Age Structure Response of Principal Groundfish to Marine Protected Areas in New England

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AGE STRUCTURE RESPONSE OF PRINCIPAL GROUNDFISH SPECIES TO MARINE PROTECTED AREAS IN NEW ENGLAND

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Atlantic cod (*Gadus morhua*), yellowtail flounder (*Limanda ferruginea*), and haddock (*Melanogrammus aeglefinnus*) were once dominant species in the New England fisheries economy, together accounting for over half of the landings value of groundfish. Over the last several decades, all three species have experienced dramatic shifts in spawning stock biomass (SSB) with current estimates for cod stocks at 3% and 7% of target biomass (Gulf of Maine and Georges Bank stocks, respectively), a strong contrast to haddock stocks that are nearly fully recovered (NEFSC 2014, 2017). As principally demersal species, they are easily targeted by trawl and gillnet, the former representing the majority of landings in New England waters. Now considered a choke species for the entire groundfish fleet, the current state of cod may signal the demise of other fish stocks if management measures are not adjusted. Despite a 2010 shift from input controls to a mixture of input controls (i.e., year-round closures) and output controls (i.e., hard quotas), along with yield-based stock assessment reference points, the outcomes for these key groundfish have been confounding. Some suggest that the failure to account for age structure of populations in management may underplay the value of old fish, those which
are generally removed by commercial fishing (Le Bris 2013, Secor 2015, Stige et al. 2017). Age truncation, vulnerability to overoptimistic assessment, and increasing amplitude of climate oscillations all put the recovery of certain species at risk (Berkeley 2004, Pershing et al. 2015). One of the key management changes enacted with the Sustainable Fisheries Act of 1996, was the implementation of year-round closures throughout New England waters. Heralded as a backstop to uncertainty, these temporary Marine Protected Areas impart a conservative management approach with the simple goal of reducing overall mortality. Nearly 25 years after the first areas were closed to fishing, research has been inconclusive about the effects on the groundfish species that they were designed to protect (Murawski et al 2005, Kerr et al 2012). Until now, no study has investigated the effects of these closures on the age structure of these three species.

To measure change, I applied three age metrics: mean age, age diversity, and catch-per-unit-effort of age 5+ fish. Together, these three metrics provide measures of change across large spatial and temporal scales.

In Chapter 1 of this thesis, I employ a Before-After Control-Impact (BACI) analysis to five year-round fisheries closures in New England. Data was drawn from over 35 years of the New England Fisheries Science Center’s bottom-trawl survey. Using stratified-random and distance-based controls, I employed generalized linear models (GLMs) and hurdle models to define significant changes to groundfish age structure. Further investigations describe the temporal response to closed areas and discuss the different ways that closure effects on age structure can manifest. Results show that in several cases, these closures function to improve age metrics in the species they were
designed to protect. Discussion of the magnitude of change and confounding management factors lead to future considerations of spatial management of groundfish.

In Chapter 2 of this thesis, I focus on Cashes Ledge Closed Area (CL). Designed to reduce groundfish mortality, its effects on the age structure recovery on Atlantic cod are unclear. Previous work here has shown that in areas where older fish range, adjacent to Essential Fish Habitat (EFH), catch inside closures can produce up to 8 times more old cod (age 5+) than surrounding open areas (Sherwood & Grabowski 2016). While the benefits of protected areas assigned EFH status seem obvious, it is unclear how age structure of the cod population in this area responds across distance and varying habitat. Results on cod from Chapter 1 show limited sampling throughout the closure, particularly over complex bottom that is difficult to trawl. With a survey designed to measure the same age metrics as Chapter 1, I sampled sites using alternate gear types (gillnet and handline) across the entire closure and adjacent fishing grounds to the Northwest. Results showing a significant positive closure effect support those of previous work (Sherwood & Grabowski 2016), but the subtle magnitude of change and results of habitat modeling, reveal that nearly 15 years after the closure was implemented, depth is the major driver of these measured age structure metrics. Highest age structure metrics manifest over habitat characterized by shallow and complex bottom, which serve as havens for a species under serious threat from fishing mortality and climate change.

Chapter 1 provides a broad perspective of change over large scales of space and time. Samples are grouped over the entire closures and before-after periods include as many as 25 years of data. Chapter 2 provides a detailed investigation of a single closure over two summer/fall sampling seasons, 15 years after closure. Together these chapters
provide perspective on what age structure health looks like and its lasting implications on the future of the groundfish fishery in New England.
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CHAPTER 1:

A BEFORE-AFTER CONTROL-IMPACT ANALYSIS OF GROUNDFISH AGE STRUCTURE IN RESPONSE TO FIVE YEAR-ROUND FISHERIES CLOSURES

ABSTRACT

Assessing the impact of marine protected areas (MPAs) on marine resources is challenging, but crucial to understanding the role this management approach can play in ecological resilience. In many cases, MPA impacts can be masked by large-scale processes (e.g., environmental change or simultaneous management action) experienced in an ecosystem. However, analysis of data collected before and after implementation of spatial closures can enable evaluation of the effects of fisheries closures on the demography of principal groundfish species (yellowtail flounder, haddock, and Atlantic cod). Growing evidence points to the importance of older fish in population recovery due to factors such as high productivity and spawning habitat selection behavior. In this chapter, I employ a Before-After Control-Impact (BACI) analysis to five year-round fisheries closures in New England. To measure age structure health, I apply three age structure metrics: mean age, age diversity, and catch-per-unit-effort of age 5+ fish. Model results show that a diminished age structure in the Gulf of Maine cod population can recover due to protection from the Western Gulf of Maine Closure. In a species with exceptionally strong recruitment events over the last 15 years, Closed Area I helped maintain healthy age structure and protect older haddock. Yellowtail flounder, a fishery with little sign of recovery, benefited from spillover effects in Closed Area II, with greatest closure benefit arising from the numbers of older fish caught inside the closure.
INTRODUCTION

Marine Protected Areas

Only recently have we begun to understand the capacity at which human impact through commercial fishing can shape community ecology on a grand scale (Hennesey & Healy 2000, Pauly et al 2005). The recent paradigm shift from single species management toward ecosystem-based approaches, has led to increased consideration of ecological and evolutionary processes in management measures (Brodziak et al 2004, Francis et al 2007, Basket & Barnett 2015). Yet, despite efforts to reduce groundfish mortality, New England fisheries management actions have stumbled to produce strong signs of recovery in several populations. The question then arises: can we create protective measures that focus on the long-term recovery of populations that face pressures such as climate induced-change and new ecological stable states?

A cornerstone of ecosystem-based fisheries management (EBFM) is the establishment of marine protected areas (MPAs, Francis et al 2007). Restricting harvest over large spatial areas can lead to increased abundance and biomass of harvested species within protected areas. MPAs have also been applied to achieve a range of fisheries objectives, including reducing groundfish mortality, spawning protections, and biomass spillover (Lubchenco 2003, Russ & Alcala 2004). However, the effectiveness of MPAs are highly dependent on characteristics of the protected area (e.g., sizing and scale) and how these features interact with the traits of fish species, structure of the ecosystem, and features of the environment they are aimed at protecting (Sanchez-Lisazo 2000, Lubchenco 2003, Basket & Barnett 2015).
Understanding the spatial and temporal scale at which fish populations will respond to spatial management is an important aspect when evaluating MPA effectiveness. The multi-generational process of demographic response can occur on a decadal scale and estimates of full biomass recovery to pre-fishing states are as high as 40 years for some fish species (Russ & Alcala 2004, Hsieh et al. 2010, Babcock et al. 2012). While it is estimated that a spatial closure is required to be approximately twice the size of the home range of the harvested species, demographic response inside the closure can be highly dependent on exploitation pressure outside (Murawski 2005, Babcock et al. 2012). Furthermore, pre-settlement larval dispersal of marine organisms can be an important outcome of spatial closures, resulting in improved recruitment success for fish stocks due to protection of critical nursery habitat (Murawski 2000, Wen et al. 2013, Basket & Barnett 2015). Another consideration is the occurrence of distinct ecotypes (e.g. resident and migratory types of Atlantic cod) as the response to closures could manifest differently across habitats and behaviors (Svedäng et al. 2007, Sherwood & Grabowski 2010, Conroy et al. 2017). Spawning site fidelity and connectivity between spawning groups (e.g. metapopulation structure) can also play an important role in the impact of spatial management (Frank & Leggett 1994, Wright et al. 2006, Zemeckis et al. 2017). For more sedentary species, which have stronger substrate- and prey-specific life histories, spatial management may present a clearer path to recovery (Bigelow & Schroder 1953, Murawski 2000). Ultimately, the spatial and temporal scales at which a population will respond to a closure depends on many factors. It is therefore crucial to deepen our understanding of closed areas and their effects on harvested species in the Gulf of Maine. If the first commandment of EBFM demands a holistic, risk-averse, and
adaptive approach to fisheries science, perhaps closures provide the hedge needed to forestall collapse (Francis et al. 2007).

**Marine Protected Areas in New England**

In response to declining biomass of principal groundfish species (Atlantic cod, haddock and yellowtail flounder) in the 1990s, the New England Fisheries Management Council enacted spatial management measures designed to reduce fishing mortality and protect critical life history processes (e.g. spawning). The closed areas include two large areas on Georges Bank (Closed Area I (CAI) and Closed Area II (CAII)) and one area off southern New England (Nantucket Lightship Closed Area (NL)) established in 1994. Closed areas I and II were implemented to protect haddock spawning and the Nantucket Lightship closure was aimed at reducing fishing mortality and enhancing spawning potential of yellowtail flounder (Figure 1.1).
Figure 1.1 Map of Closed Area Boundaries in New England waters. Closed I, Closed Area II, and Nantucket Lightship were established in 1994. Western Gulf of Maine Closures was established in 1998. Cashes Ledge closure was closed year round in 2002.
Following closures on Georges Bank, the Western Gulf of Maine closed area (WGOM) was implemented in 1998 to reduce the mortality of the Gulf of Maine cod stock which had seen steady declines over the previous decade (Northeast Multispecies Fishery Management Plan 1998). In addition, the Cashes Ledge Closed Area, in the center of the Gulf of Maine, became a year-round closure in 2002 (except for recreational fishing and exempted fishing gear) with the aim of reducing general groundfish mortality. These closures, paired with other management measures such as reduced days at sea, have improved abundance and biomass for stocks of yellowtail flounder and haddock (Murawski 2000, Brodziak et al 2004, Kerr et al. 2012). However, the evaluation of closed area impacts has been limited to date.

The southernmost New England closure, NL, was originally intended for protection of yellowtail flounder. Examination of this area after closure demonstrated that biomass of yellowtail flounder was lower within the closure than the surrounding area (Barkley 2011, Kerr et al. 2012). However, there was evidence that the closure benefited biomass of other species, including haddock and scallops. While greater haddock abundance was evident inside the closure, a 14-fold increase in scallop biomass led to the opening of a special access program (SAP), open to rotational scallop dredging (Murawski2000). This highlighted a case where regulators reached a compromise on the value of a fishery versus conservation goals such as the protection of benthic habitat and emergent epifauna within the NL closed area (Lubchenco 2003, Brodziak et al 2004).

A large portion of Georges Bank is protected by CAI and CAII (Figure 1.1). Research on CAI has shown some signs of effectiveness; Sherwood (2009) found that
haddock displayed resident behavior within the closure and Kerr et al. (2012) found a significant increase in biomass-per-tow of both haddock and winter flounder. An investigation of fishing patterns found an increase in catch of both yellowtail flounder and haddock along the closure boundary (within 4 km), suggesting a spill-over effect of Georges Bank closures (Murawski 2005). Closed Area II has seen significantly more research on habitat effects than other closures. Colonial epifaunal species diversity and abundance were significantly greater in areas free from bottom-tending mobile gear disturbance (Collie et al. 1997, Hermsen et al 2003, Collie et al 2005).

The WGOM was aimed at enhancing recovery of Gulf of Maine cod, however, evaluation has revealed mixed results with some indication of higher occurrence of cod within the closure (Grizzle et al 2009), whereas another study found no significant impact of the closure on abundance and biomass (Kerr et al 2012). A survey of the northern section of the closure showed a higher incidence of monkfish outside the closure, potentially owed to soft-sediment habitat preference or positive effect of trawling disturbance (Smith et al 2008). Despite the lack of major consensus that the closure has improved conditions for cod, the area covers vital spawning grounds for the Gulf of Maine stock (Zemeckis et al 2014).

The Cashes Ledge Closed Area is unique in the Gulf of Maine, as it contains a rare seamount called Ammen Rock. At its shallowest point, this underwater mountain range nearly breaks the surface and supports groundfish nursery habitat in the only offshore kelp forest in the Gulf of Maine (Witman & Sebens, 1992). It is the only offshore habitat that harbors distinct resident ecotypes of cod, identified by their red color pattern (Sherwood and Grabowski 2010). Recent efforts to designate it as one of the first National Marine Monuments in the Northeast U.S failed, but much like other New
England closures, there is both opposition and support for their longevity. Apart from Sherwood and Grabowski (2016), which showed positive effects on several life-history variables for cod including higher growth and median age, no studies have measured the effect of the closure on groundfish.

**Importance of Age Structure**

The demography of unfished populations is dependent on recruitment, growth, and natural mortality (Hilborn & Walters 1993). If we assume steady recruitment, growth, and natural mortality and introduce increasing fishing mortality rates, older cohorts are removed and the distribution of ages skews toward younger fish (Ricker 1975, Figure 1.2).
Figure 1.2 A simple schematic of age structure curves under varying fishing mortality rates. The x axis represents age class and the y axis represents abundance. F = fishing mortality rate. (Ricker 1975)
Several groundfish stocks in New England waters are currently “overfished” with overfishing occurring in recent decades (NEFSC 2017). In the most recent assessments of stock status, the New England Fisheries Science Center (NEFSC) concludes that both New England cod and yellowtail flounder stocks show truncated size and age structure. Understanding fishery declines is a complex problem, yet many signs are pointing toward an under appreciation of the value of older fish within populations (Berkeley et al 2004, Secor 2005, Hsieh 2010, Hixon et al 2014).

Young fish generally produce fewer and smaller eggs, spawn for shorter periods, and have lower fertilization rates (Trippel 1998, Murawski et al 1999). Furthermore, successful spawning relies on density-dependent factors, as well as hydrographic conditions, diet and nutritional conditions, such that fish may even abandon spawning when conditions are not met (Sherwood et al. 2007, Rideout & Tomkiewicz 2011). If variable conditions are the norm, selection will favor variation in timing of spawning. In this sense, older fish have a greater chance of successful spawning since they may spawn over a longer period (LeBris 2013). This increases the chances that one of their batches will encounter favorable conditions as exemplified by the match-mismatch hypothesis (Cushing 1974). Some view the truncation of age structure, leading to decreased age and size of maturation as a biological regime shift, induced by fishing pressure through short term evolutionary selection (Berkeley et al 2004, Olsen et al. 2004). It may be that overfishing of cod stocks in the Gulf of Maine for a prolonged period has resulted in the loss of critical diversity in spawning and migration behaviors required to maintain historic biomass.

When a population undergoes age structure truncation due to intensive fishing pressure, the remaining cohorts can be freed from density-dependent processes and
successful recruitment can be more dependent on environmental variability (Secor 2015). While variability in fecundity and maternal effects can dominate spawning success at high stock size, spatial and temporal variations paired with environmental oscillations can dominate the productive capacity when stocks are at low biomass (Marteinsdottir & Thoranssen 1998, Secor 2005, Le Bris et al 2013, Secor 2015). Hutchings and Myers (1993) described temporal changes in the cod fishery’s reliance on young, first-time spawners. Their results showed that young females off the Newfoundland coast displayed a shortened spawning season and suggested that this could lead to a mismatch in timing between larval emergence and peak zooplankton production, overall reducing the success of recruitment. Any mechanism that leads to lower than expected recruitment at low stock size in fish can be considered depensatory or an Allee effect (Hutchings 2013). In multi-batch spawners such as cod, the lowered likelihood of successful spawning of younger fish through reduced egg viability, can lead to stock population instability (Hixon et al 2014).

Fisheries management measures aimed to protect age class diversity, in addition to maintaining optimal stock abundance, are needed. Secor et al (2007) reasoned that the ability of a population to asynchronously respond to environmental changes may be defined by a metric termed the Portfolio Effect (PE). A high PE, contingent upon the presence of a diversity of highly productive spawners, was shown by Schindler et al (2010) to be vital to stability in the Alaskan sockeye salmon fishery (albeit not by diversity in ages but rather by diversity in spawning timing among distinct populations making up the stock complex). In our contemporary example in the US Northeast, with recent climate oscillations and rapidly warming waters, it may be increasingly important to maintain a portfolio of diverse ages and spawning components (Secor 2007, Secor
2015, Pershing et al 2016). A diverse age structure can only be built by successful recruitment and well managed exploitation. While it has been suggested that marine protected areas can reduce age structure truncation, current management schemes for groundfish in the northeast are focused solely on rebuilding or maintaining spawning stock biomass (Berkeley et al. 2004, White et al 2013, Basket & Barnett 2015).

It has long been argued that fishing at maximum sustainable yield (MSY), an outcome of single-species management, can lead to a reduction of age classes and a high proportion of young and first-time spawners (Larkin 1977). Despite mounting evidence that a well-balanced age structure contributes to resilience of a stock, it is still unclear whether managers can directly control age structure recovery in a multi-species fishery, like that of New England groundfish. Changing size-based management to include upper size limits, could protect older fish, but would be difficult to impose in a trawl dominated fishery where the discarded mortality rate is high (Reed 1980, NEFSC 2014). Simulations of various fishing effort controls on cod found no difference in age structure metrics. Furthermore, natural demographic variability and mortality, resulting in strong year classes may mask any evidence of management control (Brunel & Piet 2013). There is some evidence that maternal age effects can positively impact recruitment success and lead to higher SSB in cod (Shelton et al 2015). Given the existing groundfish scenario in the Gulf of Maine, it may be that no-take reserves are the simplest and most effective tool at protecting age structure. Sherwood and Grabowski (2016) showed that the benefits of closed areas on key life-history characteristics of cod are significant and suggested that they may be the only tool at our disposal to protect older age classes. They showed that median age of cod was consistently one year older and old cod were 8 times more abundant inside the closed areas compared with adjacent open areas. However, they did
not assess to what extent this result is influenced by scale (i.e., size of closed areas) or habitat.

The goal of my study was to evaluate the effect of marine protected areas (aka closed areas) in New England waters on the age structure of principal groundfish species. This study utilizes standardized trawl survey data to test the hypothesis that closed areas enhance the age structure of yellowtail flounder, haddock, and cod. Using BACI analyses and annual trends in age structure indices, I present a detailed account of age structure response to closed area management, and effects that may influence the future of Gulf of Maine fisheries.

**MATERIAL AND METHODS**

**Data**

Biological data for Atlantic cod, haddock and yellowtail flounder was obtained from the Northeast Fisheries Science Center (NEFSC) bottom trawl survey (1970-2016). Surveys were conducted bi-annually (spring and fall) using a stratified-random design with standardized protocols (Aarowitz 1981). The length of all fish caught were provided on a tow-by-tow basis. In addition, for each bottom trawl tow site, a subsample of each species was taken to determine biological characteristics, including age based on fish otoliths. Using the aged subsample, I constructed age-length keys for each species within their respective stock management boundaries. Age-length keys were applied to the length frequency of the entire catch data set from the NEFSC bottom trawl to generate age frequency.

Data were grouped for applying BACI analysis which requires definition of impacted (closed areas) and control treatments into equal time periods before and after
the impact. Alternative definitions of control areas were examined, including strata-based and distance-based controls. Distance controls included samples from concentric 10 km bands around each closure and were included in a multivariate model against the closure. Depending on the ranging habits of each species, these controls were designed to measure the scale at which age structure enhancement occurred because of proximity to the closure (up to 40 km away; Figure 1.3).
Figure 1.3 Distance based control rings around Closed Area I. The inner dashed red line represents the closed area boundary and each concentric line outside represents 10km buffer. Colored points indicate random sample locations used in BACI design.
Several distance-based control areas were selected to evaluate the role of distance from closed area boundary on its effects and to avoid spatial confounding amongst sites, known as ‘pseudoreplication’ (Underwood 1992). For each distance-based comparison, all samples inside the closure were included. Strata-based controls included random samples drawn from each pre-defined NEFSC trawl survey strata. Strata-based controls allowed for balance between habitat associations and are defined by the depth ranges and latitudinal species distributions (NEFSC definitions; Figure 1.4). Low treatment sample sizes (n<100) and samples from strata that overlapped with other closures were omitted from analyses.
Figure 1.4 Strata-based control samples of haddock in Closed Area I experiments. Samples were drawn from overlapping strata inside and outside Closed Area I. Gray lines denote NEFSC strata boundaries. Black crosses indicate randomly drawn sampling stations from BACI design.
Statistical Analysis

For each closed area, I compared the response of three age metrics designed to characterize age structure: mean age, age diversity (Simpson 1949, Secor 2000), and catch-per-unit effort of age 5+ fish (CPUE5+). Mean age was calculated as the mean age per tow averaged across each closed area and control area. Age diversity was calculated following methods of Marteinsdottir & Thoranensen (1998), an application of Shannon’s Diversity Index ($H$). Shannon’s $H$ is defined as:

$$H = - \sum_{i=1}^{k} (p_i \cdot \log p_i)$$

In this study, $p_i$ represents the proportion of individuals in each age class and $k$ is the number of age groups present. $H$ was calculated for each year within each treatment (closed areas and control area; before and after). $H$ values and resulting confidence intervals for annual trends were calculated using R package \{vegan 2.4-3\} (Oksanen et al 2017). Sherwood and Grabowski (2016) defined old cod as age 5+ when making broad comparisons in catch among open and closed areas. I adopted the same age cut-off to explore response of older fish to closures. CPUE5+ fish is defined as the number of age 5+ fish per tow (standardized unit of effort) and averaged across treatment.

I applied BACI analysis to test the effect of closures on the three age metrics. BACI analysis is a common approach used to assess treatment effects in many scientific disciplines (Green 1979). In ecology, BACI is typically applied to assess population changes in response to natural disturbances or management actions. A BACI design has been used to assess effects of MPAs on various metric, such as biodiversity and
abundance (Popescu et al. 2012, Moland et al. 2013, Ahmadi et al. 2015). Each BACI model was fit with the following equation:

\[ Y = time + location + time \times location \]

where time refers to periods of equal duration before and after implementation of closure, and location refers to samples drawn from either inside or outside the closure. The main effects of this model test for effects of time and location, independently, while the model interaction tests for the combined effect of time and location. Location is defined as samples drawn from either inside or outside the closure. In distance-based experiments, location is further defined by 10 km distance buffers from the closure boundary. Time is defined as grouped samples from before and after the implementation of the closure. The interaction shows the combined effect of location and Time. A significant positive interaction indicates a positive effect of the closed area on the age metric.

I applied a Generalized Linear Model (GLM) to test mean age and age diversity. A two-step, hurdle model, designed to deal with overdispersion and excess zeros, was fit for CPUE5+. The binomial portion of the two-step model tests the impact on probability of occurrence and the count portion of model tests impact on number of fish. Model input for mean age included the entire age distribution of the sample treatment, whereas age diversity was calculated by year before model input. CPUE5+ was modeled by individual tow event. Aikake Information Criterion (AIC) and Likelihood Ratio Test (LR test) were applied to assess goodness of model fit. Model diagnostics were evaluated to ensure assumptions of tests (normality and homogeneity of variance of the data) were satisfied. In the analysis of spatial scale on age, the residuals of the models were plotted on a spatial scale and interpolated using an inverse distance weighted method. To investigate
finer scale temporal changes in age demographics, each metric was summarized and plotted by year.

RESULTS

The response of Atlantic cod, yellowtail flounder, and haddock to five year-round closed areas in New England waters are summarized below. The significance of statistical tests of species responses are summarized in Tables 1-3.
Table 1.1 Results of BACI models for Atlantic Cod. Bold values show results that were statistically significant (p-value < 0.05). The effect size for each metric is displayed on a red-blue scale (negative to positive). For each control in which the interaction term was negative, the closure had a positive impact on the age metric measured. Models applied are reported below the metric name. GLM and ZANB are abbreviations for generalized linear model and zero-altered negative binomial model, respectively. Note that in the CPUE 5+ model there are two results, count and binomial. The binomial result reports the effect of the presence/absence of age 5+ fish in the sample. The relevant sample size in the right-most column includes the samples drawn from inside the closure.
Atlantic Cod

Gulf of Maine Stock. Results for Atlantic cod are summarized in Table 1. Two closures are designed to protect the Gulf of Maine Cod Stock: Western Gulf of Maine (WGOM) and Cashes Ledge (CL). Results from WGOM closed area analysis indicated the WGOM closed area had significantly greater mean age (3.5 years) than all the distance and strata-based control areas (Figure 1.5). Notably, WGOM was the only closure in New England waters that showed an increase in mean age of cod over time. There was a significant, positive effect of the closure on mean age when compared with the strata-based, 10 km and 20 km distance-based controls, suggesting that the closure had a positive effect on this age metric (Figure 1.5). Age diversity in WGOM and the control areas were not significantly different. There was a significant, greater likelihood of occurrence of age 5+ inside the closure (Figure 1.5). The number of age 5+ fish was significantly greater inside the closure when compared to the strata-based control (Figure 1.5). CPUE5+ was greater in the 10, 20, and 40 km controls. Both the occurrence and number of fish age 5+ showed a significant increase over time. The WGOM closure showed a significant, positive effect on the number of age 5+ fish in the strata control test. The occurrence of age 5+ fish was also significantly greater inside the WGOM closure compared to the 20- and 40-km control areas. These results provide evidence of a positive effect on both the number and probability of occurrence of age 5+ fish due to the closure.
Western Gulf of Maine. Atlantic Cod: before-after control-impact

Figures 1.5a-f. Atlantic Cod before-after control-impact results. The top three panels display mean values of three key age metrics from strata-based experiments: mean age (left), diversity (center), and CPUE5+ (right). The bottom panels display results from distance-based experiments on the same three age metrics. Error bars represent +/- standard error. The x-axis of each plot represents time (before and after the closure) and the y-axis represents age metric measured.
Annual trends using strata-based sampling (Figures 1.6a-c) do not show consistent increases in age metrics across years after the closure’s implementation, yet there are increases in mean age and CPUE5+ from 2001-2003 and all age metrics in 2015. The age distribution appears most symmetric in the ‘After-Closure-’ panel (Figure 1.7). While the mean age residual interpolation appears to have a weak fit due to spatial outliers (Figure 1.9), the spatial distribution of CPUE5+ shows a pattern of greater probability of occurrence of old fish over Stellwagon Bank and Jeffrey’s Ledge (Figure 1.8).
Western Gulf of Maine. Atlantic Cod: annual trends

Figure 1.6a-c Atlantic cod annual age metric trends. (Left). For each year, mean value for each metric is reported. Error bars represent +/- standard error. The x-axis represents time in years. The vertical black line in the center of the plot marks the year in which the closure was implemented. It is important to note the WGOM closure has remained open to and receive significant fishing pressure from a recreational fishery.

Figure 1.7 Atlantic cod age structure (Above). The histogram above shows the distribution of cod for each treatment in the strata based BACI experiment.
Figure 1.8 Spatial Distribution of age 5+ fish. Survey data was fitted using an inverse-distance weighted spatial model. Interpolation region is bounded by sampling effort.

Figure 1.9 Spatial Distribution of age GLM residuals. Survey data was fitted using an inverse-distance weighted spatial model. High expression of residuals to the east is likely due to weakly fitting spatial outliers.
Results from CL closed area analysis did not indicate any significant, positive impacts of the closure on age metrics of cod. Fish in the 10 and 20 km control areas had significantly greater mean age than the CL closure (Figure 1.10). In both strata-based and distance-based experiments there was a significant decrease in mean age over time. The distance-based experiments indicate a significant negative interaction effect of the closure at the 10 and 20 km controls. These results suggest that the closure resulted in a decrease in mean age. Analysis of age diversity revealed significantly greater age diversity in the closure compared to distance controls, but there were no significant differences due to the interaction effect. All tests of closure impacts on the numbers and occurrence of age 5+ fish showed greater numbers inside the closure, but overall the CL closure had no significant impact on the number or probability of occurrence of age 5+ fish.
**Cashes Ledge. Atlantic Cod: before-after control-impact**

Figure 1.10a-f Atlantic Cod before-after control-impact results. The top three panels display mean values of three key age metrics from strata-based experiments: mean age (left), diversity (center), and CPUE5+ (right). The bottom panels display results from distance-based experiments on the same three age metrics. Error bars represent +/- standard error. The x-axis of each plot represents time (before and after the closure) and the y-axis represents age metric measured.
It is likely that results from experiments in and around Cashes Ledge suffered from low sample size and infrequent survey effort. This is best explained by annual trends in age metrics (Figure 1.11). Many years lack data for cod inside the closure and years in which diversity has a zero value indicate that only one age class was captured, typically due to a single survey tow. The low sample size is best exemplified by the strata-based control experiment which had less than 150 samples per treatment over a 30-year period. The absence of a closure effect was further exemplified by similarity in age distributions among treatments (Figure 1.12).
Cashes Ledge. Atlantic Cod: annual trends

Figures 1.11a-c Atlantic cod annual age metric trends. (Left). For each year, mean value for each metric is reported. Error bars represent +/- standard error. The x-axis represents time in years. The vertical black line in the center of the plot marks the year in which the closure was implemented. It is important to note the WGOM closure has remained open to and receive significant fishing pressure from a recreational fishery.

Figure 1.12 Atlantic cod age structure (Above). The histogram above shows the distribution of cod for each treatment in the strata based BACI experiment.
The spatial distribution of residuals and CPUE5+ show some compelling patterns around the eastern portion of the closure (Figures 1.13 & 1.14), but small closure size and diversity of complex habitat likely inhibited sampling effort. These limitations are addressed through a focused sampling survey conducted in 2016 and 2017. Survey design, results and further discussion of Cashes Ledge closure is addressed in Chapter 2 of this thesis.
Cashes Ledge. Atlantic cod age model spatial residuals

Figure 1.13 Spatial Distribution of age GLM residuals. Survey data was fitted using an inverse-distance weighted spatial model. Interpolation region is bounded by sampling effort. Black dots represent sampling sites.
Figure 1.14 Spatial Distribution of age 5+ fish. Survey data was fitted using an inverse-distance weighted spatial model. Interpolation region is bounded by sampling effort. Black dots represent sampling sites.
Georges Bank Stock. Three closures exist on Georges Bank that could potentially protect the Georges Bank cod stock: Closed Area I (CAI) & II (CAII) and Nantucket Lightship (NL). Results from the CAI analysis show significant positive location effect of the closure on mean age across all distance-controls (Table 1, summarized in Figure 1.15). There was a strong significant decrease in mean age over time for all controls (0.35 years). The interaction effect of mean age was significantly negative for both strata and 10 km controls (0.18 years). Age diversity decreased significantly over time in the strata control. Results of the CPUE5+ experiments on CAI show mixed effects. The strata-based experiment was the only test that showed a significant positive location effect on the numbers of age 5+ fish, which is well exemplified in the spatial distribution of CPUE5+ (Figure 1.19). The remaining tests on the numbers and probability of occurrence of age 5+ cod showed no difference between closure and control. While the numbers and probability of older fish declined consistently over time, the probability declined significantly over time. Finally, there were no significant interaction effects on the numbers or probability of older fish in this closure. Results from this analysis in CAI indicate that while the population has seen significant declines in all age metrics over time (Figure 1.15), there is some evidence of the closure’s negative effect on mean age of cod. In the years following the closure, the area has a much higher occurrence of younger fish, with over 60% of the population represented by ages 0 and 1 (Figure 1.17). Despite the significant location effect, the trends in CPUE5+ fall flat after 2003, perhaps indicating that the region no longer supports older fish (Figure 1.16c). The spatial distribution of the age-based model residuals shows a significant northward distribution
of fish above the mean, indicating a possible loss of suitable habitat in Closed Area I and points eastward on Georges Bank (Figure 1.18).
Closed Area I. Atlantic Cod: before-after control-impact

Figure 1.15a-f Atlantic Cod before-after control-impact results. The top three panels display mean values of three key age metrics from strata-based experiments: mean age (left), diversity (center), and CPUE<sup>+</sup> (right). The bottom panels display results from distance based experiments on the same three age metrics. Error bars represent +/- standard error. The x-axis of each plot represents time (before and after the closure) and the y-axis represents are age metric measured.
Closed Area I. Atlantic Cod: annual trends

Figures 1.16a-c Atlantic cod annual age metric trends. (Left). For each year, mean value for each metric is reported. Error bars represent +/- standard error. The x-axis represents time in years. The vertical black line in the center of the plot marks the year in which the closure was implemented.

Figure 1.17 Atlantic cod age structure (Above). The histogram above shows the distribution of cod for each treatment in the strata based BACI experiment.
Closed Area I. Atlantic cod age model spatial residuals

Figure 1.18 Spatial Distribution of age GLM residuals. Survey data was fitted using an inverse-distance weighted spatial model. Interpolation region is bounded by sampling effort. Black dots represent sampling sites.
Closed Area I. Atlantic cod CPUE5+ spatial model

Figure 1.19 Spatial Distribution of age 5+ fish. Survey data was fitted using an inverse-distance weighted spatial model. Interpolation region is bounded by sampling effort. Black dots represent sampling sites.
The results of CAII analysis (summarized in Figure 1.20) indicate a significant positive location effect on mean age in all tests, excluding the 10 km control. The interaction effect was small, but negative and significant for the 10 and 20 km controls (<0.1 years), and positive and significant in the 30 and 40 km controls. Only the 30 and 40 km controls show significantly negative location effect on diversity. Both the number and probability of age 5+ fish was significantly greater due to the location effect in the strata control. The opposite trend could be seen in the 10 and 20 km distance controls; there were higher numbers of older fish outside CAII. Over time, the probability of age 5+ fish decreased significantly. The interaction effect of numbers of older fish in CAII showed mixed results; the 20 km control model showed positive significant effects, while the 40 km control showed a significant negative effect. Results from these experiments exemplify a similar trend of CAI: all age metrics decreased after the implementation of the closure. While there were some significant interaction effects on mean age, they were of small magnitude (<0.1 years). Annual trends of diversity were flat across 46 years, with a recent decline over the last 4 years (Figure 1.21b). The age distribution among treatments do appear drastically different (Figure 1.22). The CPUE5+ from the strata-based experiment shows an overall decline in catch of older fish. The spatial model of CPUE5+ (Figure 1.24) from strata-control samples shows a pattern consistent with a significant location effect, whereas the spatial distribution of age-based GLM residuals displays a weak pattern across Georges Bank (Figure 1.23).
Closed Area II. Atlantic Cod: before-after control-impact

Figure 1.20a-f Atlantic Cod before-after control-impact results for Closed Area II. The top three panels display mean values of three key age metrics from strata-based experiments: mean age (left), diversity (center), and CPUE 5+ (right). The bottom panels display results from distance-based experiments on the same three age metrics. Error bars represent +/- standard error. The x-axis of each plot represents time (before and after the closure) and the y-axis represents age metric measured.
Closed Area II. Atlantic Cod: annual trends

Figures 1.21a-c Atlantic cod annual age metric trends. (Left). For each year, mean value for each metric is reported. Error bars represent +/- standard error. The x-axis represents time in years. The vertical black line in the center of the plot marks the year in which the closure was implemented.

Figure 1.22 Atlantic cod age structure (Above). The histogram above shows the distribution of cod for each treatment in the strata based BACI experiment.
Closed Area II. Atlantic cod age model spatial residuals

Figure 1.23 Spatial Distribution of age GLM residuals. Survey data was fitted using an inverse-distance weighted spatial model. Interpolation region is bounded by sampling effort. Black dots represent sampling sites.
Closed Area II. Atlantic Cod CPUE 5+ model on Georges Bank

Figure 1.24 Spatial Distribution of age 5+ fish. Survey data was fitted using an inverse-distance weighted spatial model. Interpolation region is bounded by sampling effort. Black dots represent sampling sites.
For analysis of the NL closure, there were too few samples (n<100) to conduct a balanced strata control experiment. Distance control results indicate an overall decrease in age metrics over time (Figure 1.25). Results of the 30 and 40 km controls show a significant negative location effect on both mean age and age diversity. Despite a low mean age (<2 years), the 10 and 20 km experiments showed a significant positive interaction effect of the closure. None of the results from the CPUE5+ experiments were significant (likely due to overdispersion and low sample size), yet the overall trend showed greater numbers and probability of older fish outside of the closure due to the location and interaction effect. The overall low numbers in mean age, diversity, and older fish may indicate a weak habitat association of Atlantic cod to this region.
Nantucket Lightship. Atlantic Cod: before-after control-impact

Figure 1.25a-c. Atlantic Cod before-after control-impact results for Nantucket Lightship. Each panel displays mean values of three key age metrics from distance based experiments: mean age (left), diversity (center), and CPUE5+ (right). The x-axis of each plot represents time (before and after the closure) and the y-axis represents the age metric measured.
Haddock

Georges Bank Stock. Three closed areas were designed to protect the Georges Bank haddock stock: Closed Area I (CAI), Closed Area II (CAII) and Nantucket Lightship Closure (NL). Results of all haddock analyses are summarized in Table 3.
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Table 1.2 Results of BACI models for Haddock. Bold values show results that were statistically significant (p-value < 0.05). The effect size for each metric is displayed on a red-blue scale (negative to positive). For each control in which the interaction term was negative, the closure had a positive impact on the age metric measured. Models applied are reported below the metric name. GLM and ZANB are abbreviations for generalized linear model and zero-altered negative binomial model, respectively. Note that in the CPUE5+ model there are two results, count and binomial. The binomial result reports the effect of the presence/absence of age 5+ fish in the sample. The relevant sample size in the right-most column includes the samples drawn from inside the closure.
Results for analysis of mean age in CAI (Figure 1.26) indicate significant increases in each age metric over time from both strata and distance-based controls. Each mean age analysis also resulted in a significant positive location effect. Each control experiment suggested a significant positive interaction effect of the closure on mean age. These results alone point to a strong recovery of the haddock stock age structure in the region. For age diversity in CAI, there was a significant positive location effect of the closure. While there was a positive trend in the interaction effect on age diversity, none of the analyses revealed significant results.
Figure 1.26a-f. Haddock before-after control-impact results for Closed Area I. The top three panels display mean values of three key age metrics from strata-based experiments: mean age (left), diversity (center), and CPUE5+ (right). The bottom panels display results from distance based experiments on the same three age metrics. Error bars represent +/- standard error. The x-axis of each plot represents time (before and after the closure) and the y-axis represents age metric measured.
Annual calculations of age diversity in the haddock stock shows positive growth, with both closure and control rising together over the last 5 years (See figure 1.27b). Analysis of the numbers of age 5+ fish revealed a significant positive location effect in all controls. Due to the location effect the probability of occurrence of age 5+ fish was significantly greater in the closure when compared to the 20 and 40 km controls. Analysis of the interaction effect revealed significantly greater numbers of age 5+ fish inside the closure when compared to the 20 and 40 km controls. The probability of occurrence of older fish was significantly higher in the closure than the strata and 20 km controls. These results are supported by annual trends in age metrics. Annual trends in the numbers of age 5+ captured by the trawl survey reveal considerably high catches in the closure in the years following the closure (Figure 1.27c). The spatial model of age-based model residuals shows a preference for older fish to range over the northeastern portion of Georges Bank (Figure 1.29). The spatial distribution of older catch from the strata control analysis supports results showing a strong location effect. (Figure 1.30).
Figures 1.27a-c Haddock annual age metric trends. (Left). For each year, mean value for each metric is reported. Error bars represent +/- standard error. The x-axis represents time in years. The vertical black line in the center of the plot marks the year in which the closure was implemented.

Figure 1.28 Haddock age structure (Above). The histogram above shows the distribution of cod for each treatment in the strata based BACI experiment.
**Figure 1.29** Spatial Distribution of age GLM residuals. Survey data was fitted using an inverse-distance weighted spatial model. Interpolation region is bounded by sampling effort. Black dots represent sampling sites.
Result of CAII analysis of mean age show a significant positive location effect of the closure against all controls. The interaction effect of closure on mean age was significantly positive in the strata and 10km control, but significantly negative in the 20, 30, and 40 km controls. CAII showed a significant positive location effect on age diversity in the distance control analyses with distance-controls and the magnitude of effect increasing with distance from the closure (Figure 1.31). Much like CAI, age diversity in CAII increased significantly over time in all control experiments. The numbers of age 5+ fish was significantly higher inside the closure due to location when compared to strata, 30, and 40 km controls. The probability of occurrence of older fish inside the closure was significantly higher when compared to all controls. There were also significantly greater numbers of fish inside the closure over time. There were no significant interaction effects of the closure on numbers or probability of occurrence of age 5+ fish despite largely positive trends.
Closed Area II. Haddock: before-after control-impact

Figure 1.3a-f Haddock before-after control-impact results for Closed Area II. The top three panels display mean values of three key age metrics from strata-based experiments: mean age (left), diversity (center), and CPUE5+ (right). The bottom panels display results from distance based experiments on the same three age metrics. Error bars represent +/- standard error. The x-axis of each plot represents time (before and after the closure) and the y-axis represents age metric measured.
An examination of the distribution of ages before and after the closure reveals that nearly 50% of the haddock catch captured by the survey was comprised of 0 age fish, followed by a decrease to nearly 30% (Figure 1.33). Annual trends in age metrics also show a consistent increase in age diversity and higher catch of age 5+ fish since the closure’s implementation (Figure 1.32). The spatial distribution of age-based GLM residuals shows a trend in habitat association along the central ridge of Georges Bank (Figure 1.34). The spatial distribution of age 5+ catches shows similar habitat trends; large catches of older fish are distributed along the shallower portions of Georges Bank (Figure 1.35).
Closed Area II. Haddock: annual trends

Figures 1.32a-c Haddock annual age metric trends. (Left). For each year, mean value for each metric is reported. Error bars represent +/- standard error. The x-axis represents time in years. The vertical black line in the center of the plot marks the year in which the closure was implemented.

Figure 1.33 Haddock age structure (Above). The histogram above shows the distribution of cod for each treatment in the strata based BACI experiment.
Figure 1.34 Spatial Distribution of age GLM residuals. Survey data was fitted using an inverse-distance weighted spatial model. Interpolation region is bounded by sampling effort. Black dots represent sampling sites.
Closed Area II. Haddock CPUE5+ spatial model

Figure 1.35 Spatial Distribution of age 5+ fish. Survey data was fitted using an inverse-distance weighted spatial model. Interpolation region is bounded by sampling effort. Black dots represent sampling sites.
Results of NL experiments on mean age of haddock show a significant negative location effect, a significant decrease in the mean age (~1.8 years) over time, and a negative interaction effect of the closure when compared to all controls (Figure 1.36). Mean age decreased significantly over time (~1.8+ years). There were no significant results for effects of the closure on age diversity. In all but the 10km control, there was a significantly negative location effect on the numbers of age 5+ haddock in the closure. The probability of occurrence of age 5+ was significantly lower in the 30 and 40 km controls due to the location. There was a significant decrease in the numbers and probability of occurrence of older fish over time in the closure when compared to all controls. Due to the interaction effect of the closure, the numbers of older fish were significantly greater in the 20, 30, and 40 km controls. The probability of occurrence of older fish for the same effect was significantly higher in the 30 and 40 km controls. These results indicate that the closure negatively affected the mean and catch of age 5+ fish.
Figure 1.36a-f Haddock before-after control-impact results for Nantucket Lightship. The top three panels display mean values of three key age metrics from strata-based experiments: mean age (left), diversity (center), and CPUE5+ (right). The bottom panels display results from distance-based experiments on the same three age metrics. Error bars represent ± standard error. The x-axis of each plot represents time (before and after the closure) and the y-axis represents age metric.
Annual trends in mean age show a steady decrease in age from the early 1980s to mid-2000s (Figure 1.37a). The annual trends in CPUE5+ indicate since 1974, few older haddock were captured inside or outside the closure, providing evidence of the lack of suitable habitat in Southern New England (Figure 1.37c). This is further exemplified in the age distribution in the ‘Closure-After’ and ‘Control-After’ panels where over 80% of fish captured in the Southern New England region were age 0 (Figure 1.38).
Figures 1.37a-c Haddock annual age metric trends. (Left). For each year, mean value for each metric is reported. Error bars represent +/- standard error. The x-axis represents time in years. The vertical black line in the center of the plot marks the year in which the closure was implemented.

Figure 1.38 Haddock age structure (Above). The histogram above shows the distribution of cod for each treatment in the strata based BACI experiment.
Gulf of Maine Stock. Two closures protect the Gulf of Maine Haddock Stock: WGOM and CL. The results of experiments in the WGOM closure show a mixed effect on haddock (Figure 1.39). There was a significant positive location effect of the closure on mean age when compared to all controls. The mean age of haddock decreased significantly over time (Figure 1.39a+d). Results of the interaction effect were mixed. When compared to the strata and 10 km controls, the closure showed a significant negative interaction effect on mean age, whereas in the 20, 30, and 40 controls there were significant positive interaction effects of the closure. Age diversity and the numbers and probability of occurrence of older fish increased significantly over time. There was a strong location effect on the probability of occurrence of age 5+ fish, when compared to all controls. Analysis of the probability of occurrence showed a significantly greater probability of catching age 5+ fish inside the closure when compared to the strata, 20, and 40 km controls.
**Western Gulf of Maine. Haddock: before-after control-impact**

![Graphs showing Haddock before-after control-impact results for Western Gulf of Maine closure.](image)

**Figure 1.39a-f** Haddock before-after control-impact results for Western Gulf of Maine closure. The top three panels display mean values of three key age metrics from strata-based experiments: mean age (left), diversity (center), and CPUE5+ (right). The bottom panels display results from distance based experiments on the same three age metrics. Error bars represent +/- standard error. The x-axis of each plot represents time (before and after the closure) and the y-axis represents age metric measured.
Long-term increases in diversity since the late 1980s paired with post-closure increase in CPUE5+ provides possible indication that haddock age structure is retaining older cohorts in the region (Figures 1.40b and 1.40c). While the results of interaction on mean age are slightly confounding, there may be some selection processes by the recreational fishery in the area that may affect the age structure. The spatial distribution model of age 5+ catch shows signs of habitat preference from Jeffreys Ledge south toward Stellwagon Bank (Figure 1.43).
Figures 1.40a-c: Haddock annual age metric trends. (Left) For each year, mean value for each metric is reported. Error bars represent standard error. The x-axis represents time in years. The vertical black line in the center of the plot marks the year in which the closure was implemented.

Figure 1.41: Haddock age structure (Above). The histogram above shows the distribution of cod for each treatment in the strata based BACI experiment.
Western Gulf of Maine. Haddock: Mean Age GLM residual distribution

Figure 1.42 Spatial Distribution of age GLM residuals. Survey data was fitted using an inverse-distance weighted spatial model. Interpolation region is bounded by sampling effort. Black dots represent sampling sites.
**Western Gulf of Maine. Haddock: CPUE 5+ spatial model**

Figure 1.43 Spatial Distribution of age 5+ fish. Survey data was fitted using an inverse-distance weighted spatial model. Interpolation region is bounded by sampling effort. Black dots represent sampling sites.
Results from CL analysis reveal significant positive location effect on mean age when compared to all experimental controls (Figure 1.44). There was a significant increase in mean age over time and a significant positive interaction effect on mean age in the closure when compared to all controls except the 40 km. There were no significant results on age diversity of haddock inside and outside of CL. Much like mean age, there was a strong and significant location effect on numbers of age 5+ fish caught when compared to all but the 20 km control. When compared to the closure, the 20 and 30 km controls showed a significantly fewer age 5+ fish. Annual trends in age metrics indicate sparse sampling effort or catch of haddock in and around central Gulf of Maine over the 30-year period (Figure 1.45). The recent spike in age 5+ haddock catch inside the closure may indicate a rise in habitat use by older fish (Figures 1.45c and 1.48). Furthermore, the wider distribution of the age structure could be indicative of haddock population recovery (Figure 1.46). These results show that much like WGOM, haddock have shown signs of age structure recovery and are likely benefiting from the closure.
Cashes Ledge. Haddock: before-after control-impact

Figure 1.44a-f Haddock before-after control-impact results for Cashes Ledge closure. The top three panels display mean values of three key age metrics from strata-based experiments: mean age (left), diversity (center), and CPUE5+ (right). The bottom panels display results from distance based experiments on the same three age metrics. Error bars represent +/- standard error. The x-axis of each plot represents time (before and after the closure) and the y-axis represents age metric measured.
**Figures 1.45a-c** Haddock annual age metric trends. (Left). For each year, mean value for each metric is reported. Error bars represent +/− standard error. The x-axis represents time in years. The vertical black line in the center of the plot marks the year in which the closure was implemented.

**Figure 1.46** Haddock age structure (Above). The histogram above shows the distribution of cod for each treatment in the strata based BACI experiment.
Figure 1.47 Spatial Distribution of age GLM residuals. Survey data was fitted using an inverse-distance weighted spatial model. Interpolation region is bounded by sampling effort. Black dots represent sampling sites.
Figure 1.48 Spatial Distribution of age 5+ fish. Survey data was fitted using an inverse-distance weighted spatial model. Interpolation region is bounded by sampling effort. Black dots represent sampling sites.
Yellowtail Flounder

Yellowtail flounder is divided into three stock units in New England. The *Southern New England* stock is protected by Nantucket Lightship (NL). The *Cape Cod-Gulf of Maine* stock is protected by the Western Gulf of Maine (WGOM) and Cashes Ledge (CL) closures. The *Georges Bank* stock is protected by Closed Area II (CAII). Closed Area I protects all three stocks and analysis of this closure includes fish from each stock. Results from experiments on yellowtail flounder are summarized in Table 3.
### Table 1.3 Results of BACI models for Yellowtail Flounder

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<th>Age Diversity GLM Location</th>
<th>CPUE 5+ ZANB Location</th>
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<tr>
<td>40km</td>
<td>0.16</td>
<td>0.01</td>
<td>0.03</td>
</tr>
</tbody>
</table>

Black values show results that were statistically significant (p-value < 0.05). The effect size for each metric is displayed on a red-blue scale (negative to positive). For each control in which the interaction term was negative, the closure had a positive impact on the age metric measured. Models applied are reported below the metric name. GLM and ZANB are abbreviations for generalized linear model and zero-altered negative binomial model, respectively. Note that in the CPUE 5+ model there are two results, count and binomial. The binomial result reports the effect of the presence/absence of age 5+ fish in the sample. The relevant sample size in the right-most column includes the samples drawn from inside the closure.
Cape Cod-Gulf of Maine Stock. Due to the low occurrence and sampling effort inside the Cashes Ledge Closure (no before treatment), no BACI analysis was done on this region. Results for WGOM analysis of mean age indicate a significant positive location effect when compared to all controls (Figure 1.49). In the distance control experiments there was a small but significant increase in age (0.05 years) over time. Results show a significant negative interaction effect of the closure on mean age in comparison to all controls. Analysis of age diversity revealed only a strong negative location effect on age diversity of the closure in comparison to each control. There were no significant changes to diversity over time and no significant results of interaction effect. Results of the CPUE5+ analysis revealed a significant positive location effect of the closure on the numbers of age 5+ fish when compared to the strata, 20, 30, and 40 km controls. The probability of occurrence of age 5+ fish was also significantly greater in the strata control due to location effect.
Western Gulf of Maine. Yellowtail Flounder: before-after control-impact

Figure 1.49a-f Yellowtail Flounder before-after control-impact results for Western Gulf of Maine closure. The top three panels display mean values of three key age metrics from strata-based experiments: mean age (left), diversity (center), and CPUE5+ (right). The bottom panels display results from distance based experiments on the same three age metrics. Error bars represent +/- standard error. The x-axis of each plot represents time (before and after the closure) and the y-axis represents age metric measured.
Annual trends in CPUE5+ indicate sparse catch of older fish (Figure 1.50c) and the overall age distribution by treatment appears to be heavily skewed toward the youngest fish (Figure 1.51). Overall, these results indicate that Gulf of Maine yellowtail flounder stock does not benefit from this closure.
Western Gulf of Maine. Yellowtail Flounder: annual trends

Figures 1.50a-c Yellowtail Flounder annual age metric trends for WGOM strata experiment. (Left). For each year, mean value for each metric is reported. Error bars represent +/- standard error. The x-axis represents time in years. The vertical black line in the center of the plot marks the year in which the closure was implemented.

Figure 1.51 Yellowtail Flounder age structure (Above). The histogram above shows the distribution of cod for each treatment in the strata based BACI experiment.
Georges Bank Stock. Analysis of mean age in CAII reveal a significant positive location effect when compared to all distance controls (Figure 1.52). Mean age also increased significantly over time. The interaction effect of the closure on mean age was significantly positive when compared to the strata, 20, and 40 km controls, but significantly negative for the 10km control. In each case the magnitude of change was very low (<0.05 years). Location and time effects on diversity showed significant positive results when compared to all distance controls. Only the 40km control revealed significantly less age diversity than the closure. Analysis of both the numbers and probability of occurrence of age 5+ fish revealed a significant location effect of the closure. The same analysis indicates a significant increase in the probability of occurrence of age 5+ fish over time. While the interaction effect of the closure on the numbers of age 5+ fish was significantly negative in the strata control, the 10 km control analysis showed a significantly positive interaction effect with similar magnitude. The probability of occurrence of older fish was significantly higher in the closure when compared to the strata, 20, 30, and 40 km controls.
Closed Area II. Yellowtail Flounder: before-after control-impact

Figure 1.52a-f Yellowtail Flounder before-after control-impact results for Closed Area II. The top three panels display mean values of three key age metrics from strata-based experiments: mean age (left), diversity (center), and CPUE5+ (right). The bottom panels display results from distance based experiments on the same three age metrics. Error bars represent +/- standard error. The x-axis of each plot represents time (before and after the closure) and the y-axis represents age metric measured.
In comparison to WGOM, this region supported a more evenly distributed age structure for yellowtail flounder (Figure 1.54). The spatial distribution of older fish shows a habitat effect around the center of Georges Bank, which may be indicative of sediment type preference (Figure 1.56). Despite some mixed results in the analysis of this closure, it may be the only region where closure status has benefitted the age structure of yellowtail flounder.
Closed Area II. Yellowtail Flounder: annual trends

Figures 1.53a-c Yellowtail flounder annual age metric trends for CAII strata experiment (Left). For each year, mean value for each metric is reported. Error bars represent +/- standard error. The x-axis represents time in years. The vertical black line in the center of the plot marks the year in which the closure was implemented.

Figure 1.54 Yellowtail Flounder age structure for CAII strata experiment (Above). The histogram above shows the distribution of cod for each treatment in the strata based BACI experiment.
Closed Area II. Yellowtail Flounder Mean Age GLM residual spatial model

Figure 1.55 Spatial Distribution of age GLM residuals. Survey data was fitted using an inverse-distance weighted spatial model. Interpolation region is bounded by sampling effort. Black dots represent sampling sites.
**Closed Area II. Yellowtail Flounder CPUE5+ spatial model**

*Figure 1.56* Spatial Distribution of age 5+ fish. Survey data was fitted using an inverse-distance weighted spatial model. Interpolation region is bounded by sampling effort. Black dots represent sampling sites.
Results of analysis of mean age in CAI indicate a significant positive location effect of the closure when compared to all controls. Mean age also increased significantly over time. The interaction effect of CAI on mean age revealed a significant positive effect of the closure when compared to all but the 10 km control. There were no significant effects of the closure on age diversity. The probability of occurrence of age 5+ fish decreased significantly over time. Analysis of the numbers of age 5+ fish indicated a significant positive interaction effect of CAI when compared to the strata and 20 km controls.
Closed Area I. Yellowtail Flounder: before-after control-impact

Figure 1.57a-f Yellowtail Flounder before-after control-impact results for Closed Area II. The top three panels display mean values of three key age metrics from strata-based experiments: mean age (left), diversity (center), and CPUE5+ (right). The bottom panels display results from distance based experiments on the same three age metrics. Error bars represent +/- standard error. The x-axis of each plot represents time (before and after the closure) and the y-axis represents age metric measured.
Annual trends in mean age and diversity are difficult to distinguish among closed and control areas (Figure 1.58a–b). Spatial patterns in age-based model residuals and CPUE5+ are difficult to discern (Figures 1.60 and 1.61). The episodic pulses of catch and CPUE5+ inside the closure are likely driving the positive location trend, but interpretation is subject to a perennial limitation: shifting effort of the survey (Figure 1.59).
Closed Area I. Yellowtail Flounder: annual trends

Figures 1.58a-c Yellowtail flounder annual age metric trends for CAI strata experiment (Left). For each year, mean value for each metric is reported. Error bars represent +/- standard error. The x-axis represents time in years. The vertical black line in the center of the plot marks the year in which the closure was implemented.

Figure 1.59 Yellowtail Flounder age structure for CAI strata experiment (Above). The histogram above shows the distribution of cod for each treatment in the strata based BACI experiment.
Closed Area 1. Yellowtail Flounder Age GLM residuals spatial model

Figure 1. Spatial Distribution of age GLM residuals. Survey data was fitted using an inverse-distance weighted spatial model. Interpolation regions bounded by sampling effort. Black dots represent sampling sites.
Closed Area I. Yellowtail Flounder CPUE5+ spatial model

Figure 1.61 Spatial Distribution of age 5+ fish. Survey data was fitted using an inverse-distance weighted spatial model. Interpolation region is bounded by sampling effort. Black dots represent sampling sites.
Southern New England Stock. Analysis of yellowtail flounder mean age in NL reveals a significant decrease in mean age over time and a weak location effect of the closure. The interaction effect of the closure was significantly positive when compared to each the distance controls. Analysis of age diversity revealed a significant decrease over time and a significant positive location effect for 10, 20 and 40 km distance controls. There was a significant decrease in the number and probability of occurrence of age 5+ fish in this region. Only the 30km control showed a significant negative interaction effect of the closure on the probability of occurrence of older fish.
Figure 1.62a-f Yellowtail Flounder before-after control-impact results for Nantucket Lightship. The top three panels display mean values of three key age metrics from strata-based experiments: mean age (left), diversity (center), and CPUE5+ (right). The bottom panels display results from distance based experiments on the same three age metrics. Error bars represent +/- standard error. The x-axis of each plot represents time (before and after the closure) and the y-axis represents age metric measured.
The overall decrease in age structure metrics for yellowtail flounder in this region suggest that this fishery has struggled over the last 25 years to recover to its historic age structure. The slightly positive interaction effect on mean age may be a result of the “maintenance” effect. Annual trends in CPUE5+ show steady declines in the catch of older fish since the 1970s (Figure 1.63c). The spatial model of age-based GLM residuals show some habitat associations to the northeast and southwest of the closure, whereas spatial distribution of CPUE5+ indicates well dispersed ranging of older fish, with highest age 5+ catches inside the closure (location effect) (Figures 1.65 and 1.66).
Figures 1.63a-c Yellowtail flounder annual age metric trends for NL strata experiment (Left). For each year, mean value for each metric is reported. Error bars represent +/- standard error. The x-axis represents time in years. The vertical black line in the center of the plot marks the year in which the closure was implemented.

Figure 1.64 Yellowtail Flounder age structure for NL strata experiment (Above). The histogram above shows the distribution of cod for each treatment in the strata based BACI experiment.
Nantucket Lightship. Yellowtail Flounder Age GLM residual spatial plot

Figure 1.65 Spatial Distribution of age GLM residuals. Survey data was fitted using an inverse-distance weighted spatial model. Interpolation region is bounded by sampling effort. Black dots represent sampling sites.
**Nantucket Lightship.** Yellowtail Flounder CPUE5+ spatial model

*Figure 1.66* Spatial Distribution of age 5+ fish. Survey data was fitted using an inverse-distance weighted spatial model. Interpolation region is bounded by sampling effort. Black dots represent sampling sites.
DISCUSSION

My results add to previous studies on the effects of fisheries closures on age structure metrics of fish species (Sherwood & Grabowski 2016). This study offers a unique approach to studying closed area effects, applying BACI analysis with additional examination of temporal and spatial variation for context in interpreting results. While New England fisheries closures were not intended to protect age structure of groundfish, this study shows evidence that changes in mean age, age diversity, and numbers of oldest fish in a population can be affected by large-scale spatial management such as fisheries closures.

Atlantic Cod

For the Gulf of Maine cod stock, BACI analysis of the Western Gulf of Maine Closure revealed significant positive interaction effects on mean age and CPUE5+. Nearly all treatments in this region showed an increase in age structure metrics over time. Originally designed for the outcome of increased abundance of cod, it was unclear whether the area would support old growth. The analysis of this closure supports the hypothesis that marine protected areas can lead to age structure recovery in Atlantic cod. While thinking toward the future of WGOM closure and cod protection, results of this analysis should be interpreted in the context of fishing impacts. This area sees periodically high recreational fishing effort, unlike other closures that are typically out of reach to recreation-sized vessels. Annual trends from NEFSC trawl sampling indicate that in the 5 years directly after implementation of closed area regulation (1998-2003), CPUE5+ increased by over ten-fold and mean age increased by over 1 year. This rapid age recovery coincided with a dramatic increase in recreational fishing effort of cod in
federal waters (MA, NH, and ME landings), leading to a peak 2,300 mt removed in 2003. As rapidly as mean age and CPUE5+ recovered, both metrics fell to previously low levels. In the years that followed, recreational catch-per-unit-effort continued to increase until 2010. Not until both recreational CPUE and biomass removed dropped to their 35-year lows, did age metrics increase around the WGOM closure (2010-2016, Figure 1.6a-c). Despite recreational fishing, the overall age metrics still improved in the region, but annual relationships between this recovery and recreational effort may suggest that recreational harvest may have impeded a more substantial age structure recovery of the Gulf of Maine cod stock (Figure 1.67).
Figure 1.67 Recreation effort compared to WGOM closures. The top two panels (left) show annual mean age and CPUE5+ in the WGOM closure. The bottom two panels show biomass per-unit-effort and effort for MA, NH, and ME recreational cod fishing (NEFSC). The spikes in age metrics from 2001-2003 are followed by a time of heavy recreational fishing effort in federal waters. The period from 2008-2012 is characterized by low age metrics and high biomass per unit-effort. After this time, the amount of biomass removed by the recreational fleet drops to its lowest point in 30+ years, and is followed by another increase in age structure. Could the recreational fleet be exerting enough harvest pressure to alter the demographics of cod inside the WGOM closed area?
For the remaining analyses, the detectable effects of closed areas on cod age structure recovery are limited. The NL closure appears to be outperformed by surrounding waters on every age metric due to a location effect and much like CAI, there is a wholesale decline in all age metrics since the closure was enacted. Although there was positive age location effect detected in the 10- and 20- km control experiments, the age composition over NL is primarily composed of age 0 and 1 fish. Significant interaction effects on mean age could be optimistically interpreted as a ‘maintenance effect’ whereby the closure upheld age structure in comparison to surrounding control areas. In CAII, results of the spatial distribution of CPUE5+ (Figure 1.24) indicate a strong location effect, but despite favorable habitat for older fish, age metrics over Georges Bank continue to decrease. In concert with concerning spawning stock biomass levels, the last three years of survey data show rapid declines in age diversity and mean age (Figures 1.21a-b). The lack of significant results in BACI analysis shows weak evidence of a closure effect in a population with diminishing age structure.

**Haddock**

Haddock has seen a dramatic recovery since its 1990s lows; in 1995 the spawning stock biomass was recorded at 2,533 mt and 2016 recorded 47,821 mt (NEFSC 2017). While Northeast haddock stocks have benefitted from several successful recruitment events in the last 20 years, many point to closed area management as a major contribution to recovery success (Murawski 2005, Brodziak et al. 2005). With high recorded catch near the border of Closed Area II, it has been suggested the benefits to biomass inside the closure are spilling-over to adjacent waters (Murawski 2005). The implementation of the closures led to a significant drop in fishing mortality (from 0.5 to 0.2, 1993-1995) and
research on haddock movement suggests they may be resident to closures (Brodziak et al 2008, Sherwood 2009).

In the case of Georges Bank haddock and Closed Area I, there is strong evidence that the closure enhanced age structure. Mean age increased significantly and all other age metrics showed positive trends over time. In a region where haddock are found to have a robust age structure, (Figure 1.28) tied to a strong location effect (Figure 1.30), we see the overall recovery of a fishery that benefited from no fishing in key areas. Across all closure analyses, haddock on Georges Bank and in the Western Gulf of Maine (CAI, CAII, and WGOM) was the only species that displayed a significant and strong increase in age diversity over time. While an age diversity metric has been applied in other fisheries, the dramatic recovery of haddock and steadily increasing diversity further supports the use of this metric as a proxy for population health (Secor 2000, Marteinsdottir & Thorarinsson 1998). In some cases, a significant result of this metric for other species was likely impeded by low sampling effort and heavily truncated age structures. Nonetheless, significant results for haddock indicate that it is a suitable measure of age structure change.

In some cases, the absence of a change in mean age in response to closures may be due to recruitment of age-0 fish. As an example, the age distribution of haddock in CAII compared to the strata-based control shows that 40-50% of the catch in the control area was composed of age-0 fish, whereas age-0 represented fewer than 30% of the population inside the closure. While recent haddock recruitment success is largely influenced by environmental conditions, this finding might suggest that under a ‘no-fishing’ scenario, we might see a rebalancing of haddock age structure and a restoration of density dependence. The effects of the haddock recovery may also be seen in GOM.
stock closures. For example, in the Western Gulf of Maine and Cashes Ledge closures, the numbers of haddock captured increased by ten and twenty-fold, respectively, in the years after the closures were implemented. This rapid increase in haddock biomass has been linked to impacts on the predator-prey dynamics in the region. Haddock has been shown, through heavy predation on Atlantic herring eggs, to cause a downward shift in herring spawning stock biomass over Georges Bank (Richardson et al. 2011). While little research has been done on the effects of biomass on other groundfish, the generalist feeding habits of haddock leave larval cod and other groundfish exposed to predation. Shifts in spawning stock biomass of key groundfish predators may not be leading to a change in trophic cascade structure as suggested by Casini et al (2012) and Steneck (2012). Instead, haddock predation of larval fish may be inhibiting recovery of other species. If the Gulf of Maine is currently experiencing an altered, haddock-dominated stable-state, careful consideration of age structure management could help reduce dramatic shifts that alter the short-term economy of New England Fisheries.

**Yellowtail Flounder**

There is little evidence of age structure recovery of yellowtail flounder in Western Gulf of Maine. Although there were small changes to age structure metrics over time and no detectable location effect, there were some strong habitat associations in the region (location effect on age and CPUE5+). The age distribution appears to be negatively impacted by the closure; a significant negative interaction effect was observed on mean age. However, a closer look at annual trends and the underlying age structure tells a more compelling story. Nearly 90% of the population is composed of fish aged 0-1 (Figure 1.51) and with 1 year in the late 1980s where there was a CPUE5+ of nearly 70, every other year showed lower numbers of age 5+ catch (Figure 1.50c).
Whether the WGOM closure and surrounding habitat does not provide enough suitable habitats via sediment type, forage, or thermal range, the stock status for the yellowtail flounder fishery in this area is poor. The 2017 Stock Assessment concluded that the stock is overfished, and overfishing is occurring (NEFSC). Southern New England and mid-Atlantic yellowtail flounder stocks were at risk of extirpation as an economically-viable fishery, yet early signs of recovery were celebrated as a result of 1994 management changes, including trips limits, gear restrictions, and closed areas (Fogarty & Murawski 1998, Stone et al. 2004). After closure, from 1994-2000, CAII showed strong increases in annual measurements of mean age and CPUE5+ (Figure 1.53a-c) and distance control patterns show decreasing numbers of older fish moving away from the closure, a pattern potentially owed to a spill-over effect. In later years, age metrics converge, coincident with the timeline of the introduction of special access programs (SAPs) in 1999 to allow for rotational harvest of scallops within each of the southern closures (NL, CAI, CAII). This management change may have impeded more rapid recovery of the species. Despite recent monitoring efforts that identify and disseminate yellowtail flounder hotspots to fisherman, they remain a high bycatch species during scallop dredging operations (O’Keefe and DeCelles 2013). Without a clear understanding of the selection pressure these SAPs have on the age structure of yellowtail, managers continue to allow harvest of a high value scallop fishery, signaling a major trade-off in groundfish conservation and exploitation (Murawski 2000).

At the moment, conclusions on the direct effect of temperature on the biology of yellowtail flounder remain sparse, yet indirect environmental effects such as changes in forage distribution and seasonality support a more compelling history of collapse. Thermal range shifts detected over the last 30 years may have simply led to permanent
latitudinal shifts in species distribution that will not be undone by current fishing or management scenarios (Pershing et al 2016). The federally mandated period for stock recovery is 10 years, yet the results of this analysis indicate that closed area management is not contributing enough to recovery to meet this goal.

**Management Interactions and Environmental Change**

MPAs that allow recreational fishing as the only means of exploitation have shown decreased abundance and size composition of rockfish (Schroeder and Love 2002). If demographic recovery coincided with the expected biomass build-up, we might expect to see a spill-over effect, as demonstrated for haddock and yellowtail around Georges Bank closures (Sanchez-Lizaso et al 2000, Murawski et al 2005). Yet Murawski et al. (2005) found little evidence of this phenomenon occurring around WGOM closure from 2001-2003. If we return to the principle that older fish contribute the most to recruitment, then the subsequent biomass response would take another few years to manifest in a spill-over effect. More recent evidence found by Sherwood et al. (2016) showed decreased age, length, and growth inside the northern portion of the closure from sampling during the 2007-2009 seasons. This period corresponds to low catch of age 5+ fish. It is therefore likely that during that period, biomass and demographic recovery associated with an older population may have been mitigated by increased recreational fishing pressure. A comparable study conducted on cod on the Skaggerak coast in Norway showed 167% and 83% survival rates for small (16-44cm) and large (45-97cm) cod, respectively. The MPA, which was open only to hook-and-line fishing, would have experienced a further 100% and 44% increase in survival for younger and larger fish, respectively (Fernandez-Chacon et al 2015).
Recreational management and its effect on SSB of species like haddock and cod are complicated by unknown discard mortality rates, which can impact estimates dramatically, particularly when minimum size regulations are in place (Watson & Pauly 2011, Lee et al. 2017). If the population inside the closure approaches carrying capacity, selective removal of large individuals could reduce density-dependent processes and increase overall productivity, but few would argue that the current status of cod would indicate that this is the case. Nonetheless, the complex interaction of recreational harvest and protection is worthy of further evaluation.

With hydrological mechanisms for dispersal of larval fish in New England waters still intact, the limited signs of age structure recovery and absence of old cod in the waters south and east of Cape Cod may indicate a lack of optimal habitat. Apart from overfishing, a likely contributor to this habitat loss is the resulting distributional shifts associated with warming (Perry et al. 2005, Fogarty et al. 2008, Meng et al 2016, Pershing et al 2016). Recruitment success in cod was found to be highly correlated with bottom temperature and a mean temperature of ~9°C from 1978 to 2002 over Georges Bank exceeded a recruitment success threshold (Drinkwater 2005, Gröger & Fogarty 2011). Open ocean and shallow water temperatures, along with ocean acidification, are the primary factors projected to have the largest magnitude of change by the middle of the century. This is of great concern for each of the three species in this study; findings show they have high distribution change potential based on climate change and decadal vulnerability (Hare et al. 2017). While the specific mechanisms of temperature vary in their effect among species (i.e. changes in advection via thermohaline circulation, larval survival, enzyme reactions, prey availability etc.) few management schemes incorporate temperature with fishing mortality. A growing body of literature incorporates the direct
interaction of biological response to environmental conditions with indirect factors such as fishing effort (Meng et al. 2016, Pershing et al. 2016). As our ability to forecast temperature change in New England increases, and our understanding of basin-wide effects of mechanistic changes to the biology of critical species and trophic level response, adaptive spatial management could ensure the longevity of key groundfish predators.

**Conclusions**

This study addresses an important aspect of stock demography that is often overlooked in stock management. As expected, the age structure response differed among species, due to their differences in life history and ranging habitats, exposure to fishing pressure, and environment change. Although these temporary fisheries closures were not designed to protect or increase age structure metrics, the three examples of positive closure interaction effects coincide with the intended species whose mortality the closures were aimed at reducing.

The results of this analysis reveal several important cases of fisheries closures affecting the age structure response of Atlantic cod, haddock, and yellowtail flounder. In a region where BACI analyses resulted in significant increases in age metrics over time, mean age and CPUE5+ models provide strong evidence that the Western Gulf of Maine closure contributed to the increase in age structure metrics of the Gulf of Maine Atlantic cod stock. For haddock, a species that has seen episodic success in recruitment in recent years, Closed Area I had the strongest measured effect on age structure. With robust sampling distribution and size in CAI analyses, mean age and CPUE5+ models provide the strongest evidence of a positive closure effect in the Northeast. Mean age response
was seen immediately, and CPUE5+ increased by an order of magnitude. Despite both significant negative and positive influence effects of the Nantucket Lightship and Cashes Ledge closures, respectively, individual high-abundance tows of haddock reduce confidence in the causative effects of the closure. Although negative trends in haddock age structure response in Nantucket lightship may indicate lack of habitat for older ages, the numbers of juveniles (age-0) caught may point to favorable pelagic conditions for early life stages. Evidence of closure effects on yellowtail flounder are weakest. In the strongest case, CAII models showed mixed significant effects on mean age and CPUE5+. An initial strong response in mean age and CPUE5+ indicate a strong closure effect. Yet, the resulting convergence of the same metrics and patterns of distance response indicate a spillover effect, a pattern that may arise from a more sedentary life-history that can lead to density dependence. Importantly, CAII is the only region that saw consistent increases in the three measured age structure metrics for yellowtail flounder. CAI, showed a different effect of the closure: a maintenance effect, whereby overall age metrics decreased, and the closure helped maintain a status quo Although characterized primarily by episodic catches and decreasing metrics, the early response of yellowtail flounder CPUE5+ to the closure suggests that protection helped maintain old growth and mean age in a heavily exploited population. When positive closure effects were seen, they occurred almost immediately and persisted for the first few years of the closure. In cod, the first four years showed rapid divergence in catches of older fish within the WGOM closure. Haddock showed strong responses in mean age and CPUE5+ that persisted for the 5 years following the closure. For yellowtail flounder, the immediate response was obvious in CAII, but more episodic in CAI.
Since the 1994 restrictions on fishing over these grounds, a complex biological experiment was born. Through standardized sampling and stringent regulations, we have ecological control sites that can be used for comparison. What this study has demonstrated is that changes in age structure can be detected over long periods of time and large spatial scales. Not without sampling limitations and shifting species ranges, the NEFSC trawl survey has provided a large biological dataset to measure change. For haddock, spatial management and other changes made in the 1996 Sustainable Fisheries Act have contributed to a strong recovery. The overall trend in age metrics for yellowtail flounder and cod tell a different story: further improvements in management are in order. Maintaining a delicate balance of managing collapse and recovery, with economic and cultural considerations is inherently complicated, but a complex marine system demands a complex management structure. It would be worthwhile to consider changes to existing closures particularly if the goal is long term maintenance of stable, older populations. Such changes would require identifying specific habitats with consideration of the life history variation and seasonal distribution of these species. The results from Chapter 2 of this thesis indicate that increased age structure metrics are not ubiquitous throughout the closure. Depth driven meso-habitats within the closure lead to differential manifestation of age structure health. Furthermore, the behavioral differences between fish in these habitats may demand different spatial management applications. For example, the identification and inclusion of recruitment hotspots in future reserve structure could improve effectiveness (Murawski et al 2000, Hilborn et al 2004, Wen et al 2013). With this improved understanding of life-history strategy and habitat use, an application of a large network of smaller closures would suit the protective demands of closed area management while offering more open fishing grounds for the target of other demersal
species. More plentiful, but smaller closures would provide a higher perimeter-to-area ratio that could promote a greater spill-over effect and improve overall catch-efficiency in the groundfish fleet (Sanchez-Lizaso et al 2000, Lubchenco 2003).

The Final Rule of the Omnibus Essential Fish Habitat Amendment 2 (OEFHA2) process in April 2018 restructured closed area management in the Gulf of Maine. Notably, the ruling removed the NL and CAI closures, and implemented three smaller closures of various types: Habitat Management Areas (HMA), Dedicated Habitat Research Areas (DHRA), and Seasonal Spawning Closures. The decisions by the New England Fishery Management Council exemplifies a combination of two important considerations in the future of marine reserve management: habitat and economic output. By citing the difference in vulnerabilities of different habitat types across Georges Bank to adverse effects of fishing gear and considering the productivity of the scallop fishery over sandy substrate largely encompassed by southern closures, the restructuring will lead to a projected increase in $140-160 million in revenue for the fishing industry. Until the next ruling, the more vulnerable habitat of eastern Georges Bank will remain under protection. While the results of my study revealed a significant positive effect of Closed Area I on haddock, the fishery is currently doing well (NEFSC 2017). On the other hand, the reduction in size of the WGOM closure is worrisome. As the only closure to show strong significant protection benefits to cod, a reduction in size could detract from future age structure recovery, a biological reference point that remains on the fringe of the NEFMC’s considerations. If the future of fisheries management in New England includes an emphasis on old growth in groundfish, we must recognize that the last 25 years of closed areas were not effective enough in curbing groundfish collapse.
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CHAPTER 2:
INFLUENCE OF FISHERY CLOSURE STATUS AND HABITAT ON ATLANTIC COD AGE STRUCTURE IN THE CENTRAL GULF OF MAINE

ABSTRACT

In 2002, a historical fishing ground in the central Gulf of Maine received full protection status, creating the Cashes Ledge Closed Area (CLCA). Designed to reduce groundfish mortality, its effects on the age structure recovery on Atlantic cod are unclear. This area, with limited sampling from standardized trawl surveys, is the focal point of a two-year sampling program using gillnets and handlines to investigate the response of mean age, age diversity, and catch-per-unit effort of age 5+ cod. These age metrics are compared to acoustically derived seafloor descriptors to determine the effect of habitat on cod age response. Results show that when comparing similar strata, closure status has a significant effect on mean age. The location effect alone showed high age diversity and proportion of older fish inside the closure, but comparisons among strata show that depth-driven habitat is a stronger driver of age structure health in this area.

INTRODUCTION

The importance of habitat in the sustainable management of marine fisheries in the Gulf of Maine was formally acknowledged in the passing of the 1996 Sustainable Fisheries Act. This was applied through the Omnibus Essential Fish Habitat Amendment 2 which identified essential fish habitat (EFH), defined as substrate necessary for fish
spawning, breeding, feeding, or growth to maturity. To hedge against further fishery collapse and reduce groundfish mortality, the National Marine Fisheries Service (NMFS) enacted several fisheries closures. The focus of this study is Cashes Ledge Closure, which was fully closed in 2002 (except to recreational and exempted gear). This area, centrally located in the Gulf of Maine, contains unique offshore habitat and may provide the protection needed for demographic recovery in the overfished Gulf of Maine cod stock. The highest feature in the Gulf of Maine’s topography, Ammen Rock, is a northward trending ridgeline 56km by 10-12 km. As the defining feature of Cashes Ledge closure, this shallow promontory at its peak is only 7 m below the sea-surface and supports the Gulf of Maine’s only offshore kelp forest. With access to the productive euphotic zone and strong tidal currents, this habitat serves as a haven for benthic diversity. These benthic species, along with seasonal fluctuations in forage fish, support a predator community dominated by Atlantic cod (Witman et al 1993). At present, Gulf of Maine cod are at historically low biomass levels (Palmer 2014). Much of this is due to decades of overfishing enabled in part by overoptimistic stock assessments that did not consider the effect of unprecedented warming in the Gulf of Maine on cod stock performance (Pershing et al. 2015). In response to this collapse, fishery managers have enacted severe cuts to cod quotas. While cuts to fishing mortality should in theory enable the stock to rebuild, experience in other parts of the Atlantic would suggest that there are multiple biological and ecological factors that may impede rebuilding even in the absence of fishing pressure. For example, it is widely thought that a lack of forage fish (capelin) following a stock collapse in the early 1990’s was responsible for the slow recovery of the northern cod stock in Newfoundland (Rose & O’Driscoll 2002, Sherwood et al.
2007); this stock is currently recovering well due in large part to a resurgence of forage fish (Rose and Rowe 2015).

In addition to external food-web factors, other intrinsic biological factors may impede rebuilding of stocks at low biomass levels. Note that any factor that leads to lower than expected production at low stock abundance is termed a depensatory factor (Hutchings 2013). One such factor may be mean age of the stock which typically is skewed towards younger spawners in overfished populations (Berkeley et al. 2004). Indeed, many fisheries scientists acknowledge the importance of cod age structure to recruitment success (Marteinsdottir & Thoraninssen 1999, Hixon et al 2014, Shelton et al 2015). Particularly in multiple batch-spawning species, older females display more frequent spawning events, producing larger batches of eggs (Trippel 1998, Secor 2000, Berkeley et al 2004, Hsieh 2010, Hixon et. al 2014). This increases the chances that one of their batches will encounter favorable oceanographic conditions as exemplified by the match-mismatch hypothesis (Cushing 1974). In a fishery that heavily selects larger and older fish, a truncated size or age structure can inhibit recovery of the stock (Berkeley et al 2004, Secor 2005, Hixon et. al 2014, Shelton et al 2015). Some view the truncation of age structure, leading to decreased age and size of maturation as a biological regime shift, induced by fishing pressure through short term evolutionary selection (Berkeley et al 2004, Olsen et al. 2004). The greatest concern for Gulf of Maine cod is that the low numbers of age 5+ fish in the recent assessment may be significantly impacting recruitment success (Palmer 2014). For a more comprehensive discussion on the importance of age structure, see chapter 1.
With a lack of age-based reference points, and limited ways to manage for protection of these older fish, there may exist only one option for reducing age structure truncation: closed areas. There are currently two year-round groundfish closed areas in the Gulf of Maine: The Western Gulf of Maine Closed Area (WGOMCA, closed in 1998) and the Cashes Ledge Closed Area (CLCA, fully closed in 2002). These two closed areas are part of a larger groundfish mortality reduction strategy in New England that arose from groundfish declines in the early to mid-1990’s (see chapter 1). There has been debate about the efficacy of these closed areas and whether they are achieving their stated goal of reducing groundfish fishing mortality. Many feel that, given a shift to output controls (quotas) in 2010 for controlling groundfish fishing mortality, closed areas (an input control) are now obsolete. However, the recent collapse of cod during quota management points to the inherent risk of this system. Closed areas may provide a backstop to an even worse outcome, not only in terms of loss of stock biomass, but in terms of stock production potential (i.e., more complete age structure or older, more productive spawners). Sherwood & Grabowski (2016) reported that New England closed areas harbor 8 times more old cod (> 5 years) than adjacent open areas. While this study provided valuable data on the importance of closed areas for protecting older, larger cod, their study did not account for the potential confounding factors of habitat and scale. For instance, are cod inside of closed areas older simply because of restrictions on fishing, or do closed areas happen to encompass habitats that are more attractive to older cod? Related to this, is cod age structure enhanced throughout closed areas, or is this benefit only seen in particular habitats? The result of either of these possibilities would be that closed areas protect older cod in their current configurations. However, a greater
understanding of the scale and habitat questions could lead to more pointed closed area strategies in the future.

The current chapter focuses on studying the impact of habitat and scale on cod age structure in the Cashes Ledge Closed Area located in the central Gulf of Maine. There are several fishing grounds throughout this area that in the past, have supported catches of cod, haddock, hake and cusk (Rich 1929). While there are no known cod spawning grounds inside the closure, there is historical evidence that the area supported high cod productivity (Rich 1929, Ames 2004, Zemeckis et al 2014). Ammen Rock lies near the eastern edge of the border, but there are various structures outside of this designated EFH that may provide suitable conditions for age structure recovery of cod. Notably, Fippennies Ledge is a flat-topped bank covering the western portion of the closure. Its bathymetry and hydrography are comparable to Platts Bank, a heavily fished area north and outside of the closure. The northern section of the closure, an east-west promontory known as Sigsbee Ridge, closely resembles the peak-like structures of Three-Dory Ridge, outside the closure to the Northwest. The diversity of these bottom features may uncover clues about the spatial distribution and connectivity of cod and their age structure within the closure. Figure 2.1 shows a map of the survey area with the named fishing grounds. The complex sedimentary structure of these areas is important to food webs and should be a pertinent consideration in the analysis of spatial management of Gulf of Maine groundfish (Auster et al. 2001).
Figure 2.1. Discrete fishing grounds of central Gulf of Maine. Blue ellipsoids represent clusters of sites over various groundfish habitats throughout the closure. Black points represent sampling sites. The solid red line denotes the Essential Fish Habitat (EFH), which encompasses Ammen Rock. Sites that are not labeled are sites in deep muddy basins were cod were not captured (180+ m).
For much of the heavily fished portions of the Gulf of Maine, there is ample survey data to investigate age structure in common commercially harvested species. Sampling of Northeast Fisheries Science Center standardized bottom-trawl survey data for Before-After Control-Impact analyses yielded thousands of aged samples of cod from heavily fished grounds on Georges Bank and in the Western Gulf of Maine. Experimental results from the research outlined in Chapter 1, showed that there is a significant lack of sampling effort throughout the central Gulf of Maine, particularly inside the Cashes Ledge closure. Results from a balanced random-stratified experiment showed declines in three age structure metrics (mean age, age diversity, and CPUE5+), yet model fitting showed no significant results of the interaction effect (between location and time). With just under 150 samples per treatment, before and after the implementation of the closure, it is therefore difficult to draw a conclusion (See Chapter 1, table 1). This study aims to fill that knowledge gap through results from a random-stratified sampling survey using two gear types: gillnet and handline. Trawl sampling was not chosen for this survey due to consideration of sampling difficulty over hard, complex bottom found throughout the sampling region.

With this study, nearly 15 years after the implementation of the closure, I present results of a survey from sites inside and outside the closure conducted during survey seasons in 2016 and 2017. Applying the same age structure metrics from Chapter 1 (mean age, age diversity, and CPUE5+), I measure age structure according to location (inside; outside) and distance (km from Ammen Pinnacle). In addition to measuring the age response of cod to spatial closure, I developed a novel technique using acoustically
derived bottom habitat variables from the 2016 sampling survey to model age structure of Atlantic Cod in relation to habitat.

Holliday (2007) described nearly 80 different acoustically derived parameters for characterizing the physical and material properties of the seafloor. Still in the early stages of development, acoustic seabed classification (ASC) has tremendous potential to support ecosystem-based science due to its low cost and high spatial resolution (Anderson et al 2008). Using industrial tools developed for commercial fishing, detection of petroleum reserves, and marine research, a wide-range of methodology has been applied to fisheries habitat science. Pairing multi-beam sonar reflectivity and NEFSC trawl survey data, Auster et al. (2001) showed a statistically significant relationship between acoustic reflectivity and abundance for 12 out of 20 species tested, including Atlantic cod and haddock. On Cashes Ledge, multi-beam sonar has been used with clustering algorithms and imagery to characterize macro algae canopies and substrate type (McGonicle et al. 2011, Conroy et al. 2016). While multi-beam sonar is a useful tool for bathymetry and habitat mapping due to its wide beam swath and high-resolution, several studies have successfully characterized bottom using low-cost split-beam echosounders (Greenstreet et al 1997, Siwabessy et al. 1999). In the Gulf of St. Lawrence, discriminant analysis was applied to the backscattering strength (Sv) for successfully identifying high density scallop beds (Hutin et al. 2005). Based on these demonstrated successes, using unsupervised acoustic reflectivity variables analyzed from echosounder data collected during the 2016 season, I investigated the relationship between cod age structure and meso-habitat inside and outside the closure. I hypothesize that the most complete age structures will be seen in highly structured habitats and age
enhancement (mean age, diversity, and CPUE 5+) will decrease as a function of distance from such habitats (e.g., Ammen Rock but also Fippennies Ledge inside and Platts Bank outside). Results from this portion of the study indicate a strong effect of depth on habitat range of cod in the central Gulf of Maine.

**MATERIALS AND METHODS**

**Biological Sampling**

In the summer of 2016 and summer and fall of 2017, I conducted fishery-independent biological surveys of cod in and around the Cashes Ledge Closed Area. Strata for sampling were selected based on depth ranges of 0-45 m, 0-90 m, 90-180m and 180+ m (0-45 m sites were found only inside the closure, within EFH). Individual sites were selected at random using ArcGIS spatial analyst toolbox (ESRI). Sites are shown in figure 2.2. In 2016, aboard the *F/V C.W. Griswold*, I sampled 26 sites throughout our study area using gillnets. Fish were caught using 12-panel gillnets with mesh sizes ranging from 6.5 to 8 inches. Each gillnet was soaked for 2 hours and laid orthogonal to each acoustic transect. Each randomly selected site was subsequently sampled during soak time using a Simrad EK60 split-beam echosounder (see below for description of acoustic methods). Captured Atlantic cod were sacrificed and returned to the laboratory for biological sampling. In 2017, I sampled the same sites aboard the *F/V Lady Tracy Anne II* using hook-and-line gear. Each site was visited for approximately 1 hour of fishing effort with an average of 8 lines in the water at 1 time. Terminal gear included a mix of ‘Norwegian’-style jigs (3 hooks) and baited hooks (2 hooks, surf clams). All captured cod from both sampling seasons were sacrificed aboard the vessel. Bycatch was
identified by species and measured for length and weight before being returned to the water.
Figure 22: Cashes Ledge 2016 and 2017 sampling sites. Black dots represent sites. Red dashed line represents closed area boundaries.
Ageing

Otoliths were removed from the inner ear of captured cod and cleaned of adhering tissue. In the laboratory, otoliths were fixed in epoxy (Buehler Epothin 2) and sectioned using a low-speed saw (Buehler Isomet). Sectioned otoliths were then mounted to glass microscope slides using a thermoplastic adhesive (Crystalbond). Mounted slides were then placed under a Nikon SMZ800 dissecting microscope with a photographic lens (Q-imaging micropublisher 3.3 RTV) and captured at 2X magnification with imaging software (Image Pro Software -Cybernetics). Images were reviewed independently by two technicians who counted the annuli and assigned ages. Ageing was repeated twice by each technician before a consensus was determined.

Acoustic Sampling

21 of the sites from 2016 were sampled acoustically by conducting 7.8 km transects, travelling at 6 knots, during 2-hour gillnet soaks. Acoustic data was recorded by a Simrad EK60 multi-frequency (38-, 120-, and 200- kHz) split-beam echosounder. Each transducer was operated at 0.512ms pulse length, 500ms sampling intervals, and maximum power settings. Data from acoustic sampling includes acoustic backscattering from organisms in the water column and acoustic reflectivity of the bottom. All acoustic data was post-processed using Echoview 8.1 acoustic analysis software. Processing included bottom-selection and noise-removal algorithms. For each derived bottom variable, a depth normalization algorithm was applied to compensate for depth-specific beam width. The following bottom variables were collected from 120kHz data after post processing. 120kHz was chosen as it experienced the least interference from background
noise and provides the best compromise for calculating roughness (Anderson 2007). Each variable is listed by its definition:

**Depth** – Distance of the seafloor from the transducer face plus depth of the transducer (1m). Depth values in meters were recorded for each ping across the 7.8 km transect.

**Roughness** – derived from an integration of the tail of the first bottom return (Siwabessy et al. 1999). Higher frequencies are preferred for extracting roughness, referred to as E1 in the RoxAnn model (Chivers et al 1990, Anderson 2007). Roughness may be representative of sediment type and hydrographic conditions shaping the bottom.

**FBLN** – First bottom length normalized. There may be a correlation between lower amplitude in the first bottom echo for softer sediments (Hamilton 2001). This variable follows less discrete depth correlation pattern than Roughness.

**$S_v$** – Bottom Max $S_v$ (dB). Maximum backscatter in the first bottom echo of a ping.

**Kurtosis** – a descriptor for the outliers of the sample distribution of the bottom echo.

**Skewness** – a descriptor for the symmetry of the sample distribution of the bottom echo.

As biological samples within sampling sites are not spatially discrete, each habitat variable across transects was condensed into single number descriptive statistics (mean, range, and interquartile range (IQR)). To fit a multiple linear regression, I applied a
stepwise regression technique. This method combines forward and backward selection of variables in a linear regression and selected those that contribute to the highest variation. The hypothesized model predicts that most of the variance from acoustic data was described by six variables: Depth, Roughness, FBLN (mean and variance for each). The hypothesized model is structured in the following way and includes the location effect:

\[ y = \sum_{i=1}^{n} \beta_n x_n + \epsilon_i \]

\[ X_1 = \text{depth mean} \]
\[ X_2 = \text{depth range} \]
\[ X_3 = \text{roughness mean} \]
\[ X_4 = \text{roughness IQR} \]
\[ X_5 = \text{FBLN mean} \]
\[ X_6 = \text{FBLN IQR} \]
\[ X_7 = \text{Skewness} \]
\[ X_8 = \text{Kurtosis} \]
\[ X_9 = \text{Location (in/out)} \]

The dependent variables tested in the model included the full age distribution, age diversity, and proportion of age 5+ fish (Prop 5+). CPUE5+ was not included in the model due to lack of standardization of gear types across seasons.

**Age Structure Indicators**

A range of age structure indicators were used to assess closed area impact on cod. Identical to those used in Chapter 1, I used the age distribution, age diversity, and CPUE5+ of cod. CPUE5+ is defined as the catch-per-unit-effort of “old” cod (i.e., age 5+; Sherwood and Grabowski 2016) in each sample. Age 5+ cod likely represent repeat spawners since cod reach spawning age between 3 and 4 years old in the Gulf of Maine (Palmer 2014). Effort for 2016 is defined by the number of decimal hours of gillnet soak.
In 2017 it is defined by rod-hours (number of rods fished per site x number of hours fished per site). Thus, CPUE5+ is simply defined as:

\[
\frac{\text{Number of age 5 + cod}}{\text{Effort}}
\]

To test the response of Atlantic cod age diversity, I applied a variation of the Shannon Diversity index as adapted to age structure (Marteinsdottir & Thoranensen 1998), using the following equation for Shannon’s H (Simpson 1949):

\[
H = - \sum_{i=1}^{k} (pi \cdot (\log pi))
\]

Where \(pi\) represents the proportion of individuals in each age class and \(k\) is the number of age groups present.

**RESULTS**

A total of 461 cod were sampled during the 2016 and 2017 sampling seasons in summer and fall (105 [gillnet] and 356 [handline], respectively). Fish captured ranged from 1 to 8 years old. 323 fish were captured from random-stratified sites; the other 138 fish were captured from selected sites, either from fisherman knowledge or researcher experience. 298 fish were captured inside the closure, and 163 were captured outside. Over both seasons there were 47 site-based sampling events, of which 29 yielded cod (Table 1). A total of 293 fish were sampled over acoustically characterized bottom habitat and were included in the habitat model. 460 fish were captured at depths less than 180 m
(only 1 fish in the 180+ strata). Only the 0-90m strata sites produced fish both inside and outside the closure. In the following sections I present results of location effect, distance effect, and acoustic habitat modeling.

<table>
<thead>
<tr>
<th></th>
<th>sample size</th>
<th>SR</th>
<th>FS</th>
<th>Mean Age</th>
<th>H</th>
<th>Prop 5+</th>
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<tr>
<td>Inside</td>
<td>298</td>
<td>185</td>
<td>113</td>
<td>3.98</td>
<td>2.46</td>
<td>0.282</td>
</tr>
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<td>163</td>
<td>107</td>
<td>56</td>
<td>3.9</td>
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<td>0.196</td>
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</tbody>
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Table 2.1 Summary of age metrics from Cashes Ledge sampling. SR is the number of fish caught in stratified random sites. FS is the number of fish caught in fisherman select sites.

**Location effect**

The mean age of cod inside and outside the closure was 3.90 (SE=0.0538) and 3.97 (SE=0.0658) years, respectively. Results of a one-way ANOVA show that the difference between the age distribution due to location is insignificant (p-value=0.373). The same test was done on mean age of the predominant strata (0-90m), excluding samples from the EFH (Ammen Rock). These results showed that age was 0.22 years higher inside the closure (mean = 4.13, SE=0.0916) than outside (mean=3.91, SE=0.0660; p-value =0.0439). A direct comparison between sites on Platts Bank and Fippennies Ledge resulted in 0.29 years higher mean age inside (mean=4.29, SE=0.115) than outside (mean = 4, SE= 0.070)(p-value=0.026). This result supports the hypothesis that mean age is higher inside the closure, particularly when similar habitat/strata are directly compared. Mean age by fishing ground is presented in Figure 2.3.
Figure 2.3 Mean age by fishing ground. Black points represent grounds inside the closure. White points represent grounds outside the closure. Vertical error bars represent +/- standard error. The pairwise comparison between Fippennies and Platts Bank shows a strong difference in mean age over similar habitats that are only differentiated by closure status.
The catch-per-unit effort of age 5+ fish (CPUE5+) was higher inside the closure than outside in both sampling seasons. Only in 2017 were the results significantly different (Figure 2.4). The spatial distribution of age 5+ fish indicates suitability of habitat both inside and outside the closure (Figure 2.3). The age diversity index ($H$) was highest inside the closure and within the EFH (Figure 2.5). When compared using the location effect alone, $H$ inside the closure was 2.46 vs 2.20 outside (Table 1). Pooled samples from the 0-90 strata (excluding EFH) resulted in higher diversity outside the closure ($H = 2.19$ vs $2.07$). In a direct comparison between Platts Bank and Fippennies Ledge, diversity was also higher outside ($H=2.12$ vs $1.87$).
Figure 2.4 CPUE 5+ by season and gear type. Y-axis represents catch-per-unit effort of age 5 and over fish. Error bars represent +/- standard error. Despite differences in sampling, in both season we detect a higher catch of older fish inside the closure.
Figure 2.5 Distribution of age 5+ fish. Red bubbles represent sites where fish age 5 and over were captured. The size of the bubbles represents the relative number of older fish. Age 5+ plus fish were captured over each 0-90m fishing ground.
Distance effect

When testing the hypothesis that age structure benefits arise from EFH, results show that this is not the case. Mean age by site was highest on Peck Ridge, in the middle of the closure, but this result is confounded by low sample size (n=2)(Figure 2.6). Therefore, a pairwise comparison between Ammen Rock and Fippennies Ledge is more appropriate. Surprisingly, Fippennies Ledge sites had higher mean age than Ammen Rock. Sites around Ammen Rock had the highest diversity and CPUE5+ but were only slightly higher than those from Fippennies Ledge (Figures 2.7 and 2.8, respectively). Low values in CPUE5+ and H from intermediate and deep sites between Ammen Pinnacle and Fippennies indicate habitats of low importance to cod during the season surveyed.
Figure 2.6 Mean age by distance inside the closure. The x-axis represents distance from Ammen Pinnacle (Site 999), the shallowest site. Blue points represent sites inside the EFH, or over Ammen Rock. Green points represent sites at intermediate depth (90-180m). Red points represent sites in the 0-90m strata. Error bars on each point represent +/- standard error. Highest mean age was confounded by low samples (n=2), but interestingly in sites where many samples were captured, mean age was highest over Fippennies Bank (sites 20, 20B, and 901), not Ammen Rock (Blue).
Figure 2.7 Diversity by distance inside the closure. The x-axis represents distance from Ammen Pinnacle (Site 999), the shallowest site. Blue points represent sites inside the EFH, or over Ammen Rock. Green points represent sites at intermediate depth (90-180m). Red points represent sites in the 0-90m strata. Highest diversity by site is found on top of Ammen Rock. Comparable diversity is also found on Fippennies Bank, over 30 km from Ammen Rock (to the west).
**Figure 2.8** CPUE5+ by distance inside the closure. The x-axis represents distance from Ammen Pinnacle (Site 999), the shallowest site. Blue points represent sites inside the EFH, or over Ammen Rock. Green points represent sites at intermediate depth (90-180m). Red points represent sites in the 0-90m strata. Error bars on each point represent +/- standard error. Highest CPUE5+ was nearly identical over Fippennies and Ammen Rock. The overall higher occurrence of CPUE5+ over Ammen Rock (Blue) supports the hypothesis that contains optimal habitat for older fish. Despite vast differences in geomorphology, Fippennies Bank also provides optimal habitat for older fish.
Habitat Model

Stepwise linear regression was used to develop models to predict age diversity, the proportion of older fish (Prop 5+) and mean age by site using acoustically-derived physical descriptors of the seafloor and closure status (location). The stepwise regression failed to find a significant relationship of any of the variables with mean age. The results of the univariate relation between depth and mean age are presented in table 2. Age diversity was explained mostly by depth in a multivariate model with an $R^2$ value of $= 0.972$. A stepwise AIC regression selected 4 variables (depth mean, skewness mean, $S_v$ IQR, and location). While mean depth of site was a significant contributor to the model, $S_v$ IQR (p-value = 0.055) may also be a contributing factor to age diversity of a site (Table 2). The prop 5+ regression selected both mean depth and bottom kurtosis as contributing variables. Only depth mean was significant (p-value= 0.034, Table 2.2).
Table 2. Habitat Model Results

<table>
<thead>
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<th>Term</th>
<th>B</th>
<th>CI</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
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<td>3.66 - 9.16</td>
<td>0.002</td>
</tr>
<tr>
<td>D_mean</td>
<td>0.03</td>
<td>0.07 - 0.00</td>
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<table>
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<td>(Intercept)</td>
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<tr>
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<td>Skew_mean</td>
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<tr>
<td>Sv_iqr</td>
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<td>0.19 - 0.00</td>
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<td>Location</td>
<td>0.21</td>
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<td>0.11</td>
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<table>
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<td>(Intercept)</td>
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<td>Kurt_iqr</td>
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<td>0.05 - 0.01</td>
<td>0.115</td>
</tr>
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</table>

Observations: 7, 11, 7

R² / adj. R²: .525 / .429, .983 / .972, .721 / .581

Deviance: 0.219, 0.1, 0.024

Table 2.2 Habitat Model Results. Mean age failed to fit a stepwise regression and results are presented as a univariate relationship with depth. For both mean age and prop 5+ models, sites with low sample sizes (n=2) were omitted from analysis. In the age diversity model, a strong fit was found with depth mean, skewness mean, Sv IQR and Location. Only depth was found to be significant, although Sv IQR (a measure of the range strength of bottom reflectivity, a similar measure used in Auster et al (2001) to characterize groundfish habitat, had a low p-value (0.055). In the Prop 5+ model (proportion of older fish by site), Depth mean was statistically significant. These results indicate the habitat depth plays an important role in age structure recovery of cod, perhaps more so than closures status.
DISCUSSION

The purpose of this study was to compare a range of age structure metrics of cod inside and outside Cashes Ledge Closed Area to test the hypothesis that the fishery closure, which excludes bottom-tending commercial groundfish gear, would over time have a positive effect on age structure recovery in a heavily fished species. Fourteen years after the closure went into effect we expected to see a higher mean age inside the closure, a more robust age structure (measured by the diversity of age classes), and a higher number of older fish. This study also considers how benefits from Essential Fish Habitat, an area known to be a highly productive haven for cod, may manifest across distances inside the closure. This portion of the study was designed to address questions about the scale and size of closures in a species with considerable life-history variation across a large marine system (Olsen et al 2004, Sherwood & Grabowski 2010). The current status of cod appears to drive the distribution of the remaining fish to patches of optimal meso-habitat at shallower depths. In a unique effort to incorporate age structure in a habitat model, this study also combined unsupervised acoustic survey variables derived from the echo-return of the seafloor with biological samples to deepen our understanding of habitat selection in cod. While the influence of small differences in sediment structure were expected to contribute to differences in the presence/abundance of older fish, it is unsurprising that depth was the most significant factor contributing to positive age structure metrics. The strong collinearity of bottom habitat variables in this region is a result of depositional patterns such that depth and bottom complexity (roughness, backscatter, hardness) are interrelated. Despite a detectable closure effect on these same age metrics, habitat appeared to be a stronger factor in age structure recovery.
Ultimately, the results of this study support age structure benefits manifesting inside a closure due to lack of fishing pressure and agrees with previous findings of enhanced age structure of cod inside New England closed areas (Sherwood & Grabowski 2016). During the summer and fall months in which this survey was conducted, significantly higher values in mean age, diversity, and catch-per-unit-effort of age 5+ fish indicate that age structure recovery may be taking place inside the closure. Despite small differences (Mean Age: 0.2 years; CPUE5+: 0.21) when comparing like habitat, these results should be interpreted in the context of an already diminished age structure and low stock biomass levels throughout the stock area. Age metrics were expected to be highest on Ammen Rock, but it was surprising to find highest mean age and proportion of age 5+ fish by site on Fippennies Ledge (Figure 2.3 and 2.9). However, the higher age diversity found on Ammen Rock (Figure 2.10) does support its designation as EFH; the shallow kelp canopy and complex rocky bathymetry supports sympatry among ages and ecotypes. Furthermore, Ammen Rock provides juvenile nursery habitat; it is the only site where 1-year old fish were captured. Based on results showing high diversity and mean age on Platts Bank, it is clear that despite heavy fishing pressure, the habitat supports a healthier age structure than deeper surrounding areas. If we consider the results of Chapter 1, which showed that it was difficult to detect significant differences in diversity between control and impact, I would conclude that the mean age and numbers of age 5+ fish may be the more important metrics for measuring health, at least in the current state of diminished age structure. Therefore, the older fish inside the closure, particularly in Fippennies Ledge, are contributing the most to the recovery of the local cod population.
Figure 2.9 Proportion of age 5+ catch by fishing ground. Gray bars represent grounds inside the closure. White bars represent grounds outside the closure. The pairwise comparison between Fippennies and Platts Bank shows a strong difference in the proportion of older fish over similar habitats that are only differentiated by closure status.
Figure 2.10 Age Diversity by fishing ground. Gray bars represent grounds inside the closure. White bars represent grounds outside the closure. The highest diversity over Ammen Rock was expected. Unexpectedly, Platts Bank (outside) showed the high diversity outside of Ammen Rock.
In complement to results from Chapter 1, which utilized standardized bottom trawl survey data, this survey demonstrates the utilization of alternate gear types, gillnet and handline, in the detection of higher age diversity and a generally broader age structure over meso-habitats within a closure. From these results, it is apparent that both Ammen Rock (EFH) and Fippennies Ledge stand out as suitable habitat for demographic recovery of cod and subtle differences in demography and habitat may suggest alternate management strategies.

It is well understood that cod migrate inshore during winter and spring spawning and spend a good deal of their time in the summer and fall over offshore banks that serve as productive feeding grounds (Zemeckis et al. 2017). Despite expectations to find tagged Western Gulf of Maine cod moving to deeper waters in the winter, Lindholm et al (2007) found a high occurrence of site fidelity at deep boulder reefs throughout winter months. While Ammen Rock and some intermediate depth ridges offer similar rocky/boulder habitat, Fippennies Ledge and Platts Bank are flat-topped banks composed of sand-gravel with sand/silt/clay margins (USGS CONMAP, 2005; Conroy et al 2016). The strong tidal flow over these offshore banks, when paired with seasonal stratification and internal wave influenced depressions in the pycnocline, allow for episodic pulses in primary and secondary productivity (Whitman et al 1993, Townsend et al 2006). This productivity in turn attracts shoals of pteropods (Clione limacine) and herring (Clupea harengus) (personal observations). During field observations over Fippennies Ledge and Platts Banks, strong scattering layers and tight schools of fish were observed on the echosounder and during one sampling event, surface feeding of bluefin tuna could be seen surrounding the entire vessel. In contrast, Ammen Rock is well known for its high
benthic diversity, productive kelp forest, and nursery grounds. Studies have repeatedly demonstrated its value as a year-round haven for resident groundfish (Witman & Sebens 1992, Sherwood et al 2010, Conroy et al 2016). At this point it is unclear if cod caught over bank-like habitats have the same disposition toward residency or are simply seasonal migrants. In this study, no red cod (a more resident morphotype; Sherwood and Grabowski 2010) were caught over Fippennies Ledge or Platts Banks, but a more robust investigation into morphology, diet and/or behavior could determine ecotype of bank-associated fish (i.e. resident vs migrant). With a maximum distance of 32km between sites on Ammen Rock and Fippennies Ledge and geomorphologically distinct habitats, the level of connectivity between these populations is unclear. Within a single species, divergent habitat use can be complicated to explain. Factors such as small-scale environmental conditions and genetic adaptations can play a stronger role than the physical substrate (Dodson et al 2012, Conroy et al 2017). Robichaud and Rose (2004) identified a link between residency and low productivity and Sherwood & Grabowski (2016) identified that closed areas have a general tendency to harbor morphometrically distinct resident fish. If distinct behavioral strategies are identifiable over different meso-habitats within closures, perhaps spatial management strategies should be adapted to suit ecotypes to promote high productivity and diverse life-history strategies. Through these investigations, closed areas have been demonstrated to enhance age structure in New England groundfish, but weak effects can surely be improved through targeted and effective strategies that will more rapidly restore age structure in an ailing fishery. While we know residence strategies are not exclusive over habitat, the model results indicate that depth can predict older age structure and higher age diversity. Furthermore, the
subtle differences in biodiversity or forage availability in these habitats may influence residency behavior. Nonetheless, the results of the habitat model show that regardless of ecotype, older codfish prefer complex shallow-depth habitat. This result is an important step in recognizing, if only seasonal, the places where the age structure is healthy and likely contributing to overall stock productivity.

As we look to the future of managing cod, we must recognize and deal with an immediate threat to commercial fishing in New England: cod are in a state of crisis. Making management decisions to satisfy ecological harmony and economic viability is not without conflict (Brodziak et al 2004). The complex groundfish structure and spatial management needs to consider the importance of other species. For example, monkfish abundance does not seem to respond to closed area management, and higher numbers of juveniles have been recorded outside the WGOM closure (Smith et al 2008). Furthermore, a critical outcome of cod’s current status is that they act as a choke species for high biomass fisheries such as haddock. If management heeds the call for age-based reference points—a scenario that is inherently difficult to manage for, or continues with the status quo, a conscious reconsideration of closure design to reduce by-catch of cod—if only seasonal—could be crucial to the recovery of the stock and the economic success of other Gulf of Maine groundfish species (Shelton et al 2015). Ultimately, the cod fishery demands high recruitment, and requires many more fish to grow to old, repeat-spawning age. Age-based management, when paired with alternate gear designs and seasonal closures could help the fishing industry capitalize on healthy stocks without further depleting New England’s iconic fish.
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BIOGRAPHY OF THE AUTHOR

Julian “Julek” Chawarski was born in Tarnów, Poland in 1988. His family immigrated to the United States in October 1989 when his parents began their pursuit of advanced degrees at Yale University in New Haven, CT. Growing up around an immigrant scientist community in New Haven, Julek’s passion for science was instilled at a young age. In 2006, he began his undergraduate studies in biology at The George Washington University in D.C. During his studies he worked in the field of emergency medicine and began taking courses in animal behavior and ecology. Before the end of his studies, he was offered a National Science Foundation Partnership in International Research (NSF-PIRE) grant to study fish ecology in Bariloche, Argentina. He continued to work as a research assistant in molecular phylogenetics, before leaving for Maine to work as a fisheries observer aboard groundfish, herring, and lobster fishing boats. After inevitably leaving the observer lifestyle behind, Julek pursued jobs in environmental education and sustainable agriculture in Maine. Naturally drawn to the great outdoors, Julek offered his skills to the Maine Department of Inland Fisheries and Wildlife (MDIFW) as a River Clerk for the regional trout management plan and continued to work seasonally as a ski-patroller in Western Maine. In 2015, Julek was recruited as an intern to work at the Gulf of Maine Research Institute where he developed his quantitative research skills and began working in hydroacoustics. His multi-faceted experience in laboratory and field research made him a strong candidate for a Master’s project dealing with fisheries biology. He is a candidate for the Master of Science degree in Marine Biology from the University of Maine in May 2018.