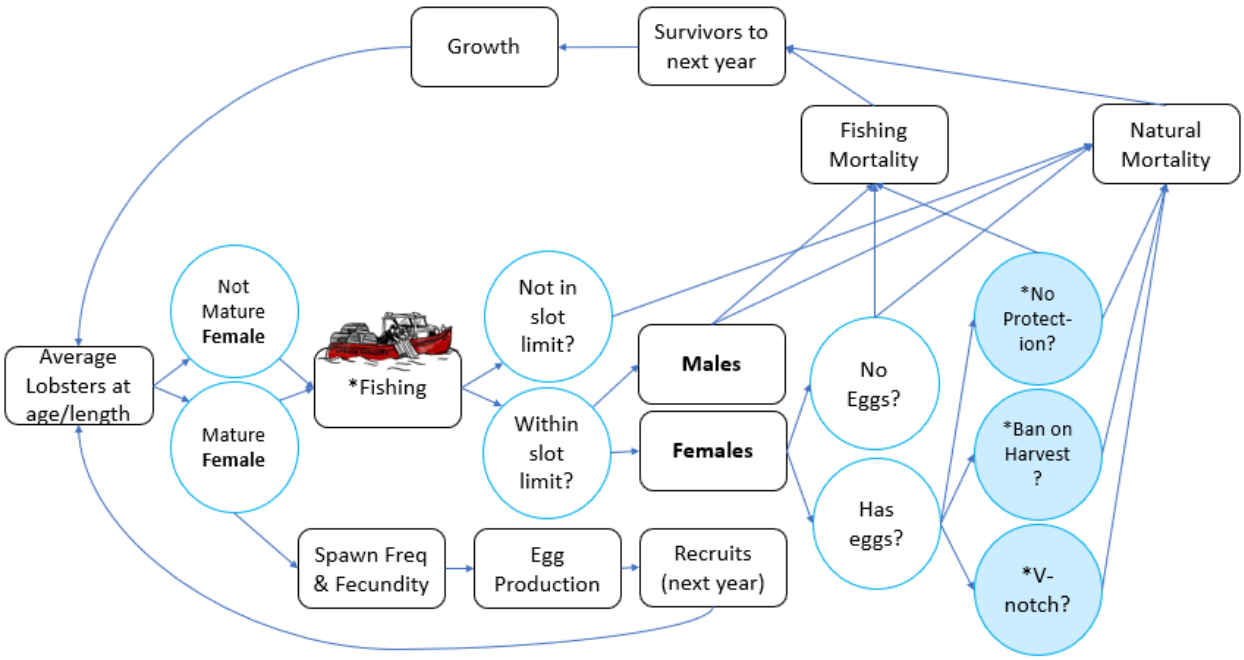

Figure 1.3. Summary of the order of events that the model simulates over time. The three filled-in circles are the different scenarios of ovigerous female protections. Items with an asterisk are variable depending on the scenario.

Growth

All data on growth for European lobster were converted from total length (*TL*) to carapace length (*CL*) for females and males using Equations 1 and 2, respectively, and are from the tag-recapture study by Sørdalen et al. (2022). To calculate growth, data on lobsters both in the protected area and the fished area were combined for a more complete span of size classes.

$$CL = 0.38 * TL - 6.84 \quad (1)$$

$$CL = 0.40 * TL - 10.91 \quad (2)$$

Growth was modelled given annual estimates of molting probability and molt increment, which were used to calculate the mean overall growth for individuals each year (Figure 1.4). Annual growth in terms of carapace length is the product of annual molting probability and molt increment. The annual probability of molting $P_{molt\ a}$ and the molt increment MI_a were calculated as a function of sex and pre-molt carapace length CL_a. For American lobster, annual probability of molting is given by a logistic equation, and molt increment is a linear function until it reaches an inflection point, after which molt increment is constant (Table 1). The relationship between molting probability and pre-molt carapace length for European lobster is given by Table 3 in Appendix A. Molt increment for European lobster females and males are linear functions of pre-molt carapace length described by Equations 3 and 4, respectively.

$$MI_a = 13.31382 - 0.05861 * CL_a \tag{3}$$

$$MI_a = 9.52874 + 0.02223 * CL_a \tag{4}$$

Annual probability of molting was then multiplied by the molt increment for each size class to calculate the mean annual growth for a given sex and pre-molt size. The estimates for molting probability and molt increment for American lobster can be found in Table 1. The model assumed that individuals of both species do not live beyond 40 years of age (ASMFC 2020). While lobsters may continue to grow and live to be 100 years old, these individuals are rare and difficult to capture (Cooper and Uzmann 1980). Capping the maximum age at 40 years old seemed appropriate given the estimates for natural and high fishing mortality that lobsters in the American and Norwegian fisheries experience.

Uncertainty and variability in growth increases when individuals reach the larger size classes since they are rarer in the wild, especially in intensively fished areas. For this study, mean estimated growth is used based on the best available information for both species. Each year, a lobster will

increase its size based on these calculations for mean annual growth until it either experiences natural mortality, is caught by the fishery, or reaches 40 years of age.

Figure 1.4. Growth of American (panel A) and European (panel B) lobsters over time. Age here is relative since these curves were generated using annual size-based probabilities of molting and molting increment for females and males.

Table 1. Growth equations and coefficients for American lobster from the 2020 stock assessment (ASMFC 2020). Note that *f* is an inflection point that represents the length at which 10% of females are mature and begin to allocate resources to reproduction instead of growth. The value for males was based on this value as well (ASMFC 2009, 2020).

	Probability of molting	**Molt Increment**
Equation	$p_{molt\ a} = \frac{1}{1 + e^{(a+b*CL)}}$	$MI = \begin{bmatrix} m + n * CL & for\ CL < f \\ m + n * f & for\ CL \geq f \end{bmatrix}$
Coefficients	a **Female**: -6.571 **Male**: -6.834	m **Female**: -3.90 **Male**: -4.51
	b **Female**: 0.05901 **Male**: 0.06046	n **Female**: 0.22 **Male**: 0.23
		f **Female**: 76 **Male**: 86

Reproduction

Female maturity was determined using the logistic equation (Equation 5) with size at 50% maturity and shape parameters in Table 2. While it has been shown that American lobster size at 50% maturity has shifted over time (Waller et al. 2019, 2021), the values used in this study were chosen for consistency across parameters, and were estimated as a weighted mean for the entire Gulf of Maine stock in the 2020 stock assessment (ASMFC 2020).

Males tend to reach physiological maturity (the ability to produce sperm and ejaculate spermatophores) at smaller sizes than females (Krouse 1973; Pugh et al. 2015). However, it is likely that males only participate in mating activities if they are at least the same size or larger than the mature females since females typically prefer larger males, and the male must be able to physically manipulate the female into mating position (Templeman 1933; Waddy and Aiken 1991a). I therefore used the data on female size-at-maturity to approximate male functional maturity in this model (Equation 5; Table 2).

$$p_{mat\ a} = \frac{1}{1 + e^{(\alpha + \beta * CL)}} \tag{5}$$

Egg production at a given point in time (E_t) was calculated by the proportion of mature females in the population in all age groups at a given time ($N_{a,t,f}$), their fecundity-at-size (Y_a), and their size-based spawning frequency (SF_a) (Equation 6). Species-specific values for this equation are in Table 2. For American lobster, female spawning frequency reflects their tendency to spawn every other year to alternate with molting years, until they are large enough to spawn twice per three years (Waddy and Aiken 1986; Waddy et al. 1995; ASMFC 2020). European lobsters tend to spawn every other year regardless of size, with some variability in the larger size classes (Sørdalen 2019).

$$E_t = \sum_{a}^{40} N_{a,t,f} * p_{mat\ a,f} * Y_a * SF_a \quad (6)$$

The population in the model reaches a stable distribution of individuals given annual birth and death rates, sex, and average individual growth before fishing begins and the population reaches a new steady state. Recruitment was deterministic and was assumed to follow the density-dependent Beverton-Holt relationship between recruitment and spawning stock biomass (Mangel 2006). Individuals are recruited to the model at 56 mm carapace length, which corresponds to roughly five years of age (ASMFC 2020). Sex ratio at recruitment was assumed to be constant at 50:50.

Fishing Dynamics

As individuals recruit to the model, their growth, maturity, reproduction, and mortality rates are determined by the parameters in Table 2. Once they reach a stable distribution, they become subject to fishing pressure ranging from $F = 0.1$ to $F = 0.9$. Both American and European lobster fisheries have experienced high rates of harvest in the past and present, so the full range of fishing pressures was tested here. For each species fishery selectivity was determined by a slot limit, with both minimum and maximum sizes.

In addition, two levels of egg-bearing female protections were simulated for both species of lobsters to reflect actual conservation practices in the fisheries. In the Norwegian fishery, egg-bearing females may not be landed, so fishers must return them to the water which results in a one-year protection for those caught females. This is the first level of protection tested. In the Gulf of Maine fishery, harvest of egg-bearing females is also banned, however fishers must make a “v-notch” in the ovigerous females’ flipper before returning it to the water. This can result in up to four years of protection when a “strict” definition of a v-notch is used (see Mazur et al. 2019). This is the second level

of protection used in the model. For both levels of protection in the model, protected females are removed from the fishable population for the applicable duration of time where they undergo growth, reproduction, and possible natural mortality until they rejoin the fishable population. For simplicity, fisher compliance for both forms of protection is assumed to be 100%. Testing both forms of female protection for both species allows for a comparison of the relationship between these possible management options for each fishery. After fishing the population, survival (*S*) to the next year is calculated as a function of natural mortality (*M*), and for age/size classes vulnerable to fishery, fishing mortality (*F*), (Equation 7). Protected females and individuals outside of the slot limit therefore only experience natural mortality and do not experience fishing mortality.

$$S = e^{(-M-F)} \tag{7}$$

Table 2. Species-specific life history and fishery parameters and equations used in this model.

Parameter / Equation Name	**American lobster (*H. americanus*)**	**European lobster (*H. gammarus*)**
Carapace length (CL) at 50% maturity	87 mm (ASMFC 2020)	96 mm (Tully 2001)
Maturity parameters	α = -17.14056 β = 0.19664	α = 14.96 β = -0.16
Spawning frequency (Mature females)	$for\ L_{mat} > CL > 120$ 0.5 $for\ CL > 120$ 0.66 (Waddy and Aiken 1986; Waddy et al. 1995; ASMFC 2020)	0.50 (Sørdalen 2019)
Fecundity at size	$Y = (0.000919833[CL^{3.580220}]) * 1.09886)$ (Estrella and Cadrin 1995)	$Y = 468.17 * CL - 33004$ (Agnalt 2008)
Beverton-Holt Stock-Recruitment functions	$R_{sex} = \frac{c * B}{1 + d} * proportion_{sex}$	$R_{sex} = \frac{eB}{1 + (B/k)^g} * proportion_{sex}$
Stock-Recruitment parameters	*B* = spawning stock biomass *c* = 1 *d* = 9E-10	*B* = spawning stock biomass *e* = 100,000 recruits per 10^8 eggs *g* = 1.0 *k*= 0.851 eggs (x10^{-8}) (Bannister and Addison 1986)
Maximum harvestable size	128 mm CL	116 mm CL (320 mm total length)
Minimum harvestable size	83 mm CL	**Females**: 86.9 mm CL **Males**: 88.6 mm CL (Converted from 250 mm total length)
Instantaneous Natural Mortality	0.15 (ASMFC 2020)	**Females**: *Small:* 0.2357 *Large:* 0.3193 **Males**: *Small:* 0.3759 *Large:* 0.6380 (Fernández-Chacón et al. 2021)
Size cutoff value for small and large natural mortality	n/a	**Females:** 88.16 mm CL **Males:** 89.09 mm CL (Converted from 250 mm TL)

Once the model runs through all fishing scenarios for each species, quantification of size structure, dimorphism, sex ratio, and egg production is possible to address each of the hypotheses presented in the introduction. The model generates a table of the number of individuals by sex and mean size at age at equilibrium with and without fishing for each level of female protection. A similar table for total annual egg production of all spawning females is also generated. Size structure is calculated by summing the number of individuals by sex per size/age group for each scenario. Size dimorphism is calculated by subtracting the mean size of mature males from the mean size of mature females for each scenario. Sex ratio, or proportion female, was calculated by dividing the total mature female population by the total mature population of males and females. Total annual egg production is calculated as the sum of eggs that are produced by all spawning females for each scenario.

Results

For both American and European lobsters, the model generated a sex-specific size structure at equilibrium in unfished populations (Figure 1.5) and fished populations. For purposes of more clearly seeing the impact of different female protections on the lobsters most vulnerable to the fishery—mature adults—juveniles were excluded after plotting size distribution (Figure 1.5).

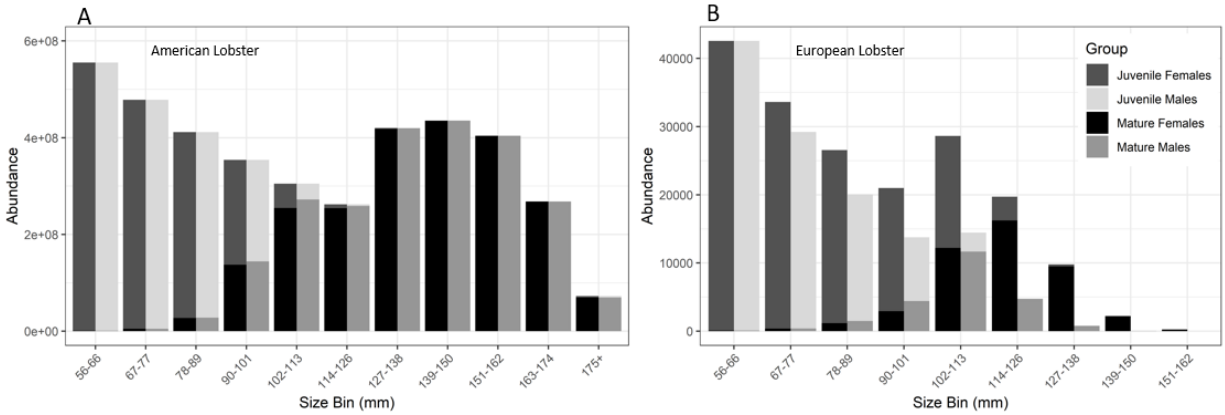

Figure 1.5. Size structures of American (Panel A) and European (Panel B) lobsters without fishing. Lighter versions of the colors for females and males indicate immature individuals, and darker colors are mature.

Size Structure

The fished size structure for mature American and European lobsters was truncated compared to the unfished structure due to few individuals surviving within and beyond the slot limit at $F = 0.8$; and the abundance of mature individuals decreased compared to the unfished scenario (Figure 1.6 Panels B and F). Fishing decreased survival, preventing many individuals from reaching larger size classes. A ban on harvest of ovigerous females increased the abundance of mature females larger than the slot limit of both species (Figure 1.6 Panels C and G). For American lobsters, this protection allowed a small number of mature females to survive long enough to reach the 175+ mm size bin, although the same is not true of mature European females, likely due to their higher natural mortality. V-notching ovigerous females protected them for four years after notching, and this protection had the greatest impact on increasing mature female abundance above the slot limit (Figure 1.6 Panels D and H). While this increase is small in European lobsters, American lobster mature female abundance rose dramatically in all size classes starting at the bin for 127 mm carapace length compared to other fished scenarios. Refer to Figure 3.1 in Appendix B for size structure plots of American and European lobster under the same management decisions but at $F = 0.2$, a lower fishing pressure that has less of an impact on survival to the larger sizes.

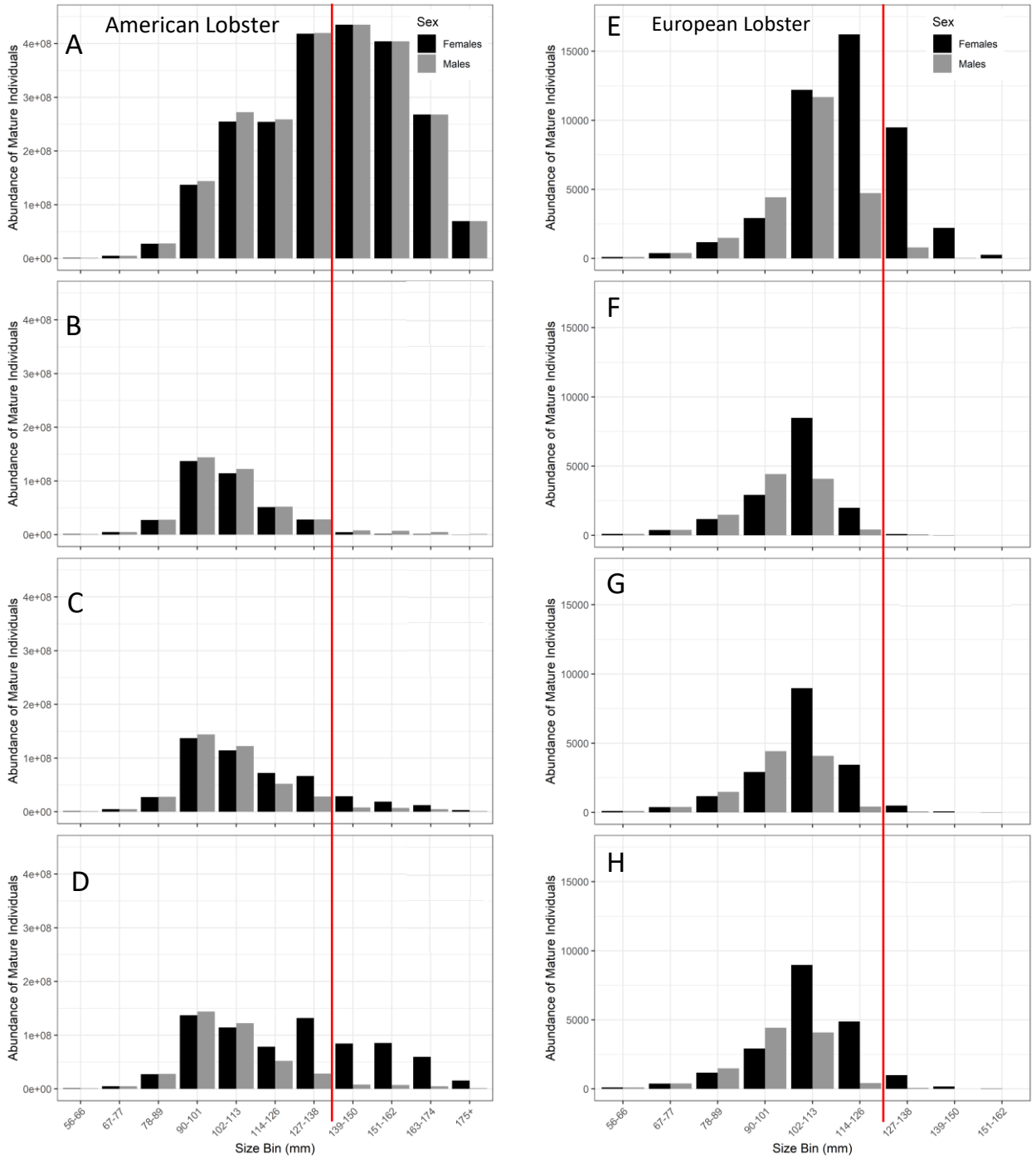

Figure 1.6. Size structures of American (left) and European (right) lobsters with and without ovigerous female protections during fishing compared to the unfished size structure. Note that these are for mature individuals only at F *= 0.8. Panels A and E are the unfished size structures. Panels B and F are fished without any ovigerous female protections. Panels C and G are fished with ban on harvest of ovigerous females. Panels D and H are fished with v-notching. The size bin to the left of each vertical red line*

contains the maximum size limit of 128 mm carapace length for American lobster and 116 mm carapace length for European lobster.

Size Dimorphism

In European lobster, mature males were on average just over 2 mm carapace length (CL) larger than females in an unfished population (Figure 1.7 panel B). This corresponds to the average female being 2% smaller than the average male. Males were up to 5 mm CL larger than females except when v-notching was used at $F = 0.9$, where mature females were 0.4 mm CL larger than mature males. When $F > 0.3$, the size difference between females and males decreased as fishing pressure increased. The greatest dimorphism occurred without any ovigerous female protections at $F = 0.4$ where females were 5 mm CL or 5% smaller than males.

American lobsters responded differently to the same ovigerous female protections and range of fishing mortality (Figure 1.7 Panel A). Without fishing, mature males were on average just over 4 mm CL, or 3%, larger than mature females. Without any protection of ovigerous females, males were on average 3 to 7 mm larger than females at any fishing level. With a ban on the harvest of ovigerous females, females were on average slightly smaller than males until a fishing level of 0.6, where males and females were on average the same size. Above $F = 0.6$, the mean difference increased so that mature females were up to 5 mm CL, or 7%, larger than males. V-notching resulted in the most extreme size dimorphism, where females were on average 2.5 mm CL larger than males at F=0.3, but as much as 8 to 16 mm larger than males at $F \geq 0.5$. In other words, at $F \geq 0.5$ the average male was 7 to 14% smaller than the average female.

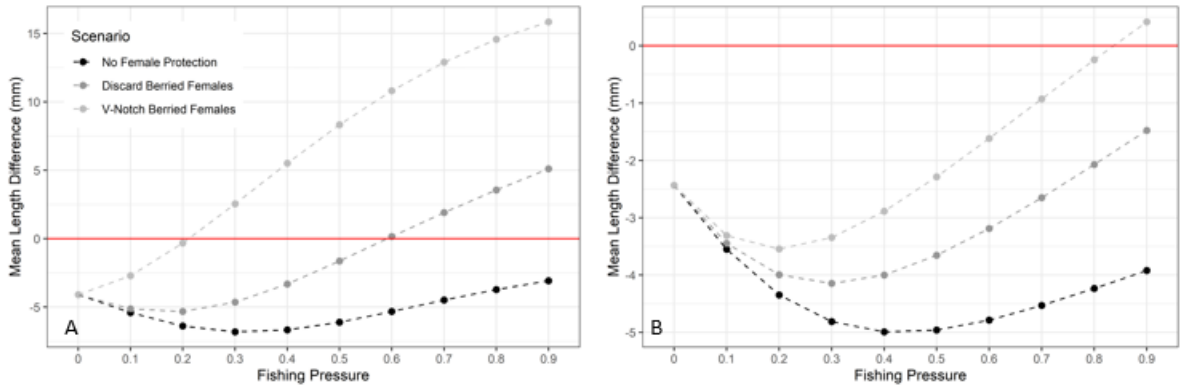

Figure 1.7. Mean size dimorphism by sex calculated by subtracting mean mature male length from mean mature female length. Panel A show mean differences in length for American lobster as mean length. Panel B shows the same for European lobster. The red lines indicate the threshold below which males are larger than females on average, or above which females are on average larger than males. The term "berried" females is synonymous with ovigerous females.

Sex Ratio

Female protections tended to increase the proportion of females in the populations of both species. In every scenario and at any fishing pressure, mature female European lobsters comprised between 58-66% of the mature population. Increasingly strict female protections and fishing pressure moved this percentage close to 60%, but rose slightly higher at $F \geq 0.8$.

While the percentage of mature female American lobsters in this simulation was around 50% without fishing, it reached 65% female at $F = 0.9$ with v-notching. Without any protections for ovigerous females, the sex ratio hovered near 50:50. With a ban on the harvest of ovigerous females alone, the proportion of females rose only slightly. V-notching at $F > 0.5$ caused the percentage of mature females in the population to exceed 60%.

Egg Production

As egg production is a function of the number of spawning females in the population, egg production is most increased with the addition of v-notching for both species, especially at the highest levels of fishing mortality. At low fishing mortality, ovigerous female protections had a small effect on European lobster egg production (Figure 1.8 Panel B). Increasingly strict protections led to slightly higher egg production relative to unfished levels at higher fishing mortalities (up to 12% higher with v-notching than without any female protections at high fishing pressure). Overall egg production with fishing ranged from 70% to 18% of unfished production levels.

American lobsters produced the highest number of eggs relative to the unfished level of production with v-notching at every level of fishing pressure, ranging from 71% to 22% (Figure 1.8 Panel A). When fishing pressure exceeded $F = 0.6$, egg production was nearly zero without any female protections. Discarding ovigerous females improved egg production slightly, but v-notching consistently led to up to 13% higher egg production at any level of fishing pressure. Overall egg production with fishing ranged from 4% to 71% of unfished production levels.

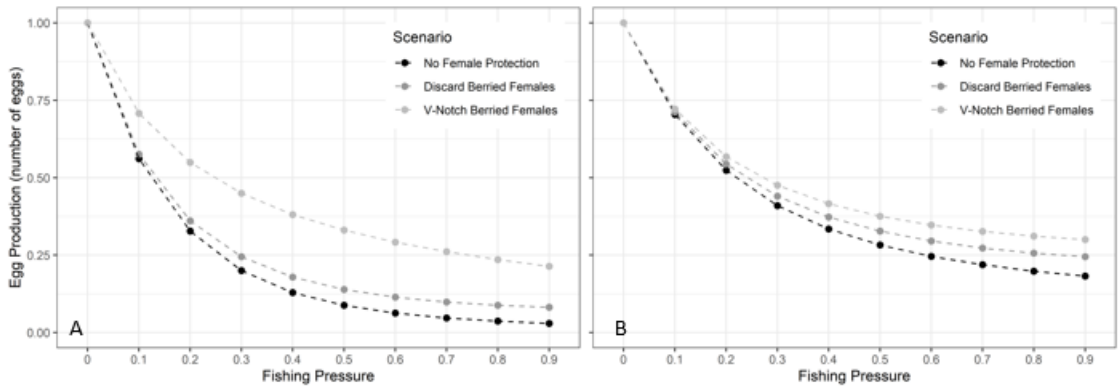

Figure 1.8. Egg production during fishing scaled to the unfished level of egg production for American (panel A) and European (Panel B) lobsters given various females protections. The term "berried" females is synonymous with ovigerous females.

Discussion

The model developed in this study is a useful tool for simulating population dynamics to predict how variables of interest change in response to different levels of fishing and a variety of management options. This model has been used to assess relative impacts of fishing styles on data-poor fisheries to provide insight on how a species might respond to specific scenarios (Kindsvater et al. 2020). In this study, the model was expanded to incorporate discontinuous growth by calculating mean size at age given annual growth probabilities which opens new possibilities for crustacean modelling. Population dynamics models are helpful for focusing on the life history of a species in the context of fishing to quantify relative changes in size structure, sex ratio, egg production, and more. Deterministic models such as this one do not incorporate environmental variability or animal abundance values from surveys, instead relying on parameters and equations that have been estimated previously through field and lab studies. This makes it easier to identify how fishing choices affect specific aspects of a species' demography. The results of models like this can be used to inform priorities for further field studies or for fishery management discussions. In this study, the model was used to evaluate the relative effects of different levels of ovigerous female protections on the demography of American and European lobsters. Results suggest that American and European lobster fisheries can benefit from these protections, however for both species there may be unintended consequences for size structure, sex ratio, and egg production that are not explicitly managed for.

Size-selective fishing is known to remove large individuals from the population resulting in an overall truncation in size structure (Law 2000). This effect is exaggerated at higher intensities of fishing. Lobsters increase their fecundity with size, so protecting spawning females is meant to preserve size-based fecundity to support overall population growth. Results of this study indicate that ovigerous female protections can help minimize the decrease in egg production due to fishing. At the same time,

size dimorphism increased as protected females are more able to survive and grow larger than their male counterparts. It is known that females prefer mating with males that have a large body and a large crusher claw (Templeman 1933; Lawton and Lavalli 1995). These traits also give the male competitive advantage when selecting a shelter, fending off other males, and attracting females (Templeman 1933; Lawton and Lavalli 1995; Talbot and Helluy 1995). While we do not yet know how v-notching has impacted the actual demography of the American lobster, in the last decade, surveys have reported increasing numbers of sublegal American lobsters of both sexes and increasing numbers of females in the size bins above the minimum size limit, although these numbers vary annually (ASMFC 2020). A Canadian study showed that males had a higher probability of capture around the minimum size limit while larger lobsters tended to be female, even without v-notching (Koepper et al. 2021). This suggests that the trends of increased average size dimorphism depicted in this simulation study may already be occurring, although we do not know to what extent or if it should be of concern to managers.

Surprisingly, each species responded differently to each level of female protection. European lobsters in this study did not experience the same drastic increase in egg production or size dimorphism as American lobsters with ovigerous female protections. The model outputs show that v-notching as a form of 4-year protection is an effective means of boosting egg production if the female is able to survive long enough to benefit from this. With a low estimated natural mortality for American lobster, females were able to survive through the 4 years of protection with v-notching to continue growing and reproducing. In species that for which estimated natural mortality is higher, such as the European lobster, v-notching will only marginally enhance egg producing potential compared to a ban on ovigerous females alone. Mature females did not outgrow mature males to the same degree as the American lobsters did. The importance of the estimated natural mortality parameter to these differences suggests that further empirical research is needed for both species.

To better understand the relevance of this work, and to identify areas for further study, it is worth examining the mating behaviors of lobsters, and how dimorphism and sex ratio may influence them. American and European lobsters are thought to exhibit similar mating patterns. Males establish and guard shelters while females select a male with desirable traits and enter his shelter (Cowan and Atema 1990; Lawton and Lavalli 1995; Talbot and Helluy 1995). Large body size and crusher claw size are typically associated with dominance in males and are sought-after traits by females, so if a choice is available, females prefer mating with larger males (Templeman 1933; Cowan and Atema 1990; Lawton and Lavalli 1995). In cases where females are on average larger than males, as seen in this study, females will not be as likely to find mates larger than themselves. While it is possible for females to mate during the intermolt period, mating most commonly occurs within 48 hours after molting when her body is better able to receive the spermatophore from the male (Talbot and Helluy 1995). In the lab, large males can mate with over 50 females in one mating season, with an average of 22 inseminations and a mean of 3.5 days between them (Waddy et al. 2017). Multiple paternity has also been observed in areas of high exploitation. A study in Canada found that 13% of females had a clutch that was sired by more than one male (Gosselin et al. 2005). They reported that this is most likely to occur in smaller females that mated with small males and did not receive adequate or high-quality sperm from their initial mating, indicating that sperm limitation may be an issue. Females can keep the viable sperm for up to two years, allowing them to utilize the stored sperm for multiple spawns in between molts if needed (Waddy and Aiken 1986). Even if sperm limitation is not an issue for males mating with larger females, they would still need to be able to engage in mating activities for successful reproduction. Further research is required on sperm limitation in American and European lobsters, especially since sperm limitation has already been shown to occur in a number of crab species including the coconut crab, *Birgus latro* (Sato et al. 2010).

Some work has been conducted on size-based mating success in American and European lobsters. A study conducted on the presence of a spermatophores in American lobster females found that many immature females had mated, while in certain regions large mature females had not (Pugh et al. 2013). The authors suspect that these large females may not have found a suitable mate or that they had received low quality spermatophores. The immature females are hypothesized to "practice" mating or to be protected during molting (Watson et al. 2017). In a study comparing traits in European lobsters in a fished area and in a no-take reserve, lobsters in the reserve were larger on average, males had bigger crusher claws, and females were more likely to mate with a male who was larger than herself (Sørdalen et al. 2018). The authors argued that fishing can alter mating activity in European lobster, and so that when females are left with mostly suboptimal mate options, they may be passing on fewer desirable traits to their offspring or choose to not mate at all. If a large, protected female is unable to mate, then her egg production for that year is effectively zero despite her high fecundity, at which point the predicted increase in egg production from this study would be overestimated. On the other hand, sperm volume increases with male size, and males may also be able to alter their spermatophore size based on the size of the female they mate with (Pugh et al. 2015; Gutzler et al. 2022), giving males flexibility to optimize mating opportunities (Gosselin et al. 2003; Pugh 2014). However, there may still be a risk of sperm limitation (Gosselin et al. 2005; Pugh 2014). Additionally, a controlled study showed that males that are 40% smaller or more than females are less likely to successfully mate, but if they do, may not pass on enough sperm (Pugh 2014). Results of this chapter suggest that at the highest fishing pressures, v-notching results in mature males that are 14% smaller than mature females, which is not the extreme studied in the work by Pugh (2014), so the risk of unsuccessful mating based on dimorphism may not be a concern. Further study on the nuanced relationship between egg production, size-based mating success, and fertilization rates in clawed lobsters is needed to more fully understand the interaction of harvest with size dimorphism and overall egg production.

Results from this study are also limited by the availability of relevant data and accurate growth information. Researchers suspect that males will reach a point where they will put less resources into growing longer and more resources into growing their crusher claw to attract more mates (Sørdalen et al. 2020), which may affect male growth in larger size classes. On the other hand, most of the parameters used in this study for European lobster are based on recent tag-recapture data that estimated molting probability and molt increment (Sørdalen et al. 2022), while the parameters for American lobster are mainly from older data that have been recycled over a number of stock assessments (ASMFC 2020). This could be an indication that updated estimates of natural mortality, growth, and fecundity are necessary for American lobster management into the future, especially since it has already been shown that their size at maturity has been changing over time (Waller et al. 2019). For example, if we are currently underestimating natural mortality of American lobster, then we may be overestimating the effectiveness of v-notching. Additionally, if mature females are on average larger than mature males, then egg production may also be overestimated if this dimorphism affects reproductive success. This may be something to keep an eye on moving forward as lobsters and fishers in the Gulf of Maine adapt to environmental changes.

The results of the simulation models presented in this study may be helpful indications of the types of data that should be collected to confirm or contest the trends in size structure, dimorphism, sex ratio, and egg production described for both species. By comparing the management strategies of both the American and European lobster fisheries, we are able to more clearly see how species biology interacts with harvest to alter population demographics. This is especially true for fisheries whose management goals include increasing egg production to grow the population and increasing the number of large legal-sized individuals. In the case of the model presented in this study, results were sensitive to the values used for natural mortality. Because protections for ovigerous females have a temporal component, overall survival determines how impactful longer-term protections such as v-notching are

to total egg production. If values for natural mortality are underestimated, for example, the results from this study would be overestimating total annual egg production as well as the relative impact of v-notching compared to a simple ban on harvest of ovigerous females.

As climate change brings both predictable and unexpected changes to the world's oceans and fisheries, stakeholders are expressing concern for building resilience into fisheries so that we can more easily adapt to these new changes. The state of Maine, for example, has included fishing in its climate resilience plan, "Maine Won't Wait," indicating that they are concerned about the future of their fisheries as a major part of their economy (Maine Climate Council 2020). Building climate resilience is not a simple task, but it is one that can be supported with up-to-date information as well as quantitative predictive modelling that incorporates those data. As climate change is a global issue, communicating and collaborating across boundaries to solve new challenges supports everyone.

Chapter 2: The Potential of Marine Protected Areas to Enhance Egg Production and Restore Size Structure of an Exploited Species

Abstract

The European lobster (*Homarus* gammarus) fishery in southern Norway uses a harvest slot limit in combination with a network of small no-take reserves as an effort to boost the lobster population. Lobster abundance in this region is low due to historical overfishing. Intense fishing pressure is also known to truncate the size and age structure of exploited species. Slot limits are a management tool used to protect small individuals long enough to reproduce, as well as large individuals with high fecundity. Implementing no-take reserves or marine protected areas (MPAs) can be a beneficial tool to preserve size-structure in exploited populations while also creating the opportunity to study how fishing changes population demographics by comparing lobsters in protected areas with nearby fished areas. Because slots limits and MPAs are very different methods of preserving size structure and increasing egg production, it can be difficult to empirically study the interaction of the two methods and examine their individual contributions. In this study, a deterministic model is used to compare these two management strategies to quantify their relative impacts on size structure and egg production of a simulated population of European lobsters. Results suggest that combining a slot limit with a MPA is more effective at preserving larger individuals and maximizing egg production compared to a slot limit alone.

Introduction

Fisheries managers use a variety of tools to help them combat effects of overfishing such as size structure truncation or skewed sex ratios. In crustaceans as well as in finfish, large individuals tend to have higher reproductive output than smaller ones (Estrella and Cadrin 1995; Agnalt 2008), so that when these individuals are removed from the population by fishing, overall fecundity and egg production is also greatly reduced. When size distribution is changed by fishing, size-based life history traits such as size at maturity can lead to population-level reductions in productivity and phenotypic variability (Hutchings and Fraser 2008). Fishery managements targets that seek to maximize productivity should therefore use restorative methods to help reverse size structure truncation, reduced egg production, and other effects of overfishing.

A restorative method that is gaining popularity around the world is the implementation of marine protected area (MPA) networks. These protected areas are also sometimes called no-take zones or reserves. While a MPA may be described in many different ways, Marcos et al. (2021) summarize the definition of a MPA as a designated space that protects the ecosystem, habitats, species, and more, while also providing social, economic, and cultural benefits or services. Because of the many benefits that reach beyond the exploited species, MPAs are a management tool that can help fisheries move towards an ecosystem management approach. MPAs range in size depending on the region and goals for implementation (Marcos et al. 2021). A common motivation to implement a MPA is to support nearby fisheries by increasing species abundance, size, reproductive output, or protect traditional fishing methods (Carter et al. 2017; Marcos et al. 2021).

While studies providing evidence for the benefits of MPAs are becoming more common, MPAs are still a somewhat novel management strategy for fisheries. Building on our understanding of how exploited species respond to this style of protection is essential for future decision-making and fishery

sustainability. Fisheries that are size- and/or sex- selective may alter the size structure and mating systems of exploited species like clawed lobsters (Sørdalen 2019; Moland et al. 2021). This in turn can affect population recruitment and productivity. Many studies have shown that MPAs effectively increase the abundance and size distribution of exploited species (see Marcos et al. 2021). They also may be more effective at preserving larger, older individuals in the population than a maximum size harvest limit or slot limit (Berkeley et al. 2004). It is less clear how a MPA interacts with other fishery management strategies such as slot limits, fishing seasons, or other protections.

Another widely used management strategy is a maximum harvestable size limit with a minimum size limit, otherwise known as a slot limit. Slot limits can protect the smallest individuals so that they can mature and reproduce at least once before being caught by the fishery as well as protecting the largest most fecund individuals. Protecting large individuals with a slot limit can be important for restoring mating and reproductive behaviors. Although the age and size structure of the species will be truncated by fishing mortality regardless of the slot, the slot limit will potentially conserve population structure more than fishing with no maximum size limit (Berkeley et al. 2004). Unfortunately, when fishing pressure is intense, few individuals may survive long enough to be protected by the upper size limit of the slot, defeating the purpose of the conservation measure, especially in species with high mortality (Kindsvater et al. 2020).

In this study, a population dynamics model is used to simulate the dynamics of fishing to test for quantitative changes in annual egg production and in European lobster population size structure for males and females under management strategies that represent regimes used in Norway currently, as well as in other regions. This chapter addresses the gap in current knowledge for how the interactions between a slot limit and a MPA lead to changes in size structure and reproductive output by modelling growth and egg production, using European lobster (*Homarus gammarus*) as a case study. The model

used is the same as the one used in Chapter 1 with expansions for protections due to the implementation of a MPA. Specifically, this study aims to quantify how a MPA with and without a slot limit can be expected to restore a more natural size structure, reduce sexual dimorphism, and enhance egg production. No protections for ovigerous females are included so that it is possible to focus on just the effects of size- and spatially- based protections. Empirical studies of the MPA network in southern Norway measuring net movement (Huserbråten et al. 2013) and mean size- and sex- specific survival (Fernández-Chacón et al. 2021) were used to parameterize the model.

I hypothesize that 1) spatially protecting a percentage of a fished population will increase overall egg production and 2) restore some of the size structure in the largest size classes with increased fishing effort. Slot limits are less effective at higher fishing pressures as individuals do not survive long enough to be protected by the maximum harvest limit size. Incorporating a MPA will provide protection for individuals in all size classes, making it possible for some individuals to grow to larger sizes. In addition, I hypothesize that 3) the size structure within the MPA will be less truncated than the size structure in the fished population, even with some movement of lobsters from the MPA to the fished area. The purpose of this study is to examine the combined effects of both size-based and spatially-based protections on European lobsters, with a focus on egg production, sex ratio, and size dimorphism. Using a simulation approach is a useful method of evaluating the relative effectiveness of management strategies in maintaining fishery productivity and size structure.

Methods

The methods for this chapter follow those used in Chapter 1 with a few adjustments representing different management scenarios. The key difference is that ovigerous females are no longer protected, and the model instead uses a hypothetical no-take MPA, with and without a maximum

harvestable size (116 mm carapace length) in the fished population (see Figure 2.1). Minimum size restrictions (88.16 mm carapace length for females and 89.09 mm carapace length for males; converted from 250 mm total length) were retained in all fished scenarios.

The simulation model was run for European lobster without fishing until the population reached a stable size distribution. Fishing was introduced with a minimum harvest size limit and with or without a maximum size limit until the population equilibrated. This model is not technically a spatial model, so to mimic the establishment of a MPA, 20% of the population was protected from fishing, and everything was allowed to reach a new equilibrium with 80% of the population continuing to experience fishing. When the MPA was established, it was assumed that individuals were evenly distributed and that the total area had uniform habitat and resource availability. During spawning within the model, mature females in both the fished area and the MPA produce eggs. It was assumed that once eggs are hatched, planktonic larvae from the MPA and the fished area enter a well-mixed larval pool, with 80% settling into the fished area and 20% settling into the MPA (proportional to the original size of the MPA). The net movement from the MPA to the fished area was assumed to fixed at 4.7% based on a study looking at lobster movement between a MPA and a fished area in southern Norway (Huserbråten et al. 2013). Additional parameters for natural mortality, recruitment, and others are the same as those in Chapter 1 Table 2 for European lobster.

Using the model outputs, total egg production and sex-specific size distribution were quantified in the following combinations of management scenarios: 1) Unfished, 2) Fishing with a minimum size limit (no slot), 3) Fishing with a minimum and maximum size limit (slot), 4) Fishing with no slot limit and n MPA, and 5) Fishing with a slot limit and a MPA. These combinations provide an opportunity to examine interactions between a slot limit and a MPA to quantify relative egg production and mean size dimorphism for females and males. The relative differences between each of these scenarios were then

quantified and plotted for analysis following the same procedures used in Chapter 1 with one exception. To compare the sizes of each sex in the fished area with those in the MPA, with and without a slot limit, mean size for each sex in each location was calculated for mature individuals only. Then, for each of the four scenarios, the mean length of each sex in the fished are was subtracted from the mean length of each sex in the MPA for $F = 0.0$ to $F = 0.9$.

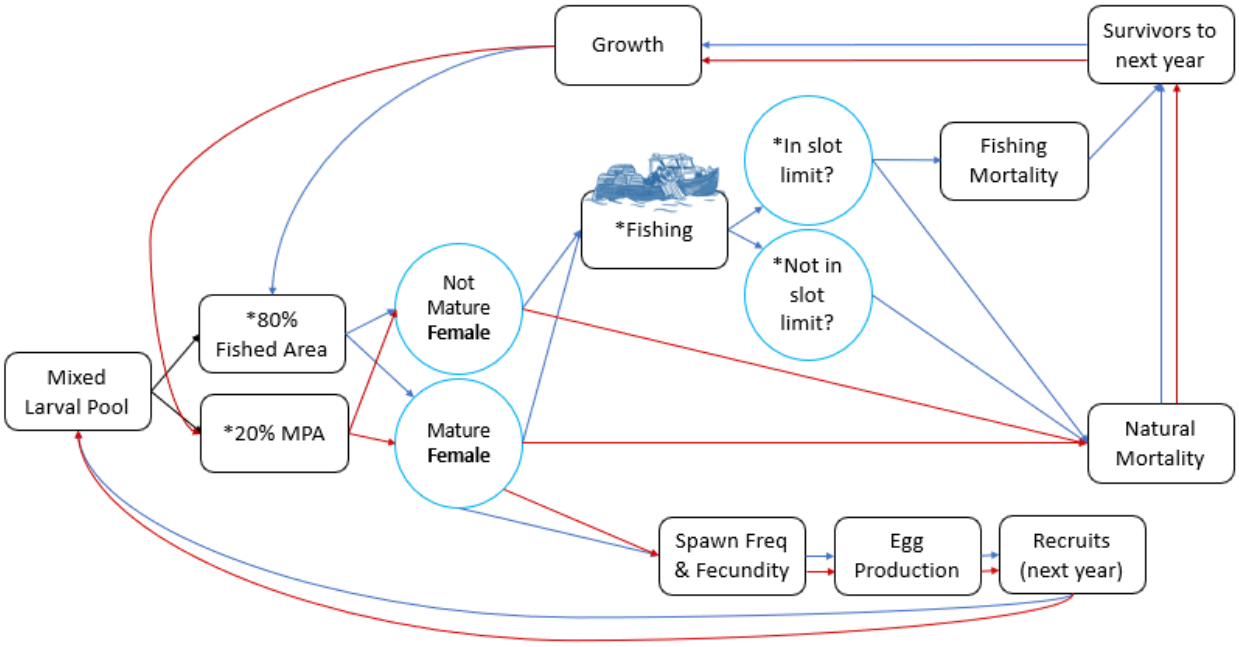

Figure 2. 1. Summary of the order of events that the model simulates over time. Items with an asterix are variable depending on the scenario. Blue lines follow the fate of lobsters in the fished area, and red lines follow the fate of lobsters in the MPA.

Results

A stable size distribution for European lobster was achieved by the model for each of the fished scenarios with and without a maximum harvest size limit, and with and without a marine protected area (MPA). The unfished size structure for both juvenile and mature lobsters can be seen in Figure 2.2. This

equilibrium size structure was calculated from the stable age structure, using the growth curve for European lobster in Chapter 1. As mature individuals are the main targets for the fishery, juveniles were removed from the rest of the plots for easier interpretation of the effects of different management solutions on mature lobsters. In every scenario, regardless of fishing pressure, slot limits, or presence of a MPA, mature females comprised 59 to 66% of the total mature population.

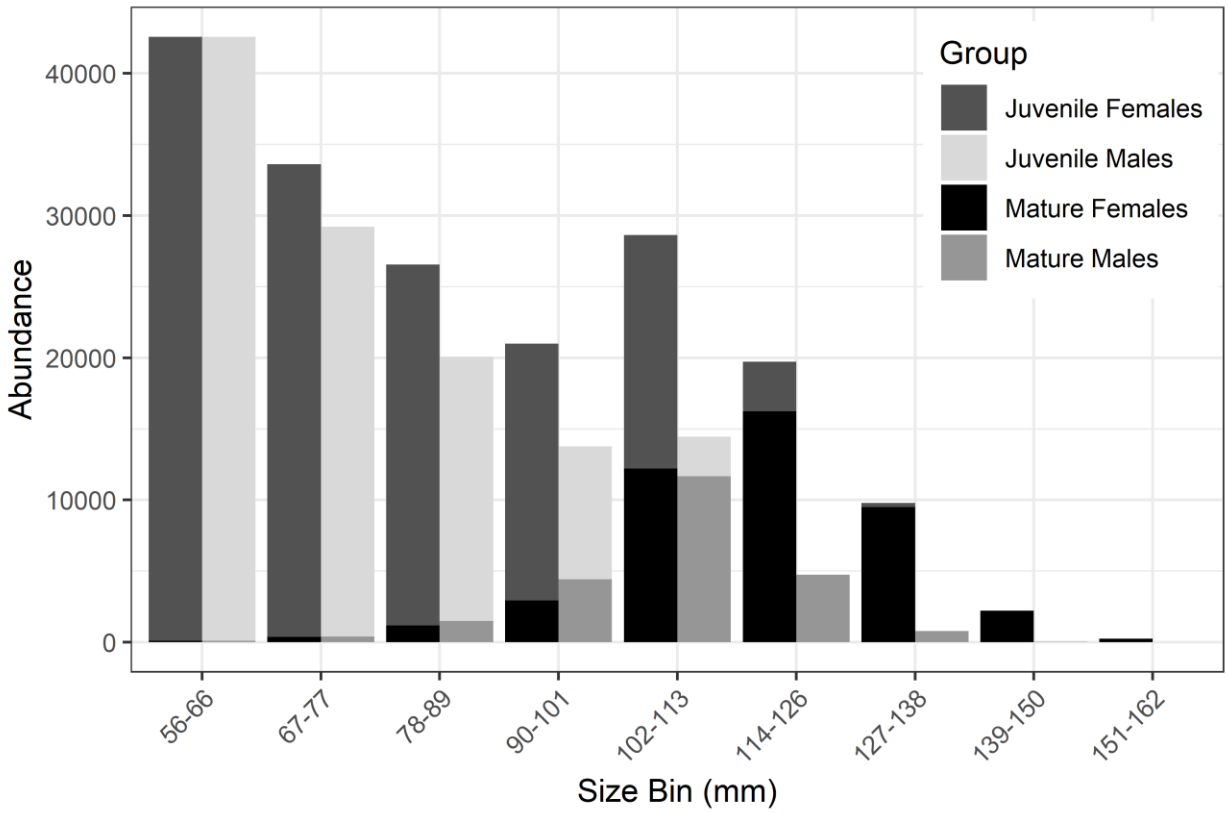

Figure 2. 2. Size structure of European lobster without fishing or a protected area. Lighter versions of the colors for females and males indicate immature individuals, and darker colors are mature.

Size Structure

Fishing with a slot limit and a MPA provided the largest increase in mature individuals in the largest size classes (Figure 2.3). With only a slot limit and no MPA, very few mature individuals—male or female—survived long enough to be protected by the slot limit at a fishing pressure of 0.8. The

maximum harvestable size limit was 116 mm carapace length, however, there was still high natural mortality beyond this length due to high natural mortality. Implementation of a MPA without using a slot limit was enough to increase survival within the length group that contained the maximum harvestable size for both females and males. Adding a slot limit in addition to a MPA added very few individuals to the largest three size classes. This was true for both males and females; however, it was slightly more evident in females since they have a lower natural mortality than males. Overall, the MPA provided far more benefit to rebuilding size structure in the largest size classes than a slot limit. Refer to Figure 3.2 in Appendix C for size structure plots for European lobster under these same management decisions but at *F* = 0.2, a lower fishing pressure with increased survival into the largest size classes.

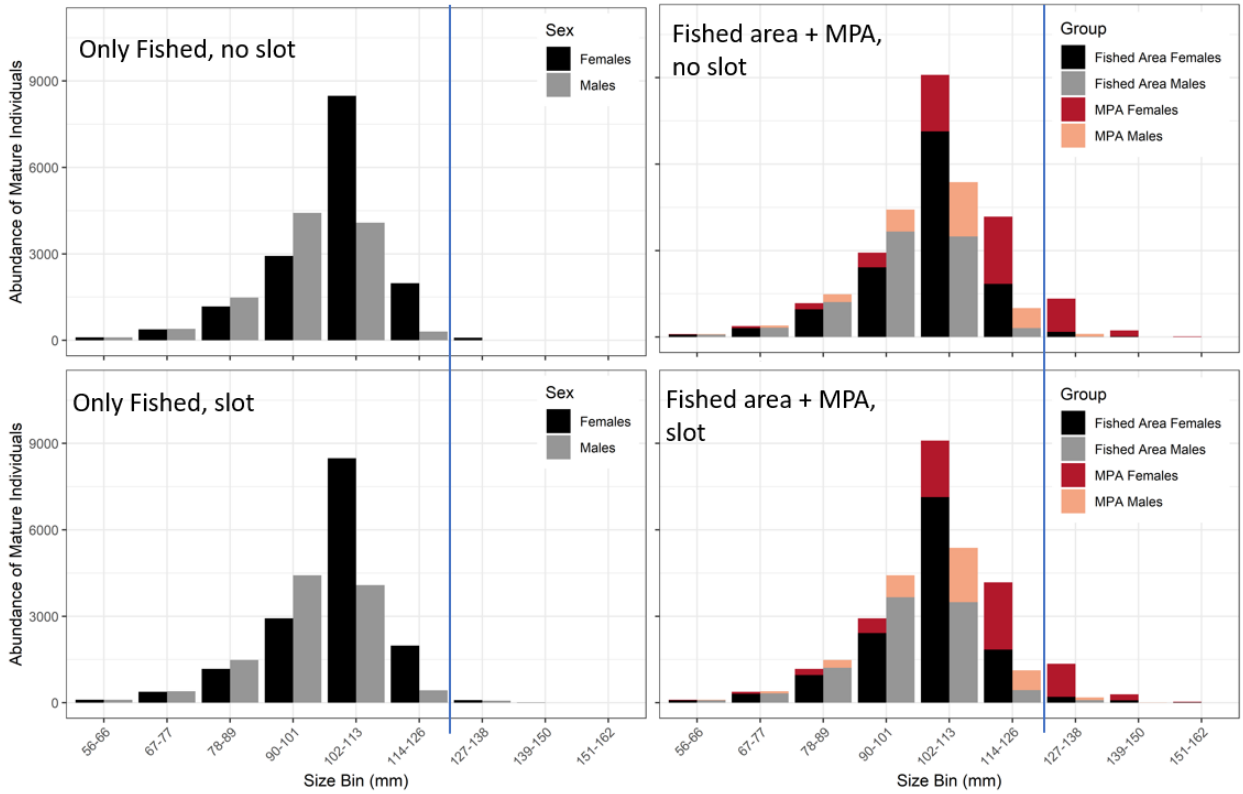

Figure 2. 3. Size structure of mature female and male European lobsters at F *= 0.8. The left column shows the size structure for a fished population with and without a slot limit. The right column shows the same with the implementation of a MPA. Shades of red are used to represent the lobsters found within the MPA as opposed to those vulnerable to the fishery. The size bin to the left of each vertical blue line contains the maximum size limit of 116 mm carapace length.*

Size Dimorphism

Mean length difference between females and males ranged from just over 2 mm carapace length in the unfished scenario, to 5 mm carapace length in the slot fishery at $F = 0.4$ (Figure 2.4). Males were always larger than females regardless of the scenario. Each scenario saw increased dimorphism with fishing until roughly $F = 0.5$, then decreased dimorphism as all populations became overfished. The fishery without the slot limit and the fishery with a MPA and a slot limit exhibited similar trends in dimorphism over all levels of fishing pressure, but the average sizes were larger with the MPA and the slot (Figure 2.4). The fishery with the slot limit consistently had the highest dimorphism over all levels of fishing pressure and the fishery with a MPA and no slot consistently had the lowest dimorphism (Figure 2.4). The two "extreme" scenarios—fishing with a MPA and a slot limit, and fishing without a MPA or slot limit—followed a similar trend in mean dimorphism over fishing pressures. However, interpreting Figure 2.4 with Figure 2.3 for reference, the individuals in the scenario with a MPA and a slot limit were on average several millimeters larger than those without the MPA or a slot limit.

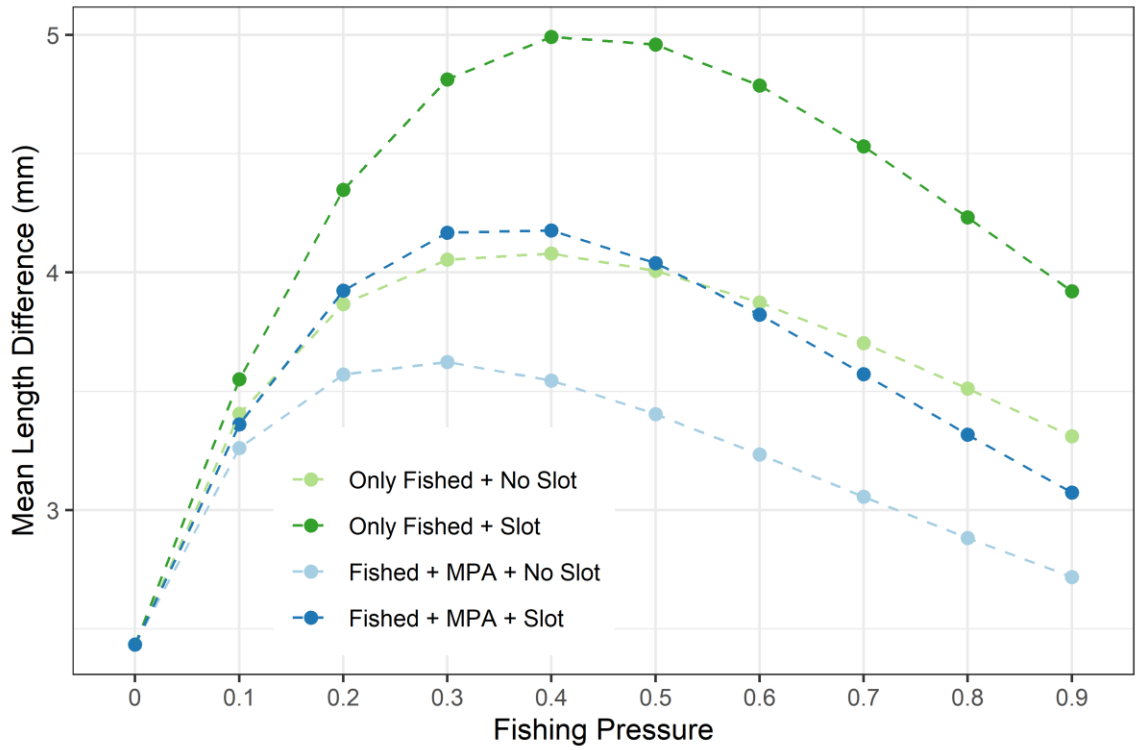

Figure 2. 4. Mean difference in length of mature male and female European lobsters. Males are larger than females.

Figure 2.5 shows the mean difference in size by sex of lobsters in the MPA and the lobsters in the fished area when a MPA is implemented with or without a slot limit. As fishing pressure increased, so did the difference in size between individuals in the MPA and the fished area with or without a slot limit. The inclusion of a slot limit led to overall lower mean differences as some of the larger individuals in the fished area were protected by the slot. Without a slot, females and males in the MPA were up to 11 mm CL larger than their counterparts in the fished area. With a slot, they were up to 10-11 mm CL larger. Overall, females in the MPA experienced the highest increase in size compared to the fished area when fishing pressure exceeded 0.2. The smallest difference in size between the MPA and fished area was seen for males when a slot limit was used.

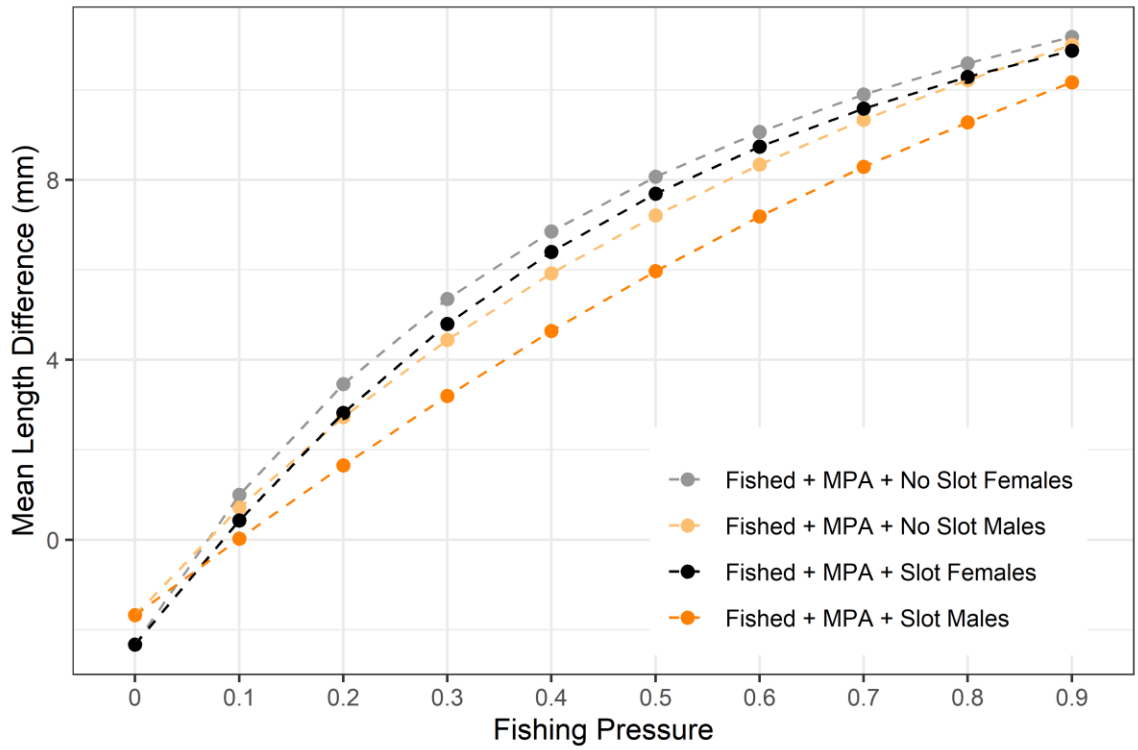

Figure 2. 5. Mean difference in length by sex between European lobsters in the MPA compared to the fished area when a MPA is implemented with or without a slot limit.

Egg Production

Total egg production was most influenced by presence of a MPA and fishing pressure (Figure 2.6). In general, as fishing pressure increased, egg production decreased. Slot limits improved egg production slightly (by 2-3% when scaled to the unfished level of egg production) when $F < 0.4$, but made little difference in egg production at higher levels of F compared to when only a minimum size limit was used, because fishing mortality was intense enough that few individuals survived to outgrow the slot. Implementation of a MPA, through protecting 20% of the adult population, led to increased egg production (relative to the no-MPA scenarios) as fishing pressure increased, ranging from a relative increase of 4% of production scaled to unfished levels at $F = 0.1$ to an increase of 11% at $F = 0.9$ (Figure 2.6).

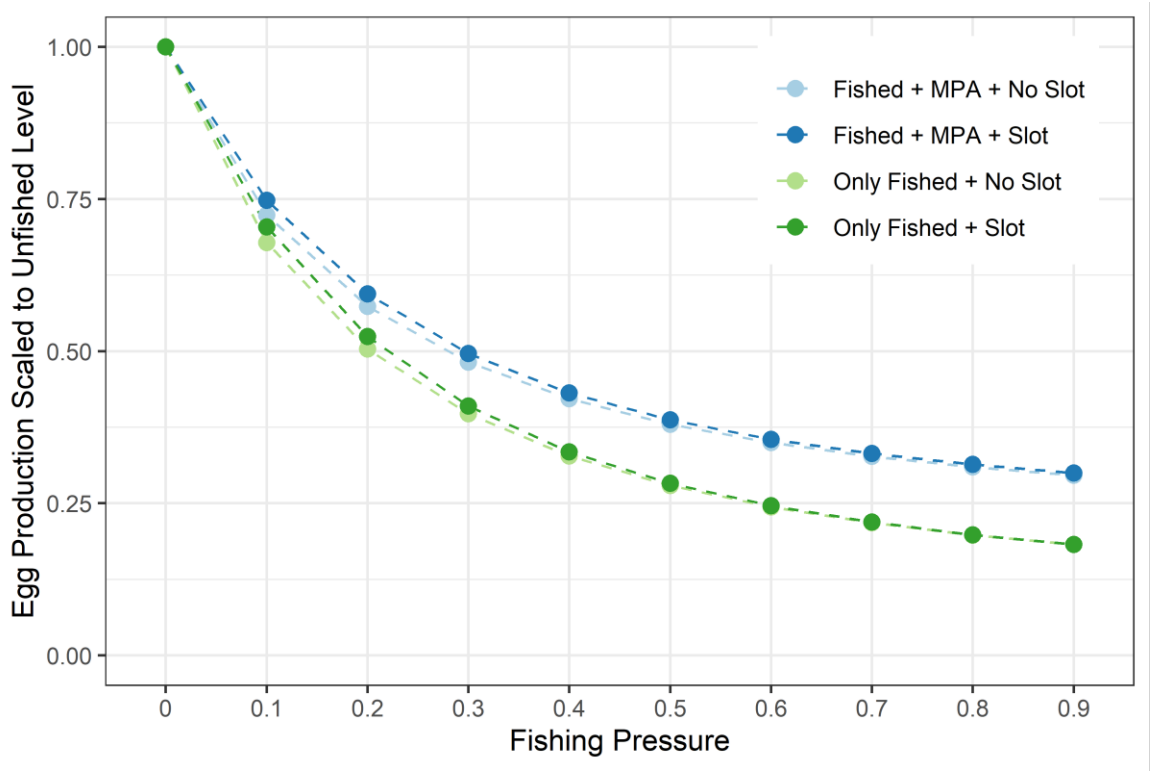

Figure 2. 6. Total egg production over a range of fishing pressure scaled to unfished levels. Darker shades indicate inclusion of a slot limit, and lighter shades indicate inclusion of a minimum harvestable size only.

Discussion

The model used in this chapter, like in Chapter 1, is a tool that can be used to quantify relative differences in egg production, size structure, and size dimorphism under different management styles. In this study, the model was expanded to incorporate protection for a proportion of the population as a simplified version of a MPA. This is intended to understand some of the benefits this type of protection might give to an exploited species at a basic level. Because no form of environmental variation or interaction with other species was included, there are limitations to this model as it is not spatially explicit. However, this model does succeed in simulating the population dynamics of European lobster in the context of protecting a portion of the population. A similar management tool to this is a quota, in

which fishers are only allowed to harvest a certain number of individuals. The relevant difference between a quota and a MPA in this case would be that the MPA protects a slice of the population according to location, also providing ecosystem benefits. The quota is more focused on single-species management and protection. With that said, population dynamics models can quantify relative changes in size structure, sex ratio, egg production, and more given different fishing intensities and management choices. Without the need for animal abundance data, this type of deterministic modelling is helpful for revealing relative trends in variables of interest, which can be challenging using noisy data alone. The model results can be used to discuss plans for management. In this study, the model was used to evaluate the relative effects of MPAs and slot limits on the demography of European lobsters. Results suggest that European lobster fisheries can benefit from these protections, however the slot limit provided little benefit to size structure and egg production compared to the MPA.

Results of this study indicate that MPAs can help restore natural size structures and patterns of dimorphism while boosting egg production considerably more than a slot limit alone. Slot limits alone provided only a minimal increase in egg production and relative abundance at larger sizes at low fishing mortality. At higher levels of fishing mortality, not enough individuals were able to survive through the slot to benefit from the protection, so egg production with and without a slot limit at these higher values of *F* were essentially the same. Protecting a fraction of the population from fishing altogether will allow for individuals to reach these large sizes and contribute more offspring to the overall population, thus supporting total fishable abundance, assuming there is movement between the protected area and the fishable area (Thorbjørnsen et al. 2018). One study in Australia found up to 152% higher egg production of an exploited species in a protected area compared to fished areas (Carter et al. 2017). Slot limits can select against fast growing individuals who recruit to the fishery more quickly and exhibit bolder behavior that leads to higher catchability (Biro and Sampson 2015). In this sense, a slot limit alone would not be enough to rebuild natural size structures, as seen in this study. Conversely,

MPAs in this study protected more individuals in large size classes and increased egg production more as fishing pressure increased relative to fishing without a MPA. In this sense, optimizing egg production using a slot limit and a MPA also depends on the intensity of fishing pressure. As fishing pressure increases, fewer and often smaller females are available for reproduction. For this reason, clawed lobster fisheries, including European lobster fisheries and the American lobster (*Homarus americanus*) fishery, that experience intense fishing pressure protect ovigerous female (v-notching, ban on harvest) to boost egg production by keeping proven breeders in the population while maintaining high fishing pressure (Daniel et al. 1989; Mazur et al. 2019).

When the MPA was a part of the management regime in this model, individuals were on average larger in the MPA than in the fished area, especially at higher fishing pressures. This is a trend that has also been seen in Southern Norwegian MPAs for European lobster (Sørdalen et al. 2018, 2020). This benefit could potentially be seen beyond just the increased body length alone, as it is hypothesized that male European lobsters, once they reach a large enough size, might instead focus on growing their crusher claw rather than increasing their length to improve mating success (Sørdalen et al. 2020). Another study has shown that lobsters with larger claws are more likely to be caught due to their increased competitive ability to guard the baited traps and ward off other lobsters (Moland et al. 2019).

Implementation of a MPA had a larger impact on egg production and preservation of larger lobsters than the slot limit alone. At lower levels of fishing pressure, the slot limit may help boost these numbers a little more when overall mortality is low enough that individuals can survive through the maximum size limit. While a slot limit loses effectiveness at higher levels of fishing mortality, a MPA protects lobsters at all sizes. Movement studies have shown that European lobsters that do leave the MPA tend to be large (Thorbjørnsen et al. 2018). Fishers in southern Norway will often “fish the line” of a MPA to take advantage of medium to large lobsters that leave the MPA but are still within legal size

limits (Nillos Kleiven et al. 2019). There is a possibility that lobsters that exceed the legal-size limit also leave the MPA and mate with lobsters in the fished areas, although there is no evidence for this yet. If this is occurring, it would have important implications for the evolution of lobster growth through countering fishery induced selection for smaller sizes (Sørdalen et al. 2022). Protecting these larger individuals by implementing a no-take MPA keeps these lobsters in the population to contribute to egg production rather than being removed by the fishery.

In reality, site selection for a MPA is challenging. The review by Knutsen et al. (2022) describes the process that Norwegian managers followed to select areas. According to that study, the key attributes a MPA should exhibit include: avoiding popular fishing areas, having a variety of habitats, being located where it can be easily monitored, and have fisher support (Knutsen et al. 2022). Depending on water currents in the vicinity of the MPA, larvae originating from the MPA and adjacent fished areas might mix together to improve overall recruitment compared to fishing alone without a MPA. However, for species for which recruitment is more localized, the benefit of a MPA on overall recruitment may be limited to the population within the boundaries of the MPA.

Thoughtful incorporation of fishery management strategies is important for achieving goals in fishery sustainability. Increasing egg production and preserving large individuals to restore natural mating dynamics and size structure are common goals of sustainable fisheries management. While these goals are typically inclusive of using slot limits, and more recently MPAs, more empirical work is needed to understand how these strategies directly or indirectly impact egg production and size structure. However, this case study suggests that while combining these two methods (MPAs and slot limits) led to the largest improvement to egg production and size structure, the role of a slot limit is limited, appearing to provide little improvement for larger values of *F*, and improvements only at low *F*. Egg production and size structure restoration are most benefitted from the MPA.

Rather than assuming that egg production can be approximated by population density or size structure alone, we should also consider additional variables that contribute to overall egg production (Carter et al. 2017). This study reveals that fishery management decisions do influence egg production and mean size structure of the European lobster population, but this model is only a first step, and its conclusions are preliminary. In reality, factors not included in this model such as potential for sperm limitation, likelihood of mating success given mean size dimorphism, and sex ratio, should be investigated as potential contributors to fishery-driven depletion of egg production (Pugh 2014). Fishing may also exaggerate skewed sex ratios that result from variation in temperature, depth, salinity or other environmental factors (Jury et al. 2019; Koepper et al. 2021). The model outputs from this study are useful tools for considering the relative effects of slot limits and no-take reserves on the demographics of European lobsters, however there are additional management strategies that can be used in tandem with these options, such as protections for ovigerous females, to reach our sustainable management goals. Understanding how these decisions and combinations of strategies impact a fishery is necessary to ensure its sustainability. Furthermore, results from Chapter 1 suggest that the protection of females while ovigerous or with a v-notch are likely to intensify sexual dimorphism and skew sex ratios even more than we considered here as fishing pressure increases. The role of the MPA is likely even more important given these consequences of protecting females. For this reason, managers of species with size-based mating behaviors and size- and sex-selective fishing practices should consider a combination of spatial protection (such as MPAs) and size-based regulations (such as slot limits) to achieve their sustainable management goals.

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Appendix A. Length-Proportion Molting Key for *H. gammarus*

Table 3. Probability of molting given pre-molt carapace length (CL) for females and males of species *H. gammarus*. Data is from Sørdalen et al. (2022).

Pre molt CL	Probability Molting	
	Female	**Male**
56	0.954438	0.998032
57	0.951875	0.997854
58	0.949056	0.997675
59	0.945928	0.997459
60	0.942785	0.99723
61	0.93953	0.996999
62	0.9361	0.996749
63	0.932807	0.99645
64	0.929357	0.996128
65	0.925385	0.995805
66	0.921234	0.995418
67	0.916776	0.995005
68	0.911843	0.994589
69	0.906924	0.994089
70	0.902283	0.993558
71	0.896988	0.993023
72	0.891413	0.992377
73	0.886097	0.99163
74	0.879958	0.990856
75	0.873675	0.990035
76	0.866951	0.989122
77	0.859425	0.988222
78	0.852112	0.987164
79	0.845206	0.985996
80	0.837312	0.984842
81	0.829186	0.983594
82	0.821436	0.982141
83	0.812478	0.98051
84	0.802719	0.978914
85	0.793065	0.977048
86	0.784099	0.974972
87	0.774081	0.972935
88	0.763528	0.970546
89	0.753681	0.967912
90	0.742565	0.965321
91	0.731203	0.962273
92	0.720504	0.958945
93	0.70734	0.955662
94	0.693841	0.951792
95	0.6823	0.947606
96	0.669446	0.943471
97	0.656279	0.939029
98	0.644049	0.933856
99	0.630305	0.928179
100	0.616654	0.922635
101	0.602488	0.91617
102	0.587108	0.90915
103	0.572675	0.902291
104	0.559467	0.894289
105	0.546175	0.885699
106	0.531627	0.87731
107	0.516899	0.867523
108	0.503462	0.857146
109	0.488632	0.847024
110	0.47273	0.835228
111	0.457912	0.822887
112	0.443497	0.810875
113	0.428896	0.796905
114	0.416458	0.782497
115	0.401268	0.768517
116	0.386254	0.753918
117	0.374399	0.737259
118	0.359801	0.71995
119	0.34544	0.703471
120	0.334156	0.684753
121	0.320325	0.665627
122	0.306783	0.64964
123	0.296191	0.626156
124	0.283265	0.604382
125	0.270663	0.586642
126	0.260849	0.564143
127	0.251267	0.541395
128	0.239636	0.52306
129	0.228355	0.500058
130	0.219613	0.477057
131	0.20904	0.458721
132	0.198821	0.440496
133	0.190929	0.417955
134	0.181417	0.395729
135	0.172254	0.378258
136	0.165199	0.356878
137	0.156721	0.336017
138	0.148578	0.319787
139	0.142326	0.300124
140	0.134833	0.281124
141	0.127654	0.266481
142	0.122157	0.255807

Appendix B. Size Structure Plots at F = 0.2 for American and European Lobster with Ovigerous Female Protections

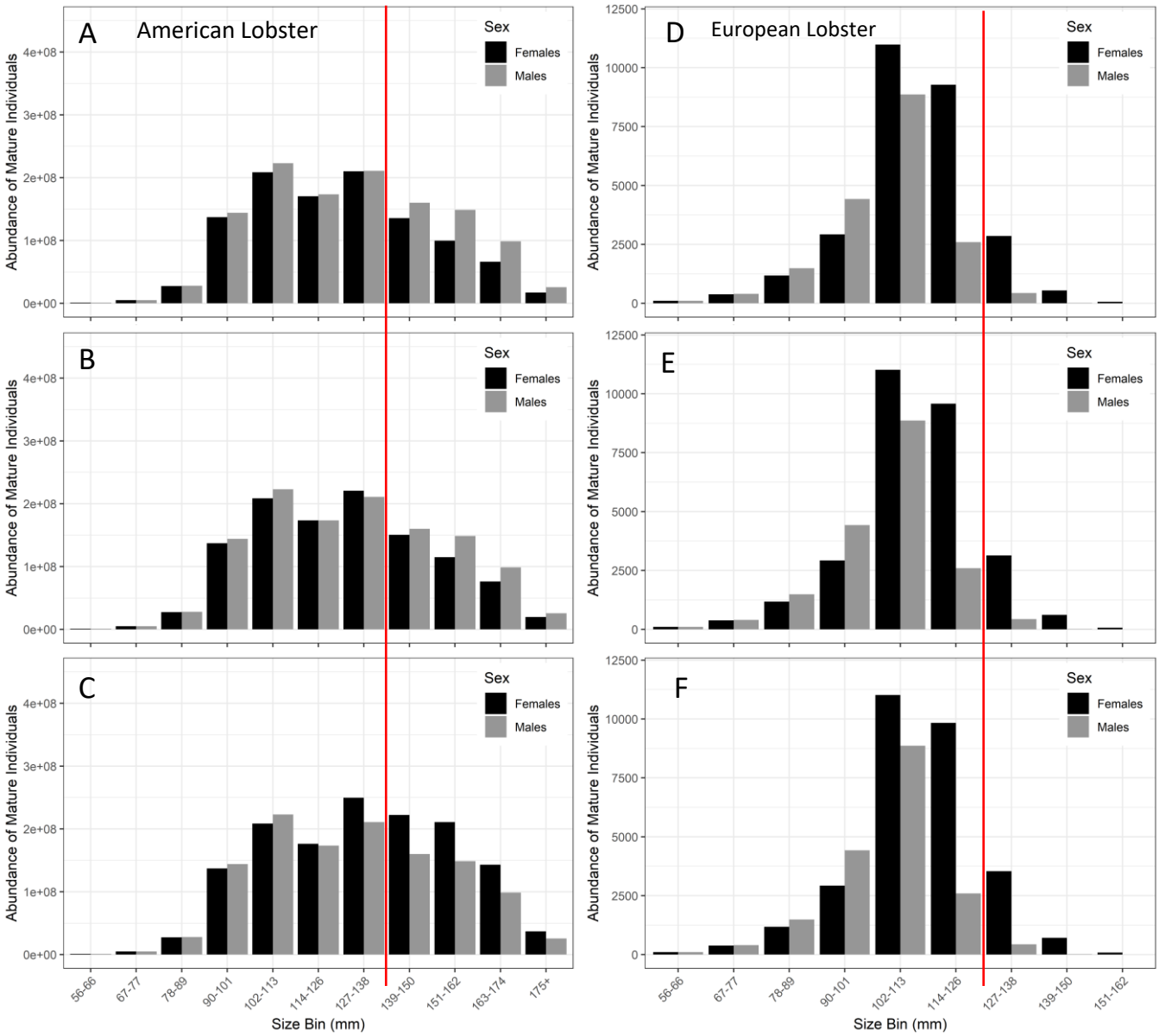

Figure 3. 1. Size structures of American (left) and European (right) lobsters with and without ovigerous female protections during fishing compared to the unfished size structure. Note that these are for mature individuals only at F *= 0.2. Panels A and D are fished without any ovigerous female protections. Panels B and E are fished with ban on harvest of ovigerous females. Panels C and F are fished with v-notching. The size bin to the left of each vertical red line contains the maximum size limit of 128 mm carapace length for American lobster and 116 mm carapace length for European lobster.*

Appendix C. Size Structure Plots at F = 0.2 for European Lobster with Slot Limits and a MPA

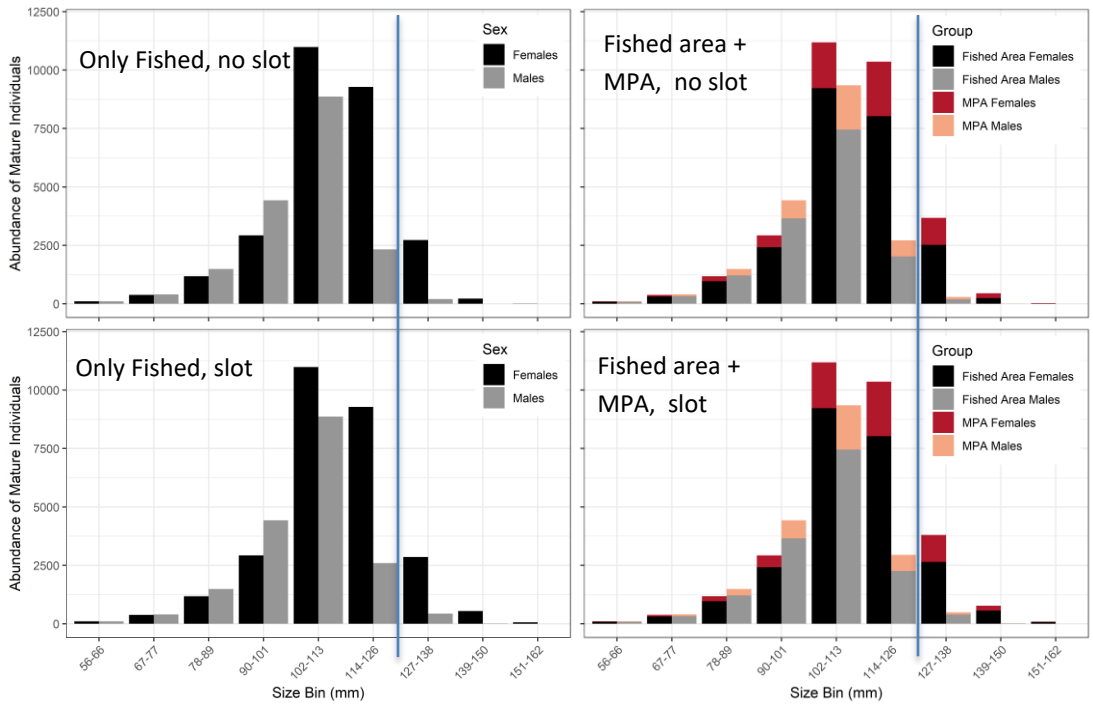

Figure 3. 2. Size structure of mature female and male European lobsters at F *= 0.2. The left column shows the size structure for a fished population with and without a slot limit. The right column shows the same with the implementation of a MPA. Shades of red are used to represent the lobsters found within the MPA as opposed to those vulnerable to the fishery. The size bin to the left of each vertical blue line contains the maximum size limit of 116 mm carapace length.*