Ecological and socioeconomic implications of a northern range expansion of black sea bass, 
*Centropristis striata*

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Abstract of dissertation

Species’ range shifts have become an increasingly common ecological phenomenon in recent decades, as global temperatures have warmed and species have shifted to avoid thermal stress. This is particularly evident in the Northwest Atlantic, where many fish stocks have undergone a poleward shift in distribution. Although efforts to project future range shifts and theorize potential outcomes have recently accelerated, the ecological and socioeconomic implications of range shifts are still not well understood. Black sea bass, *Centropristis striata*, historically ranged from the Gulf of Mexico to Cape Cod, but in recent years they have become abundant in the southern Gulf of Maine (GOM), and have been reported as far north as midcoast Maine. In this dissertation, I documented the ecological and socioeconomic impacts of black sea bass in the GOM.

In Chapter 1, I conducted seasonal scuba surveys in midcoast Maine (ME) (i.e., range edge), northern Massachusetts (MA) (i.e., newly expanded range) and Narragansett Bay, Rhode Island (RI) (i.e., native range) to document the distribution and abundance of young-of-year (YOY), juvenile and adult sea bass. Juvenile and adult sea bass were found in all regions, but in very low abundance in MA and RI when compared to other data sources. YOY sea bass were significantly more abundant in RI compared to MA, and were also significantly more abundant in the fall compared to the summer. YOY sea bass were most abundant between 3-4 m depth, which is a range not targeted by trawl, trap and seine surveys.

In Chapter 2, I compared life-history traits of black sea bass collected from 2013-2016 from the northern most point of the historic range of the northern stock (southern Massachusetts) and from two areas in the newly expanded range (northern Massachusetts and Maine). I found significant latitudinal differences in size, diet, condition, maturity and sex ratio across this range.
Overall, sea bass in the newly expanded range had a less diverse diet and lower condition, but reached maturity at a younger age. I also found greater length- and age-at-maturity estimates from all study regions combined compared to the most recent sea bass stock assessment.

In Chapter 3, I investigated the effects of sea bass on the behavior of juvenile American lobsters, *Homarus americanus*. I manipulated the presence of sea bass olfactory cues and observed shelter use and foraging behavior of lobsters from three regions in the GOM with different exposure histories to sea bass. Sea bass presence increased shelter usage and reduced foraging in lobsters, but exposure history influenced the strength of these behavioral responses. Lobsters with no previous exposure to sea bass did not significantly increase shelter usage or decrease movement in their presence, but there was a significant reduction in their foraging rate on mussels. Lobsters with the longest exposure history to sea bass significantly increased shelter usage when sea bass were present; however, they exhibited limited movement and foraging behavior in both the absence and presence of sea bass. Finally, lobsters with a short exposure history to sea bass exhibited increased shelter usage, reduced movement, and reduced mussel consumption in the presence of sea bass, revealing that juvenile lobsters quickly adapt anti-predator defenses to avoid this novel threat.

In Chapter 4, I surveyed commercial lobster fishers in Maine and Massachusetts to document their observations and perceptions of the northern range expansion of black sea bass. Fishers reported historic trends of sea bass bycatch in their lobster traps, including distribution, abundance and habitat information. Overall, 73.3% of fishers reported sea bass being most abundant between 2012-2015, and 56% of fishers believed increased sea bass abundance was due to an increase in water temperature. 48% of fishers believed that sea bass eat lobsters, and this belief influenced whether fishers perceived the range expansion as an opportunity or a threat.
However, 57% of all respondents believed that sea bass becoming more abundant would be ‘somewhat’ or ‘very beneficial,’ indicating an optimistic viewpoint of the northern range expansion. Meanwhile, 67% of fishers in Massachusetts reported that they were not satisfied with current sea bass management, and many specifically called for higher quotas now that sea bass are more abundant.

This dissertation presents empirical data on the ecological and socioeconomic implications of the northern range expansion of black sea bass, as well as biological stock metrics of sea bass in their newly expanded range. These findings indicate that geographic variation in life-history traits may arise during range expansion, and provide a greater understanding of the relative consumptive and nonconsumptive effects of range expanding predators. Furthermore, this study documented fishers’ observations and perceptions of the northern range expansion of black sea bass, which will help inform efforts to manage this species in the Gulf of Maine. Overall, this dissertation offers a model for quantifying the range expansion of an economically important fish species, and consequently may aid in ongoing and future management efforts for species with shifting distributions.
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**Introduction**

The warming of the world’s oceans has begun to restructure marine communities and impact system productivity (Walther et al. 2002, Harley et al. 2006, Mooney et al. 2009, Hoegh-Guldberg and Bruno 2010). This climate-induced environmental forcing is occurring at a rapid rate, increasing the need for efficient assessment of climate change impacts to local ecosystems. One of the consequences of warming ocean temperatures is that species ranges often expand or contract to avoid temperature stress (Parmesan & Yohe 2003, Perry et al. 2005, Poloczanska et al. 2013).

The Gulf of Maine (GOM) provides an excellent platform for studying range shifts because of the steep temperature gradient that exists in the Northwest Atlantic. In the past, this temperature gradient impeded many species from moving northward. However, accelerated warming trends over the past several decades (Pershing et al. 2015), as well as the 2012 warm water temperature anomaly that ranged from Cape Hatteras, NC to Labrador Canada (Mills et al. 2013), have resulted in a northern shift of many temperate species (Nye et al. 2009, Pinsky et al. 2013, Hare et al. 2016).

The impacts of range shifting species on the structure and function of the ecosystems they are expanding into is not well understood; however, the role of predation in regulating ecological communities has been well established (e.g., Hairston et al. 1960, Paine 1980, Sih et al. 1985, Werner and Peacor 2003). Predators impact populations through the direct removal of prey, also known as consumptive effects (CE) (Hairston et al. 1960, Paine 1980, Estes et al. 1998), and by inducing behavioral, morphological or physiological responses, also known as nonconsumptive effects (NCE) (Lima 1998, Trussell et al. 2002, Werner and Peacor 2003, Schmitz et al. 2004). NCEs may have equal or larger impacts on community structure than CEs; however, the strength
of NCEs is context dependent and is influenced by both biotic and abiotic processes (Peacor and Werner 2001, Preisser et al. 2005, Peckarsky et al. 2008, Schmitz et al. 2008).

Newly emerging species present an opportunity to study predator-prey dynamics over a gradient of exposure histories, including at the range edge, where naïve prey may be exposed to novel predators. The ‘naïve prey hypothesis’ suggests that prey exhibit ineffective defenses against novel predators (Cox and Lima 2006, Freeman and Byers 2006, Sih et al. 2010). However, the type of naiveté that prey exhibit (Banks and Dickman 2007), as well as the similarity of the invaded habitat to the native habitat of the predator (Sih et al. 2010), may affect the strength of the interaction among naïve prey and novel predators. Furthermore, some prey species have been found to respond effectively to novel predators (Sih et al. 2010, Kimbro et al. 2013, Ferrari et al. 2015).

Species undergoing range shifts may be subjected to different selective pressures at the range edge that alter life-history traits and increase spatial heterogeneity among populations (Burton et al. 2010, Phillips et al. 2010). For example, the r-K selection theory suggests that populations constrained by density-dependent effects are often K-selected because successful propagation is related to fitness in high density areas (Roughgarden 1971, Charlesworth 1971). Conversely, populations not constrained by density-dependent effects often invest less in competitive ability (K) and more in reproductive ability (r) (Roughgarden 1971, Charlesworth 1971). Therefore, one might expect low-density range-edge populations to be r selected, and high-density range-center populations to be K selected (Burton et al. 2010, Phillips et al. 2010). Environmental heterogeneity across a species’ range can also drive life-history variation (Brander 2010). In particular, temperature and the length of the growing season strongly
influence growth and the timing of maturation in fishes (e.g., Pauly 1980, Conover 1990, Pörtner et al. 2001), and likely vary from the edge to the center of a species’ range.

The black sea bass (Centropristis striata) is a temperate reef fish that ranges along the east coast of the United States and Gulf of Mexico (Moser and Shepherd 2009). The northern stock ranges from Cape Hatteras, North Carolina to the GOM and is jointly managed by the Atlantic States Marine Fisheries Commission and the Mid-Atlantic Fishery Management Council (ASMFC 2016). Historically, black sea bass were thought to be rare in the waters north of Cape Cod (DeWitt et al 1981, Drohan et al. 2007). In recent years, however, there is evidence from recreational and commercial fishers that black sea bass have become abundant in the southern GOM, and are frequently encountered as far north as midcoast Maine (Chapters 2 and 4).

Moreover, McMahan (Chapter 2) has collected over 50 black sea bass samples from fishermen in the midcoast Maine area and has directly observed black sea bass via SCUBA and video as far north as Muscungus Bay, Maine (Chapter 1).

At the northern end of its range, black sea bass distribution varies seasonally. Black sea bass typically migrate offshore and then move south during the cold winter months, but will return to northern inshore areas in the late spring and early summer (Shepherd 2008). Typically, black sea bass are found in waters ranging from 18-22°C (Steimle et al. 1999). The GOM has historically been much colder than the surrounding waters of the Northwest Atlantic, with a mean sea surface temperature of 7°C (Shearman and Lentz 2010). However, the GOM has recently been warming at a rate faster than 99% of the world’s other oceans (Mills et al. 2013, Pershing et al. 2015, Figure 1.0A). In particular, the average temperature in midcoast Maine from June through September, when black sea bass are typically found in nearshore areas, was 14.9°C in the 1990s and 16.9°C in the 2000s, an increase of 2°C (MDMR 2013, Figure 1.0B).
This observed warming of sea water temperatures is likely enabling the northern range expansion of black sea bass.

In addition to warming water temperatures, the lack of large bodied predators in the northern GOM may be facilitating the range expansion of black sea bass. Atlantic cod (*Gadus morhua*) were once dominant in the GOM, but are now functionally absent in nearshore coastal areas due to overexploitation (Steneck 1997, Jackson et al. 2001, Ames 2004). The most recent stock assessment shows that cod spawning stock biomass is currently estimated to be at 3-4% of the target level (Palmer 2015). Other potential predators such as cusk (*Brosme brosme*) and Atlantic wolffish (*Anarhichas lupus*) are also at low biomass levels (AWBRT 2009, NEFSC 2006). The drastic decline in cod and other top predator stocks over the past several decades has altered the GOM food web, resulting in increased mesopredator populations such as cunner (*Tautogolabrus adspersus*) and sculpin (*Myoxocephalus scorpius*) (Witman and Sebens 1992, Steneck 1997), and has even been linked to influencing American lobster (*Homarus americanus*) populations (McMahan et al. 2013). The functional absence of many of the GOM’s top predator may similarly be allowing black sea bass to expand into new territory with little top-down control exerted on their population.

Black sea bass are protogynous hermaphrodites. They are typically born female and transition to male as they increase in size and age. However, black sea bass are distinguished from typical protogynous hermaphrodites in that secondary mature males and large females also occur in the population (Blaylock and Shepherd 2016). In the Mid-Atlantic, black sea bass reach 50% maturity at a length of 21.0 cm total length (NEFSC 2016). Spawning occurs in the spring in nearshore coastal waters (Drohan et al. 2007). Black sea bass can form harems consisting of one dominant male and several females that the male aggressively defends; however, very little
is known about black sea bass behavior during spawning in their native range (Nelson et al. 2003). Furthermore, there have been no studies assessing sex ratio, maturity, or spawning patterns of black sea bass in the northern GOM. This information will help in determining if black sea bass are reproducing in the northern GOM, or if the northern range expansion is limited by recruitment pulses from further south.

Adult black sea bass are generalist carnivores that feed on a variety of invertebrates, small fish and squid (Drohan et al. 2007). Black sea bass south of Cape Cod have been found to consume a diet largely comprised (>50%) of decapod crustaceans (Garrison and Link 2000). Within the GOM, black sea bass are found in similar habitats as the American lobster (Chapter 1 and 4), which is the most valuable fishery in the United States (NMFS 2015). The degree to which the northward expansion of black sea bass is affecting lobster populations is unknown; however, fish predators can reduce lobster movement and foraging behavior and may potentially influence lobster population dynamics (Wahle 1992, Spanier et al. 1998, McMahan et al. 2013, Wilkinson et al. 2015). Therefore, there may be both ecological and socioeconomic impacts of the recent increase of black sea bass in the GOM.

In its traditional range, black sea bass are a highly sought game fish and represent a valuable recreational and commercial fishery. In the past century, the GOM has suffered from the depletion and loss of many fisheries due to overfishing. The economic diversity of marine resources in the state of Maine has drastically declined in the past 20 years, leaving fishermen almost entirely dependent on the lobster fishery (Steneck et al. 2011). While a newly emerging potential predator of lobsters is cause for concern, black sea bass may also provide new economic opportunities. The establishment of recreational and commercial fisheries for black sea bass in the northern GOM could provide an economic subsidy for a region that has very few
recreational sport fish and even fewer commercial fishery resources. Early management efforts of black sea bass, as well as support from recreational and commercial industries, will be critical in aiding the development of black sea bass fisheries.

Black sea bass are a data poor species, which can increase uncertainty in stock assessment models and makes management challenging (Shepherd 2008, Pilling et al. 2009). The lack of basic biological metrics for black sea bass in their newly expanded range further complicates matters. Current stock designations are based on population metrics of black sea bass collected south of Cape Cod, but it is unclear if characteristics of black sea bass in the GOM differ from those for populations farther south. Meanwhile, management has struggled to keep pace with this and other rapidly shifting species (Pinsky and Fogarty 2012), which has caused tension in the recreational and commercial fishing industries, and has given rise to a political debate over quota allocation at both state and federal levels. Furthermore, black sea bass fisheries have recently developed in the northern GOM, outside of stock assessment areas, potentially making this population vulnerable to rapid depletion (Link et al. 2011).

Fisheries-independent data for black sea bass is primarily collected by federal- and state-led bottom trawl surveys which provide a measure of relative abundance of each fish species that is caught. However, black sea bass are typically found in structurally complex habitat, such as oyster and rocky reefs (Peterson et al. 2003, Drohan et al. 2007), that is not conducive to sampling with otter trawls. Trawl surveys also avoid sampling in shallow coastal areas where juvenile black sea bass have been found to be abundant (Drohan et al. 2007, Chapter 1). Within the GOM, trawl surveys rarely encounter black sea bass, despite recreational anglers (K. Cheung personal communication) and commercial fishers (Chapter 4) reporting dramatic increases in abundance in recent years. Therefore, trawl surveys may not be an accurate measure of black sea
bass distribution and abundance (Shepherd 2008). Efforts to describe black sea bass abundance and distribution in coastal waters of the GOM are a necessary first step in understanding the dynamics of their range expansion.

The purpose of this dissertation was to quantify the ecological and socioeconomic impacts of the northern range expansion of black sea bass. In Chapter 1, I conducted scuba surveys to observe the distribution and abundance of black sea bass in the GOM (i.e., newly expanded range) and southern New England (i.e., historic range) from 2013-2016. I tested if (1) black sea bass would be least abundant in the GOM and most abundant in southern New England and (2) there would be a higher ratio of adults to juveniles in the GOM where water temperatures are colder and migration distances are longer. In Chapter 2, I compared life-history traits of black sea bass collected from southern Massachusetts (i.e., historic range) and from two areas in the GOM, northern Massachusetts and midcoast Maine (i.e., newly expanded range). My hypotheses were that (1) the diet of black sea bass in the GOM would consist of more crustaceans than those from southern Massachusetts, (2) patterns of growth, condition and reproduction would differ between GOM and southern MA black sea bass, but not between populations within the GOM, and (3) seasonal variations in diet, condition and reproduction would occur in all regions. In Chapter 3, I performed experiments to investigate the effects of black sea bass on the behavior of juvenile American lobster from three regions within the GOM where exposure history to black sea bass varied. I hypothesized that the presence of black sea bass would induce lobsters to increase shelter usage and decrease foraging, and that this response would be stronger for lobsters with a longer exposure history to black sea bass. In Chapter 4, I built on my earlier biological and ecological research by conducting stakeholder surveys of commercial lobster fishers in Maine and Massachusetts to document their observations and perceptions of the
northern range expansion of black sea bass. I hypothesized that lobster fishers would perceive
the range expansion of black sea bass as a threat to their livelihood. Alternatively, I hypothesized
that MA lobster fishers may already benefit from the recreational or commercial harvest of black
sea bass, and therefore may perceive the range expansion as a benefit. In addition, I hypothesized
that MA lobster fishers would not be satisfied with current black sea bass regulations due to low
quotas and a limited season.
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Figure 1.0. Sea surface temperature (SST) in the Gulf of Maine. A) SST record from the Gulf of Maine showing 15-day (blue line) and annual (gray circles) variability. Linear trend in daily anomalies has a slope of 0.026°C yr\(^{-1}\) (black line) for the entire record. After 2004, the rate increased to 0.26°C yr\(^{-1}\) (red line). From Mills et al. 2013. B) Average annual SST in midcoast Maine from 1993-2010. Trendline = linear regression of temperature over time \((p < 0.05)\). Data from MDMR 2013.
Chapter 1: Surveying the distribution and abundance of black sea bass (*Centropristis striata*) in the Gulf of Maine and southern New England

Abstract

Black sea bass, *Centropristis striata*, have recently expanded their distribution northward into the Gulf of Maine. Fisheries independent trawl surveys rarely detect sea bass in the Gulf of Maine, likely because they prefer structured habitat. Therefore, critical ecological data for sea bass, such as their distribution and abundance, is lacking in their newly expanded range. I conducted seasonal scuba surveys in midcoast Maine (ME) (i.e., range edge), northern Massachusetts (MA) (i.e., newly expanded range) and Narragansett Bay, Rhode Island (RI) (i.e., native range) from 2013-2016 to document the distribution and abundance of young-of-year (YOY), juvenile and adult sea bass. Surveys were conducted at four sites with similar structured habitat within each region, and ranged in depth from 3-10 m. YOY sea bass were most abundant between 3-4 m depth, which is a range not targeted by trawl, trap and seine surveys. YOY sea bass were significantly more abundant in RI compared to MA, and were absent in ME. They were also significantly more abundant in the fall compared to the summer. Finally, YOY sea bass abundance was significantly greater in RI in the fall of 2014 compared to 2013, 2015 and 2016. Juvenile and adult sea bass were found in all regions, but in very low abundance in MA and RI when compared to other data sources and reports from fishers. Therefore, scuba surveys may not be ideal for observing juvenile and adult abundance. Overall, these results indicate that scuba surveys may aid in identifying black sea bass nursery habitat and documenting YOY abundance in shallow, structured habitat that has historically been underrepresented in other survey techniques. Documenting fish settlement patterns is important for understanding how early life history processes influence population dynamics, and is also useful for the stock assessment process and identifying essential fish habitat.
Introduction

Black sea bass, *Centropristis striata*, are a temperate reef serranid that range along the east coast of the United States and Gulf of Mexico. The northern stock ranges from Cape Hatteras to the Gulf of Maine (GOM), but sea bass were rarely found north of Cape Cod historically (DeWitt et al. 1981, Drohan et al. 2007). However, the center of stock biomass has shifted poleward in recent years (Bell et al. 2015), and sea bass have expanded into the GOM. Fisheries-independent state and federal trawl surveys rarely detect sea bass in the GOM, likely because sea bass prefer structured habitat that is not conducive to sampling with otter trawls (Peterson et al. 2003, Drohan et al. 2007, Cullen and Stevens 2017). Trawl surveys also are not conducted in shallow coastal areas where juvenile sea bass have been found to be abundant (Drohan et al. 2007, Ares and ManNamee 2016). However, GOM lobster fishers have reported catching hundreds of pounds of sea bass bycatch daily in their lobster traps, indicating that sea bass have become very abundant in some parts of the GOM (Chapter 4).

The lack of basic ecological data on black sea bass in their newly expanded range makes assessment and management challenging. The Northeast Data Poor Stocks Working Group has suggested using alternative survey techniques for measuring sea bass distribution and abundance, including ventless trap surveys (Shepherd 2008). Beyond utilizing alternative gear, the basic design of fisheries independent surveys may also need to be reexamined. Random stratified surveys that meet the rigorous criteria required for inclusion in stock assessment models may not accurately reflect the abundance of species with patchy or clustered distributions (Christman 1997). Indeed, Cullen and Stevens (2017) found that adaptive cluster sampling (Thompson 1990) was a more efficient method than random sampling for estimating sea bass abundance in the Mid-Atlantic Bight.
Scuba surveys may provide an additional assessment method for black sea bass, and are ideally suited for shallow, structured habitats. Scuba survey techniques were first developed in the 1950s, and have since been widely applied in many ecosystems around the world (reviewed in: Witman et al. 2013). They are cost effective, easily repeatable, relatively quick and non-destructive (Harvey et al. 2004, Witman et al. 2013).

Efforts to describe black sea bass abundance and distribution in their newly expanded range are a necessary first step in understanding the dynamics of their range expansion, and will be essential to ongoing management efforts. The goal of this study was to document the distribution and abundance of black sea bass in their native (i.e., southern New England) and newly expanded (i.e., GOM) range using scuba surveys. I hypothesized that black sea bass would be least abundant in the GOM and most abundant in southern New England. I also hypothesized that there would be a higher ratio of adults to juveniles in the GOM where water temperatures are colder and migration distances are longer.

**Methods**

*Dive Surveys:*

Underwater surveys of black sea bass were conducted in midcoast Maine (ME) (i.e., range edge), northern Massachusetts (MA) (i.e., newly expanded range) and Narragansett Bay, Rhode Island (RI) (i.e., historic range) from 2013-2016 (Figure 1.1). Within each region, four sites with rocky bottom habitat were sampled. Each site was sampled seasonally in the spring (May-June), summer (July-August) and fall (September-October) from 2013-2014, in the summer and fall of 2015, and the fall of 2016. Surveys were conducted in a 2-m wide area along four randomly placed 30 m transects between 3-10 m depth. Divers slowly swam the length of each transect, recording the abundance and size category of all sea bass encountered. Size
categories included young-of-year (YØY) (1-10 cm total length (TL)), juvenile (11-20 cm TL) and adult (21+ cm TL) sea bass (NEFSC 2016). Water temperature was recorded prior to the start of each dive, and depth was recorded at the beginning and end of each transect.

Data Analysis:

The Kolmogorov-Smirnov (K-S) test was used to compare the cumulative depth frequency distribution among size classes from all regions combined. All abundance data were non-normal and were analyzed using General Linear Mixed Models (GLMMs) with a poisson distribution using the ‘lme4’ package in R (R Core Team 2017). Size classes were modelled using separate GLMMs. Region, year, season, and their interactions were included as fixed effects, and site nested within region was included as a random effect, in all GLMMs. The significance of main effects and their interactions was tested using type II Wald’s $\chi^2$-tests. Post-hoc multiple comparison analyses were conducted using the glht function in the ‘multcomp’ package, which conducts simultaneous tests and confidence intervals for GLMs (Bretz et al. 2010, Hothorn et al. 2008).

Results

Sea bass were not present in any region during spring sampling in 2013 and 2014, and spring surveys were not conducted in 2015 and 2016. Surveys were also not conducted in the summer of 2016. YØY sea bass were significantly more abundant in shallow water compared to juveniles (K-S test, $p < 0.05$) and adults (K-S test, $p < 0.05$; Figure 1.2). YØY sea bass were most abundant at a depth of 3 m (Figure 1.2A), while juveniles and adults were most abundant at 5 m and 7 m, respectively (Figure 1.2B and 1.2C).

YØY sea bass were only found in MA in 2013 and 2014, and no YØY sea bass were found in ME (Figure 1.3). The interaction of region and season ($\chi^2 = 11.9, p = 0.003$) and the
interaction of season and year ($x^2 = 7.2, p = 0.03$) both significantly affected YOY abundance. YOY sea bass were significantly more abundant in RI compared to MA in the fall of 2013 (Tukey’s HSD, $p = 0.03$) and 2014 (Tukey’s HSD, $p < 0.001$). Meanwhile, there were no significant differences between the abundance of YOY sea bass in MA and RI in the summer of 2013 (Tukey’s HSD, $p > 0.05$) or 2014 (Tukey’s HSD, $p > 0.05$). In RI, YOY sea bass were significantly more abundant in the fall compared to the summer from 2013-2015 (Tukey’s HSD, $p < 0.05$ for all tests), and more abundant in the fall of 2014 than the fall of 2013, 2015, or 2016 (Tukey’s HSD, $p < 0.05$ for all tests).

Juvenile sea bass were most abundant in MA and RI in 2015, and most abundant in ME in 2013. Season ($x^2 = 13.5, p < 0.001$) and the interaction of region and year ($x^2 = 24.8, p < 0.001$) significantly affected juvenile abundances (Figure 1.4). Juvenile sea bass were significantly more abundant in the fall compared to the summer (Tukey’s HSD, $p < 0.001$). Regional abundance did not significantly differ among years (Tukey’s HSD, $p > 0.05$ for all tests).

Overall, adult sea bass were rare in surveys, and entirely absent from summer surveys in 2013, 2014 and 2016 (Figure 1.5). Therefore, only data from the fall season was analyzed. Adult abundances varied as a function of the interaction of region and year ($x^2 = 20.7, p = 0.002$), which was driven by the absence of sea bass in RI in 2013, in MA in 2013 and 2014, and in ME in 2014.

**Discussion**

Black sea bass are a data poor species that have been particularly challenging to assess in their northern range. This is due, in part, to the lack of assessment techniques that can target structured habitat where sea bass aggregations are often found, or shallow habitat that may be
important to juvenile life history stages (Drohan et al. 2007, Shepherd 2008). My study utilized scuba surveys to estimate the distribution and abundance of black sea bass in RI, MA and ME. I found the highest density of sea bass in the fall in all regions, which may reflect a seasonal shift in habitat use from deeper spring spawning grounds (Musick and Mercer 1977, Drohan et al. 2007) to shallow coastal areas accessible by scuba. In particular, YOY sea bass were very abundant in RI in the fall, which is when the majority of settlement likely occurs (Drohan et al. 2007). My results also provided evidence of YOY sea bass in the GOM, as well as juvenile and adult distributions extending as far north as midcoast ME.

While sea bass were not present in dive surveys in the spring, they are found in RI and southern MA during this time, as evidenced by trawl surveys (Ares and McNamee 2016, MDMF 2016, URI 2017) and samples collected from recreational anglers (Chapter 2). The absence of sea bass in dive surveys in the spring may be due to habitat preferences during the spring spawning season. Spawning aggregations are thought to occur primarily in nearshore habitat between 20-50 m (Musick and Mercer 1977, Drohan et al. 2007), which is deeper than the range where scuba surveys were performed. Therefore, scuba surveys likely did not provide an accurate reflection of sea bass abundance in the spring. Surveys capable of targeting deeper, structured habitat, such as trap or video surveys, may be better suited to surveying sea bass abundance during the spawning season.

The high density of YOY sea bass in the fall in RI (i.e., Narragansett Bay) suggests that this may be an important nursery habitat for sea bass. Ichthyoplankton surveys have found very few sea bass eggs or larvae (Bourne and Govoni 1988) in Narragansett Bay, and trawl surveys have not caught many juveniles (Reid et al. 1999, Drohan et al. 2007). However, neither survey type targets the YOY size class (i.e., here designated as 1-10 cm). YOY sea bass live close to the
sea floor and are not commonly found in the water column where ichthyoplankton surveys occur. They are also too small to be targeted by the Narragansett Bay trawl survey (URI 2017), which generally does not catch sea bass smaller than 10 cm (J. Zottoli, personal communication). Seine surveys find YOY sea bass in Narraganset Bay, but can only target depths less than 2 m (N. Ares, personal communication). My surveys found that YOY sea bass predominantly occurred at a depth of 3-4 m, which is too shallow for trawl and trap surveys conducted from boats to target, and too deep for seine surveys. This finding suggests that previous surveys may have been underestimating the abundance of YOY sea bass in RI, and possibly other areas as well, and emphasizes the need for alternative survey methods that are able to target relatively shallow, structured areas. Moreover, my study suggests that diver surveys are an effective method to sample this critical life history stage.

I found evidence of increased settlement in RI in the fall of 2014. YOY density increased by roughly 115% compared to 2013, 2015 and 2016. This increase was not reflected in RI seine survey data from the fall of 2014; however, a sharp increase was seen in the seine survey in the fall of 2015 (Ares and McNamee 2016). RI seine surveys are conducted in a similar habitat to my scuba surveys; however, the depth of the majority of my YOY sightings were deeper than where seine and shallower than where trawl surveys can effectively be conducted, and may partially explain the observed differences in YOY density among methods. The fall 2014 spike I found in RI was reflected in the MA Division of Marine Fisheries trawl survey, which found a roughly 300% increase in YOY sea bass abundance in southern MA from 2013 to 2014 (MDMF 2016). The increase in sea bass abundance in deeper habitat where trawl surveys sample may be due to density-dependent processes that cause black sea bass to leave their ideal habitat when at high densities, similar to what has been shown with YOY Atlantic cod (Laurel et al. 2004,
Robichaud and Rose 2006). Due to variation in the winter survival of YOY sea bass, fall YOY abundance may not reflect subsequent year class strength (Miller et al. 2015, NEFSC 2016). However, observing settlement trends is an important part of understanding population dynamics and identifying essential fish habitat.

YOY sea bass are thought to be rare in the GOM (Drohan et al. 2007); however, I found YOY sea bass at multiple survey sites in MA (i.e., north of Cape Cod) in 2013 and 2014. Previously, Kolek (1990) had observed spawning as far north as Nantucket Sound. The presence of YOY sea bass in MA, combined with the presence of spawning capable adults in this area (Chapter 2), suggests that spawning may now be occurring in the GOM. Meanwhile, the absence of YOY sea bass in MA in 2015 may be due to temperature. Water temperature in the GOM was below average in the winter and spring of 2015 (NERACOOS 2017), which may have restricted spring spawning activity to warmer southern waters. However, water temperature was higher than average in the winter and spring of 2016, and yet YOY sea bass remained absent at survey sites in MA. Environmental conditions experienced by sea bass in overwintering areas along the continental shelf impact survival, year class strength (Miller et al. 2015) and migration (Moser and Shepherd 2009), and may also influence spawning patterns, and subsequent settlement. Other oceanographic conditions in the GOM and southern New England may also affect the advection of eggs and larvae, and the resulting settlement patterns. Although we did not examine what is driving nearshore patterns of YOY sea bass abundance in the GOM in this study, their presence in this region in 2013 and 2014 is further evidence of the extent of the northern range expansion.

Anecdotal evidence from recreational anglers indicates that juvenile and adult sea bass are very abundant in Narragansett Bay (Chapter 4); however, I found very low densities at my
survey sites. The Narragansett Bay trawl survey also found higher abundance estimates of juvenile and adults than my surveys in both the summer and fall (URI 2017). This difference could be due to a behavioral tendency of sea bass to avoid divers, which would bias abundance estimates. Yet, YOY sea bass have high site fidelity and move very little (Able and Hales 1997), and therefore may be more suited to surveys via scuba. The adult sea bass that were encountered during surveys in this study did not appear to be avoiding divers, and in some instances even exhibited aggressive and territorial behavior toward divers. Another possible explanation for the observed low abundance of juveniles and adults is that I may not have been targeting areas where these sea bass age classes aggregate. Cullen and Stevens (2017) found that adaptive cluster sampling (Thompson 1990) was a more effective method for surveying sea bass in the Mid-Atlantic Bight when compared with random sampling. Although my sites were not randomly selected (i.e., I was limited by shore access for scuba divers), I did not specifically target areas where aggregations were known to occur. Therefore, juvenile and adult sea bass density may be much higher in RI than what I found in my surveys (Cullen and Stevens 2017), and possibly higher than what is reflected in the Narragansett Bay trawl survey, which targets random areas (URI 2017). Reports from commercial lobster fishers that indicate very high abundances of sea bass in some areas of MA (Chapter 4) also suggest that my surveys underestimated juvenile and adult abundances. Sea bass abundance is very low in ME compared to MA and RI, but it is unclear if my survey results accurately reflect abundance in this area. I suggest that future survey efforts, including scuba, video and trap surveys, incorporate adaptive cluster sampling techniques to more accurately reflect sea bass abundance.

My efforts to quantify sea bass distribution and abundance through scuba surveys revealed that this technique was best suited for estimating YOY abundance in the fall, and that
traditional survey techniques may be underestimating YOY abundance in some areas. Identifying nursery habitat in southern New England and the GOM will be critical to managing the northern stock of black sea bass as they continue to expand northward. Furthermore, range expansions are predicted to continue along the US Northeast Continental Shelf as ocean temperatures warm (Kleisner et al. 2017). Therefore, incorporating non-traditional survey techniques may be important for accurately assessing populations in their newly expanded ranges, particularly structure oriented, aggregating species.

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Figure 1.1. Map of black sea bass scuba survey regions in midcoast Maine (ME), northern Massachusetts (MA) and Narragansett Bay, Rhode Island (RI).
Figure 1.2. Cumulative depth frequency histogram of black sea bass sightings during scuba surveys for all regions combined from 2013-2016. A) young-of-year sea bass, B) juvenile sea bass, and C) adult sea bass.
Figure 1.3. Mean young-of-year black sea bass abundance from scuba surveys conducted from 2013-2016 in Rhode Island (RI), Massachusetts (MA) and Maine (ME). Error bars represent ± 1 SE.
Figure 1.4. Mean juvenile black sea bass abundance from scuba surveys conducted from 2013-2016 in Rhode Island (RI), Massachusetts (MA) and Maine (ME). Error bars represent ± 1 SE.
Figure 1.5. Mean adult black sea bass abundance from scuba surveys conducted from 2013-2016 in Rhode Island (RI), Massachusetts (MA) and Maine (ME). Error bars represent ± 1 SE.
Chapter 2: Geographic variation in life-history traits of black sea bass (*Centropristis striata*) during a rapid range expansion

Abstract

The warming of the world’s oceans has resulted in the redistribution of many marine species. As species undergo range shifts poleward, the expanding edge of the population often experiences novel environmental and demographic conditions which may cause variations in life-history strategies to emerge. The northern stock of black sea bass, *Centropristis striata*, has recently shifted its distribution poleward and expanded into the Gulf of Maine. Management has struggled to keep pace with this rapid range shift, in part, because very little is known about the expanding population. I compared life-history traits of black sea bass collected from 2013-2016 from the northern most point of the historic range of the northern stock (southern Massachusetts) and from two areas in the newly expanded range (northern Massachusetts and Maine). I found significant latitudinal differences in size, diet, condition, maturity and sex ratio across this range. Overall, sea bass in the newly expanded range had a less diverse diet and lower condition, but reached maturity at a younger age. I also found greater length- and age-at-maturity estimates from all regions combined compared to the most recent sea bass stock assessment. This study represents one of the first observations of life-history traits of sea bass in the Gulf of Maine, and suggests that range expanding sea bass exhibit life-history strategies that differ from their southern counterparts. These findings provide a greater understanding of population dynamics within the northern sea bass stock, and may aid in ongoing and future management efforts for species with shifting distributions.

Introduction

Climate-induced range shifts have become common in recent decades. Species are shifting their distributions to avoid climatic stress, which is altering the structure and function of
many ecosystems (e.g., Parmesan & Yohe, 2003, Perry et al. 2005, Poloczanska et al., 2013, Pecl et al. 2017). This movement is expected to intensify, and may already be occurring at unprecedented rates (Lawing and Polly 2011, Pecl et al. 2017). As species undergo range shifts, they encounter unique selective pressures that may alter life-history traits and lead to increase spatial heterogeneity among populations (Burton et al. 2010, Phillips et al. 2010). This can complicate conservation and management efforts, particularly if the impact of range expansion on a species’ population dynamics is not well understood.

Geographic variation in life-history traits often arises in response to different environmental and demographic gradients experienced across the range of a species (e.g., Roff 1993, Brown 1995). For instance, populations not constrained by density-dependent effects often invest less in competitive ability ($K$) and more in reproductive ability ($r$, Roughgarden 1971, Charlesworth 1971). In contrast, populations that are density-dependent are often $K$-selected because successful propagation is related to fitness in high density areas (Roughgarden 1971, Charlesworth 1971). Although the ‘abundant center’ distribution does not always occur in natural populations (e.g., Sagarin and Gaines 2002), range expanding species are expected to exhibit lower population density along the expanding range edge in comparison to more centralized populations (Burton et al. 2010, Phillips et al. 2010). Environmental heterogeneity across a species’ range can also drive life-history variation (Brander 2010). In particular, temperature and the length of the growing season can strongly influence growth and the timing of maturation in fish (e.g., Pauly 1980, Conover 1990, Pörtner et al. 2001). Spatial variations in predation pressure (e.g., Reznick et al. 1990, Benard 2004), harvesting (e.g., Jorgensen et al. 2007) and prey availability (e.g., Sherwood et al. 2007) have also been shown to influence life-history traits in fish.
Recently, emphasis has been placed on incorporating spatial heterogeneity into marine fisheries management (Ciannelli et al. 2008, Cadrin and Secor 2009, Pascoe et al. 2009, Lorenzen et al. 2010). Traditionally, stock populations have been managed over large geographic areas where demographic and environmental variables were considered homogenous (Ciannelli et al. 2008). Spatial heterogeneity has largely been ignored due to the substantial complexity it adds to stock assessment models (Pascoe et al. 2009). However, demographic and environmental conditions are rarely homogenous throughout a species’ range, and ignoring this may lead to a misunderstanding of the mechanisms regulating population dynamics (Ciannelli et al. 2008, Lorenzen et al. 2010). Incorporating spatial heterogeneity may be of particular importance for range expanding species that can undergo rapid evolution of life-history traits (Burton et al. 2010). Yet, a big impediment to adaptively managing range shifts is that there often is little information about these species in their newly expanded distributions.

The black sea bass, *Centropristis striata*, is a temperate serranid that is distributed from the Gulf of Mexico to the Gulf of Maine (GOM) (Drohan et al. 2007). Within that range, they are managed as three separate stocks: Gulf of Mexico, South Atlantic and North Atlantic. The North Atlantic stock undergoes seasonal migrations, moving between the outer continental shelf winter habitat to nearshore spring and summer spawning habitat (Moser and Shepherd 2009). They support important commercial and recreational fisheries throughout their range.

Historically, the North Atlantic stock ranged from Cape Hatteras, NC to Cape Cod, MA, but in recent years the center of stock biomass has shifted poleward (Bell et al. 2015) and sea bass populations have expanded into the GOM. Very little is known about the population dynamics of sea bass in the GOM. Current stock designations are based on differences in seasonal migrations and life-history traits of sea bass south of Cape Cod, yet it is unclear if these
characteristics of sea bass in the GOM differ from those of populations farther south. Furthermore, sea bass fisheries have recently developed in the northern GOM, outside of stock assessment areas, potentially making this population vulnerable to rapid depletion (Link et al. 2011).

Sea bass are protogynous hermaphrodites (i.e., they are typically born female and transition to male as they increase in size and age), which can complicate management, particularly if accurate information on sex ratios and the mean size at which individuals change sex is not available (Alonzo et al. 2008, Provost and Jensen 2015). Furthermore, latitudinal variation in growth and maturity has been observed in both the North Atlantic (Kolek 1990, Caruso 1995) and South Atlantic sea bass stocks (McGovern et al. 2002). Kolek (1990) and Caruso (1995) found that sea bass collected in southern Massachusetts grew faster than sea bass from New York and Virginia, and Caruso (1995) also noted that sea bass recruiting to this area were predominantly mature. In addition, McCartney et al. (2013) observed genetic variation across a latitudinal gradient in the northern stock. These studies provide evidence that life-history variation exists within the northern stock, and further emphasize the need to understand how the northern range expansion is influencing population dynamics.

The purpose of this study was to examine life-history traits of sea bass collected from southern Massachusetts (SMA) (i.e., native range) and from two regions within the GOM (i.e., newly expanded range). I hypothesized that the diet of black sea bass from the GOM would have a higher crustacean content than those from SMA. I also hypothesized that patterns of growth, condition and reproduction would differ between GOM and SMA black sea bass, but not between populations within the GOM. Finally, I hypothesized that seasonal variations in diet, condition and reproduction would occur in all regions.
Methods

Sampling Design:

To determine if life-history traits of black sea bass differed between native and newly expanded populations, I collected samples from three regions: southern Massachusetts (SMA) (historic northern range limit delineated by Cape Cod), northern Massachusetts (NMA) (newly expanded range north of Cape Cod) and midcoast Maine (ME) (expanding range edge), between May and November from 2013-2016. In SMA, fish were collected by the Massachusetts Division of Marine Fisheries trawl and trap surveys, as well as by commercial lobstermen who caught sea bass as bycatch in their lobster traps. State and federal trap and trawl surveys rarely find sea bass in NMA, so fish were collected via hook and line by recreational fishermen, as well as bycatch from lobster traps. Collecting fish caught as bycatch in lobster traps was the only successful method in Maine. Recreational and commercial sea bass fishing does not occur in this area, and state and federal trawl surveys do not encounter sea bass. Therefore, the only capture method that was the same across regions was bycatch from lobster traps.

The date, location, depth, habitat type and capture method were recorded at each site where fish were collected. Fish were collected from depths of 5-60 m in various habitats, including rock/cobble, sand, mud and kelp. Fish were frozen immediately after capture and transported to the laboratory for processing. Sea bass were thawed in the laboratory prior to processing. The total length, standard length and total weight were measured for each fish prior to removing vital organs. Weight was also recorded after the removal of vital organs to obtain the gutted weight. The gonads and liver were weighed individually, and stomachs were retained for stomach content analysis. Sagittal otoliths were removed to determine age and calculate
growth rates. Small core subsections (~1 g) were taken from muscle tissue samples to conduct stable isotope analysis.

**Size Distribution and Growth:**

Size-frequency histograms were used to explore regional differences in black sea bass distributions. Age determination was conducted to compare growth rates of sea bass among regions. Aging techniques were adapted from the Massachusetts Division of Marine Fisheries Fish Aging Protocol for black sea bass (Elzey et al. 2015). Sagittal otoliths were immersed in mineral oil on a black background and viewed under a microscope. The number of annuli on each otolith was counted outward from the core to estimate age. Annuli were defined as continuous dark bands with no breaks.

Growth was modelled using the Von Bertalanffy growth function (VBGF):

\[ L_t = L_{\text{inf}} \left( 1 - e^{-k(t-t_0)} \right) \]

where \( L_t \) is length (cm) at age \( t \), \( L_{\text{inf}} \) is the asymptotic length, \( k \) is the Brody growth coefficient and \( t_0 \) is the age at which length is 0.

**Diet:**

Stomach contents were used to compare the diet of sea bass among regions. Stomachs were dissected and contents were weighed, counted and identified to the lowest possible taxon. Prey items were divided into the following groups: pelagic fish (bay anchovy, butterfish, herring, etc.); demersal fish (sculpin, scup, black sea bass, etc.); squid (long-fin squid); crabs (various species); shrimp (various species); lobster; benthic invertebrates (molluscs, polychaetes, amphipods, algae, etc.); and unidentified fish. Partial fullness index (PFI) of prey was calculated for each fish and mean PFI was used to compare the relative importance of prey groups among
regions. Mean PFI provides a length standardized way to determine relative volumetric prey importance (Bowering and Lilly, 1992), and was calculated as:

$$\text{Mean PFI} = \frac{1}{n} \times \sum \frac{w_{ij}}{L_j^3} \times 10^4$$

where $w_{ij}$ is the weight of prey $i$ for fish $j$, $L_j$ is the length of fish $j$ and $n$ is the total number of fish sampled.

Stable isotope ratios of nitrogen ($\delta^{15}$N) and carbon ($\delta^{13}$C) can be used to determine the trophic position of an organism (Zanden and Rasmussen 1999) and the source of carbon (e.g., benthic, demersal, pelagic, etc.) in marine food webs (Sherwood and Rose 2005), respectively. Muscle tissue samples were dried in a drying oven at 60°C for 48 h, ground to a fine powder using a mortar and pestle, and weighed and packaged in 4 x 6 mm tin capsules. Samples were sent to the Colorado Plateau Stable Isotope Laboratory (Northern Arizona University, Flagstaff, AZ, USA) for analysis. Samples were combusted to produce CO$_2$ and N$_2$, from which stable nitrogen and carbon isotope ratios were analyzed using an elemental analyzer followed by gas chromatograph separation interfaced via continuous flow to an isotope ratio mass spectrometer. Stable carbon and nitrogen ratios were expressed in delta ($\delta$) notation and defined as parts per thousand deviations from the following standard materials: Pee Dee Belemnite for $\delta^{13}$C, and N$_2$ in air for $\delta^{15}$N. To determine the level of precision of my isotope results, 8% of the samples were analyzed in duplicate.

**Condition:**

The length-weight relationship was estimated using the following equation:

$$W = aL^b$$

where $W$ is the whole body weight (g), $L$ is the total length (cm), $a$ is the intercept of the regression and $b$ is the regression coefficient.
I considered two indices of physiological condition; Fulton’s condition factor $K$, and liver-somatic index (LSI). $K$ is primarily an indicator of energy reserves available for somatic growth (i.e., muscle mass), while LSI is a measure of energy reserves available for reproduction (i.e., lipid storage). A length-standardized measure of Fulton’s condition factor was calculated to determine the effects of region and season on condition (Le cren 1951, Froese 2006):

$$K_{rel} = \frac{W_g}{aL^b}$$

where $W_g$ is the gutted fish weight (g), $L$ is the total length (cm), and $a$ and $b$ are the parameters of the length-weight relationship defined above. I also calculated Fulton’s condition factor by standardizing for season, rather than size, in order to examine how condition varies with size and related diet ontogeny (Sherwood et al. 2007):

$$K_{adj} = K - K_{avg}$$

where $K$ is Fulton’s condition factor and $K_{avg}$ is the average condition factor (all sizes and regions) by season (spring, summer and fall). LSI was calculated as:

$$LSI = \frac{W_l}{W_g} \times 100$$

where $W_l$ is the liver weight and $W_g$ is the gutted fish weight. A seasonally adjusted value was also calculated for LSI:

$$LSI_{adj} = LSI - LSI_{avg}$$

where $LSI_{avg}$ is the average $LSI$ (all sizes and regions) by season (spring, summer and fall).

Reproduction:

Sex and reproductive stage of black sea bass were determined using macroscopic and histological techniques similar to Klibansky and Scharf (2015). Reproductive stage was categorized as immature, developing, spawning capable, spent, resting and transitional.
Macroscopic gonad analysis was sufficient for identifying developing, spawning capable and spent stages. Gonad samples that could not be clearly identified macroscopically were sent to the University of Maine for histological analysis. Processing began with fixing gonad tissue in 10% formalin for 14 days. Samples were then sequentially dehydrated in ethanol for successive 30-minute dehydration periods (30% to 70%), followed by 10-minute dehydration periods (80% to 100%). Once dehydrated, samples were cleared in toluene for three successive 30 minute periods, placed in wax for three successive eight hour periods, and finally poured into a wax mold. Embedded samples were sliced (> 5μm) using a microtome and mounted on slides. Slides were stained with Masons Trichrome stain and observed under a compound microscope to determine reproductive stage.

The gonadosomatic index (GSI) of each fish was calculated using the following equation:

$$GSI = \frac{W_g}{W_t - W_g} \times 100$$

where $W_g$ is gonad weight and $W_t$ is total weight. The sex ratio-at-length was determined separately for males and females using the following equation:

$$p = \frac{1}{1 + e^{-k(L-L_{50})}}$$

where $p$ is the proportion of males or females at length $L$, $k$ is a slope parameter, and $L_{50}$ is the length at which 50% of the fish are male or female, respectively. Maturity-at-length for both sexes combined was determined using the same equation, where $p$ is the proportion of mature fish at length $L$, and $L_{50}$ is the length at which 50% of the fish are mature. Sex ratio-at-length and maturity-at-length were calculated using all regions combined, due to the small sample size within each 1 cm size bin when regions were separated. Age-at-maturity for both sexes
combined was determined for all regions combined, as well as each region separately, using the following equation:

\[ p = \frac{1}{1 + e^{-k(A-A_{50})}} \]

where \( p \) is the proportion of mature fish at age \( A \), \( k \) is a slope parameter, and \( A_{50} \) is the age at which 50% of the fish are mature. I chose to combine sexes to determine length-at-maturity and age-at-maturity because this was the method used in the most recent black sea bass stock assessment (NEFSC 2016).

**Data Analysis:**

The Kolmogorov-Smirnov (K-S) test was used to compare the cumulative size frequency distribution among regions. I also compared the cumulative size frequency distribution among capture types in SMA and NMA (only one capture type was used in ME). VBGF curves were established for SMA, and all regions combined. Separate growth curves were not established for NMA and ME fish due to low sample sizes of the youngest and oldest age classes in each region. Growth models were compared using an F-test (Chen et al. 1992).

Distinctions in the overall diet among groups were assessed using a permutational multivariate analysis of variance (PerMANOVA) using the ‘vegan’ package in R (R Core Team 2017). Specifically, PerMANOVA was used to test the effects of region, sex, season and their interactions on the PFI’s of each prey group. PerMANOVA requires the use of a matrix of dissimilarity indices, rather than raw response values, which I calculated prior to analysis. I used Gower’s index as the dissimilarity measure because it allows for the use of double zeroes (Gower 1971). To test for potential violations of PerMANOVA assumptions, I compared the multivariate dispersions of each group matrix using beta diversity tests.
I employed a two-step modelling approach using GLMs to analyze individual prey categories, similar to Stefánsson (1996). First, the presence of prey was analyzed using generalized linear models (GLMs) with binomial error distribution and logit link functions. Second, prey category abundance (i.e., PFI ≠ 0) was analyzed using GLMs with gamma error distributions and identity link functions. A similar approach using generalized additive models has also commonly been employed in diet studies (Stefansson and Palsson 1997, Santos et al. 2013, Buchheister and Latour 2015); however, GLMs are more appropriate when utilizing multiple factors (Stefánsson 1996, Stefansson and Palsson 1997). Fixed effects in both binomial and gamma GLMs included region, sex, season, and all interactions. Capture method was also included as a fixed effect, but not as an interaction term because capture method was unequally represented across the levels of the other factors. I included total length as a covariate when analyzing prey presence, but not abundance, since PFI is a length standardized measure. Akaike information criteria (AIC) was used to assess fit and select the most parsimonious model(s). Separate three-way ANOVAs were used to test the effect of region, season and size class on carbon and nitrogen stable isotope ratios. Size classes were categorized as 10-19 cm (juveniles), 20-29 cm (50-95% mature), 30-39 cm (reproductive adults), and 40+ cm total length (≥ 50% male).

A length-weight relationship equation was derived for all sea bass combined, using the ‘FSA’ package in R. To control for the effect of size on LSI and GSI, I used the standardized residuals from the least-squares regression of total length and LSI or GSI, respectively. \(K_{rel}\), residual LSI and residual GSI were analyzed using separate two-way ANOVAs where region, season, and their interaction were included as fixed effects. Post-hoc multiple comparison tests were conducted using the glht function in the ‘multcomp’ package, which conducts simultaneous
tests and confidence intervals for parametric models (Bretz et al. 2010, Hothorn et al. 2008). Regional differences in $K_{adj}$ and $LSI_{adj}$ were qualitatively explored within 2-cm size intervals. Finally, I explored whether the proportion of males and females, as well as the proportion of mature and immature fish, differed among region using Chi-Square tests.

**Results**

*Size Frequency and Growth:*

Of the 289 sea bass collected between 2013-2016, 132 were captured in SMA, 108 in NMA and 49 in ME. Sea bass collected in NMA were significantly larger than those collected in ME and SMA, and this pattern was observed in trap caught fish as well as all capture methods combined (K-S test, $p < 0.05$, Figure 2.1). Length-at-age was greater for all regions combined compared to SMA alone (Figure 2.2); however, there was no significant difference in the VBGF curves when comparing all regions combined with SMA alone (F-test, $p > 0.05$). VBGF parameters varied among regions, with the lowest $k$ value and highest $L_{inf}$ value in SMA (Table 2.1).

*Diet:*

Sea bass diet varied among region (Figure 2.3) and season, and also varied with size (Figure 2.4). Demersal fish, pelagic fish and squid comprised 47-66% of sea bass diet in SMA, but only 20-29% in NMA and 8% in ME. Meanwhile, crustaceans (e.g., shrimp, crabs, lobster) accounted for 31-53% of sea bass diet in SMA, 69-76% in NMA and 78% in ME. The best fitting binomial and gamma GLMs included various combinations of explanatory variables. Region and season were typically the two most important factors in the models, emphasizing the importance of both spatial and temporal dynamics in trophic interactions. Sex did not
significantly influence the presence or abundance of prey. Overall, total length and capture method did not significantly influence presence or abundance for the majority of prey groups.

The presence of demersal fish was significantly influenced by region \( (x^2 = 23.5, p < 0.001) \), season \( (x^2 = 39.2, p < 0.001) \) and total length \( (x^2 = 9.5, p = 0.002) \). Demersal fish were significantly more frequent in the stomachs of SMA fish compared to NMA (Tukey’s HSD, \( p < 0.001 \)) and ME (Tukey’s HSD, \( p = 0.01 \)), and significantly more frequent in the fall compared to the summer (Tukey’s HSD, \( p = 0.001 \)). No demersal fish were found in the stomachs of fish collected in the spring. Demersal fish regularly occurred in the diet of sea bass measuring 24-40 cm total length, but were more variable in smaller and larger fish. None of the factors tested significantly influenced the abundance of demersal fish, despite overall mean abundance being greater in SMA (mean PFI = 0.64) compared to NMA (mean PFI = 0.18) and ME (mean PFI = 0.02), and greater in the fall (mean PFI = 0.81) compared to summer (mean PFI = 0.16).

The presence of squid was significantly influenced by region \( (x^2 = 10.86, p < 0.001) \) and season \( (x^2 = 21.59, p < 0.001) \). Squid were significantly more frequent in the stomachs of fish collected in the fall compared to the summer (Tukey’s HSD, \( p = 0.008 \)) and spring (Tukey’s HSD, \( p = 0.009 \)), and significantly more frequent in SMA fish compared to NMA fish (Tukey’s HSD, \( p = 0.003 \)). No squid were found in the diet of fish captured in ME. None of the factors tested significantly influenced the abundance of squid; however, there was a trend of greater abundance in the fall (mean PFI = 0.66) compared to spring (mean PFI = 0.005) and summer (mean PFI = 0.08), and a greater abundance of squid in SMA (mean PFI = 0.50) compared to NMA (mean PFI = 0.14).

The presence of shrimp was significantly influenced by the interaction of region and season \( (x^2 = 21.81, p < 0.001) \). Shrimp were significantly more frequent in the stomachs of fish...
collected in SMA in the spring compared to summer (Tukey’s HSD, \( p = 0.012 \)) and fall (Tukey’s HSD, \( p = 0.013 \)). The abundance of shrimp was significantly influenced by the interaction of region and season \( (x^2 = 3.35, p = 0.001) \). Shrimp were less abundant in SMA in the fall compared to spring (Tukey’s HSD, \( p < 0.001 \)) and summer (Tukey’s HSD, \( p < 0.001 \)), and more abundant in the summer in SMA compared to ME (Tukey’s HSD, \( p = 0.03 \)). There was an overall trend of lower shrimp abundance in NMA (mean PFI = 0.08) compared to ME (mean PFI = 0.15) and SMA (mean PFI = 0.17), and lower abundance in the fall (mean PFI = 0.05) compared to spring (mean PFI = 0.20) and summer (mean PFI = 0.18).

The presence of crabs was significantly influenced by region \( (x^2 = 29.70, p < 0.001) \) and season \( (x^2 = 26.64, p < 0.001) \). Crabs were significantly more frequent in the stomachs of fish collected in NMA compared to ME (Tukey’s HSD, \( p < 0.001 \)) and in the fall compared to the spring (Tukey’s HSD, \( p < 0.001 \)). The abundance of crabs was significantly influenced by capture method \( (x^2 = 9.35, p = 0.012) \). There was a significantly greater abundance of crabs in the stomachs of hook and line caught fish compared to trap (Tukey’s HSD, \( p = 0.022 \)) and trawl (Tukey’s HSD, \( p = 0.05 \)) caught fish.

The consumption of benthic invertebrates (e.g., molluscs, polychaetes, tunicates) was significantly influenced by region \( (x^2 = 14.15, p < 0.001) \) and season \( (x^2 = 34.99, p < 0.001) \). The presence of benthic inverts was significantly greater in SMA compared to ME (Tukey’s HSD, \( p = 0.012 \)), and significantly lower in the summer compared to spring (Tukey’s HSD, \( p = 0.011 \)) and fall (Tukey’s HSD, \( p < 0.001 \)). The lobster and pelagic fish prey groups were not modeled using GLMs due to a small sample size. However, it is worth noting that lobsters were found in the diet of fish from all regions, while pelagic fish were only found in SMA and NMA fish.
Stable isotope analysis suggested that sea bass diets differ among region and season, but not size class (Figure 2.5). There was a significant effect of season on both δ\textsuperscript{13}C (ANOVA, F\textsubscript{2,160} = 3.52, p = 0.03) and δ\textsuperscript{15}N (ANOVA, F\textsubscript{2,160} = 3.95, p = 0.02), and there was a significant effect of region on δ\textsuperscript{15}N (ANOVA, F\textsubscript{2,160} = 12.87, p < 0.0001), but not on δ\textsuperscript{13}C. There was also a significant interactive effect of region × season on both δ\textsuperscript{13}C (ANOVA, F\textsubscript{4,160} = 5.94, p = 0.0002) and δ\textsuperscript{15}N (ANOVA, F\textsubscript{4,160} = 2.55, p = 0.04). The overall trend of δ\textsuperscript{13}C values showed that SMA and NMA fish were more pelagic in the spring, and ME fish were more pelagic in the fall. δ\textsuperscript{13}C values were significantly lower for ME fish in the fall compared to the spring and summer (Tukey’s HSD, p < 0.001), and significantly lower for NMA fish in spring compared to fall. There was a trend of lower δ\textsuperscript{13}C values for SMA fish in the spring compared to summer and fall, but this effect was not significant. Finally, δ\textsuperscript{13}C values of ME fish in the spring were significantly higher than those for SMA and NMA fish (Tukey’s HSD, p < 0.05 for both comparisons). Similarly, in the fall, δ\textsuperscript{13}C values of NMA fish were significantly greater than those of ME fish (Tukey’s HSD, p < 0.001), and there was a trend of greater δ\textsuperscript{13}C values in fish in NMA than in SMA fish (Tukey’s HSD, p = 0.15).

There was a trend of higher δ\textsuperscript{15}N values in SMA fish compared to those in NMA and ME. δ\textsuperscript{15}N values were significantly higher for SMA fish compared to NMA fish in the spring, summer and fall (Tukey’s HSD, p < 0.05), and significantly higher than ME fish in the summer. In addition, δ\textsuperscript{15}N values of ME fish were significantly higher than those of NMA fish. Finally, δ\textsuperscript{15}N values for ME fish were significantly higher in the fall compared to spring and summer, for SMA fish were significantly higher in the summer compared to spring and fall, and for NMA fish were significantly higher in the fall compared to spring (Tukey’s HSD, p > 0.05 for all comparisons).
**Condition:**

The equation $W_g = 0.02L^{2.85}$ explained > 97% of the variance between length and weight of sea bass from all regions combined (Figure 2.6). There was a significant interaction effect between region and season on $K_{rel}$ (ANOVA, $F_{4,253} = 2.56, p = 0.04$, Figure 2.7A). $K_{rel}$ was significantly greater for NMA and ME fish in the fall compared to the spring and summer, and significantly lower for SMA fish in the summer compared to spring and fall (Tukey’s HSD, $p < 0.05$ for all comparisons). $K_{rel}$ was also greater for SMA fish in the spring compared to ME fish (Tukey’s HSD, $p = 0.009$). Mean (± 1SE) values of $K_{adj}$ (binned into 2-cm sea bass length intervals) varied greatly; however, there was a decreasing trend in $K_{adj}$ between 28-36 cm for all regions combined (Figure 2.8).

There was a significant interaction effect of region and season (ANOVA, $F_{4,251} = 7.36, p < 0.001$, Figure 2.7B) on residual $LSI$. Residual $LSI$ was significantly lower for SMA fish in the fall compared to the spring and summer, significantly greater for ME fish in fall compared to summer, and significantly greater for NMA fish in fall compared to spring (Tukey’s HSD, $p < 0.05$ for all comparisons). $LSI$ was also greater in the fall for NMA and ME fish compared to SMA fish, and greater in the summer for NMA fish compared to ME and SMA fish (Tukey’s HSD, $p < 0.05$ for all comparisons). Mean (± 1SE) values of $LSI_{adj}$ (binned into 2-cm sea bass length intervals) also varied greatly, but contrary to $K_{adj}$ results, there was a trend of increasing $LSI_{adj}$ between 26-36 cm for all regions combined (Figure 2.8).

**Reproduction:**

Reproductive stage varied greatly among region and season; however, the presence of spawning capable fish decreased from spring to fall in all regions (Figure 2.9). There was a significant interactive effect of region and season (ANOVA, $F_{4,240} = 7.36, p < 0.001$) on residual
Residual GSI was lower for NMA and ME fish in the fall compared to spring
and summer, and greater for SMA fish in the spring compared to summer and fall (Tukey’s
HSD, \( p < 0.05 \) for all comparisons). Residual GSI was also lower in the spring for SMA fish
compared to NMA fish, and lower in the summer compared to both NMA and ME fish (Tukey’s
HSD, \( p < 0.05 \) for all comparisons).

There were significantly more females than males in SMA and ME \( (\chi^2, p < 0.05, \text{ Figure } 2.10A) \), and slightly more males than females in NMA, but this was not significant. The black
sea bass sex ratio-at-length for all regions combined is shown in Figure 2.11A. The length at
which 50% of the population was female was 33.5 cm. Mean length at 50% maturity for all
regions combined was 26.6 cm (Figure 2.11B), and the age at 50% maturity for all regions
combined was 1.85 (Figure 2.12). Age-at-maturity varied among regions, with SMA having the
highest age-at-maturity and NMA having the lowest (Figure 2.12). There were significantly more
mature than immature sea bass collected in NMA \( (\chi^2, p < 0.05, \text{ Figure } 2.10B) \). The proportion of
mature fish collected in SMA and ME did not differ \( (\chi^2, p > 0.05) \).

**Discussion**

Observations of black sea bass from SMA (i.e., historic northern range limit), NMA (i.e.,
newly expanded range) and ME (i.e., upper limit of newly expanded range edge), revealed
variation in life-history traits across a relatively small geographic area. I observed significant
spatial differences in size, diet, condition, maturity and sex ratio. These findings suggest that
range expanding sea bass may exhibit life-history strategies that differ from their southern
counterparts.

The length-at-age estimate for sea bass from all regions combined was greater than the
length-at-age estimate for SMA sea bass alone. Furthermore, length-at-age estimates for both
SMA and all regions combined were greater than the length-at-age estimate established in the 2016 Black Sea Bass Stock Assessment, which combines length and age data from populations throughout the northern range, from Cape Hatteras to Cape Cod (NEFSC 2016). I also found that sea bass from NMA and ME were reaching reproductive maturity at a younger age than sea bass from SMA, and that the length-at-maturity for all regions combined ($L_{50} = 26.6$ cm) was greater than the length-at-maturity utilized in the most recent sea bass assessment ($L_{50} = 21$ cm; NEFSC 2016). These observed differences may have arisen from latitudinal variation in temperature and the length of the growing season. Organisms at higher latitudes may be locally adapted to grow within a lower range of temperatures, may have growth rates that evolve inversely with the length of the growing season (i.e., countergradient variation), or may exhibit some combination of these adaptations (Yamahira and Conover 2002). For instance, Conover and Present (1990) found that fish from colder regions were adapted to a shorter growing season and grew faster than their southern counterparts. This effect may be due, in part, to northern fish having greater food conversion efficiencies (Present and Conover 1992). Regardless of the mechanism driving this pattern, latitudinal variation in growth and maturity could have far reaching management implications as the northern stock of sea bass continues to shift poleward (Pinsky and Mantua 2014, Hare et al. 2016, Kleisner 2016, 2017).

Demographic patterns of abundance may also be influencing sea bass growth and reproduction. Range expanding sea bass populations, which are likely at lower densities and consequently may not be subject to density-dependent competition (Burton et al. 2010, Phillips et al. 2010), appear to be exhibiting a greater tendency to be $r$-selected, which follows the $r$-$K$ selection theory (Roughgarden 1971, Charlesworth 1971). Faster growth rates result in fish achieving reproductive maturity at a younger age, which promotes rapid population growth.
Spatial variation in conspecific density has been found to influence life-history traits in fish, including growth, maturation, and diet (Jones 1987, Samhouri 2009, Caselle et al. 2003, 2011). For example, Caselle et al. (2011) found that high density populations of California sheephead were smaller in size, had lower fecundity, and changed sex at smaller sizes, and Samhouri (2009) found that aggressive interactions in high density populations of damselfish resulted in reduced growth and reproductive output. Similar density-dependent effects may be influencing the spatial variation in black sea bass life-history traits I observed among my study sites, as well as between my data and the most recent sea bass stock assessment from farther south where these effects are likely stronger (NEFSC 2016).

Interspecific competition may also differ between the GOM and regions farther south. Atlantic cod, a historically dominant large bodied predator in the GOM, has rapidly decreased in abundance in recent decades, and spawning stock biomass is currently estimated to be at 3-4% of the target level (Palmer 2015). In general, large groundfish species are functionally absent in the nearshore ecosystem, and have been largely replaced by smaller-bodied fish, such as sculpin and cunner (Witman and Sebens 1992, Steneck 1997). Sea bass are an aggressive and territorial species, and may easily outcompete small-bodied native GOM fish. For example, SCUBA and video surveys in NMA and ME have captured sea bass aggressively interacting with cunner and small pollock, generally driving them away from sea bass territories (McMahan and Grabowski, unpublished data). Therefore, in addition to experiencing reduced intraspecific competition, sea bass in the GOM may also be subjected to reduced interspecific competition in comparison to those in southern regions, further minimizing the reproductive trade-offs sea bass would face in a highly competitive environment (Burton et al. 2010).
I found regional and seasonal variability in $K_{rel}$, but overall there was a decreasing trend with latitude, which also follows the $r$-$K$ selection theory of more dense populations being more $K$ selected (Roughgarden 1971, Charlesworth 1971, Burton et al. 2010, Phillips et al. 2010). Diet is also likely impacting condition. I found that the diversity and quality of prey items in the diet of sea bass also decreased with latitude. The diet of SMA sea bass was dominated by lipid rich demersal and pelagic fish, as well as squid, whereas the diet of NMA and ME sea bass was dominated by small crustaceans. Diet trends in NMA and ME were similar to results from previous studies suggesting that sea bass rely heavily on crabs and other benthic invertebrates (Mack and Bowman 1983, Steimle and Figley 1996, Garrison and Link 2000). Within my study area, heterogeneity in prey availability is likely driving regional differences. For instance, many prey items found in the diet of SMA sea bass (e.g., bay anchovy, scup, squid) are rare or found in lower abundance in the GOM. However, it is unclear why SMA sea bass would consume more fish and squid than populations farther south.

Stable isotope signatures reflected many of the dietary trends revealed in the stomach content analysis. The mean $\delta^{13}C$ value of SMA fish indicated more pelagic prey in the diet, whereas $\delta^{13}C$ values of NMA and ME fish indicated more benthic prey in the diet (Sherwood and Rose 2005, Grabowski et al. 2009). The mean $\delta^{15}N$ value of SMA fish also indicated a higher trophic position (Sherwood and Rose 2005). ME fish had the highest $\delta^{13}C$ values in the spring, which was also when the most shrimp and benthic invertebrate prey were found in their diet. SMA and NMA fish had higher $\delta^{13}C$ values in the fall, which was when the greatest amount of crabs were found in their diet. $\delta^{13}C$ values were lowest for SMA and NMA fish in the spring; however, this was also the period of time when very few fish and squid were found in their diet. Therefore, there may be a prey source that these fish consume in the spring (i.e., when sea bass
are migrating from the continental shelf to nearshore spawning habitat) that was not found in stomach content results.

Ontogenetic trends in diet revealed that feeding habits also fluctuated with fish size and that $K_{adj}$ closely tracked diet trends. I was unable to compare ontogenetic trends in diet and condition among regions due to low sample sizes. However, when examining $K_{adj}$ for all regions together, I did find a general decrease in feeding, and a shift in diet from predominantly squid and fish to crabs, occurred between 28-36 cm total length, when a decrease in $K_{adj}$ was also observed. Sherwood et al. (2002) found that prey switching often occurs when condition starts to decline, suggesting that these diet changes may be necessary to overcome energetic bottlenecks. Yet, counterintuitively, $LSI_{adj}$ increased within this size range, suggesting that further research will likely be needed to resolve whether it is an energetic bottleneck. It is also possible that the allocation of energy shifts during certain growth phases, causing liver and somatic condition to diverge.

The range of $LSI$ and $GSI$ values obtained in this study were similar to values previously reported for sea bass collected in SMA (Wuenschel et al. 2013). $LSI$ varied among season, but was highest in the fall for NMA and ME, and was inversely correlated with $GSI$. This finding may indicate that sea bass in the GOM are using energy reserves in the liver while spawning, and that those reserves are replenished when spawning concludes in the late summer and fall. However, the opposite trend was found in SMA. $LSI$ decreased from spring to fall and was positively correlated with $GSI$. $LSI$ values in SMA were also lower than in NMA and ME. I speculate that this could have been related to increased consumption in SMA. As spawning decreased from spring to fall for SMA fish, consumption may have rapidly increased. A substantial increase in body weight would sharply increase the denominator of the $LSI$ equation,
leading to decreased LSI values (Brown and Murphy 2004). Overall, these results suggest that sea bass in SMA may exhibit different energetic strategies than sea bass in the GOM, but further investigation of how energetic strategies vary with latitude is warranted.

Regional differences in GSI may reflect a latitudinal gradient in the length of the spawning season. Sea bass in SMA are likely able to spawn earlier in the spring due to warmer temperatures and a shorter migration from offshore winter habitat. I collected sea bass between mid-May and mid-June in the spring season. In SMA, GSI may have already begun to decrease during this period if spawning began earlier than mid-May. Conversely, GSI was much higher in NMA and ME during the spring, perhaps because spawning is delayed at higher latitudes. In the summer season, GSI was greatly reduced in SMA and began to decline in NMA and ME as spawning likely ends, and GSI values were similarly low among all regions in the fall.

I found that the sex ratio of all regions combined was 100% female for the smallest sizes and approached 100% male for the largest sizes. This pattern is typical of a hermaphroditic species that matures as a female and transitions to male as it grows; however, it is markedly different from previous black sea bass work that has found sex ratios of approximately 30% male below 30 cm, and 30-40% female above 45 cm (Wuenschel et al. 2011, NEFSC 2012, NEFSC 2016, Blaylock and Shepherd 2016). Indeed, the northern stock of black sea bass is distinguished from typical protogynous hermaphrodites because of the presence of secondary mature males and the abundance of large females in their population (Blaylock and Shepherd 2016). Blaylock and Shepherd (2016) concluded that black sea bass are likely more resilient to fisheries exploitation because of these unique sex ratios. My results did not reveal a similar abundance of smaller males and larger females, which may be a consequence of small sample sizes of the smallest and largest black sea bass size categories. I analyzed a total of 289 sea bass, whereas the
stock assessment utilizes results from thousands of sea bass throughout the northern range (but south of Cape Cod). However, it is also possible that range expanding populations do not reflect the same sex-ratio trends as populations near the center of their range.

In addition, I found that sex ratio varied with region, with 20-30% males and 70-80% females in SMA and ME, and 55% males and 45% females in NMA. I also found that sea bass were larger in NMA and predominantly mature. Caruso (1995) observed that the majority of sea bass recruiting to SMA where mature, and at the time of these observations (early 1990s), SMA was considered the range edge of the northern stock. My results indicate that sea bass populations have shifted, and that large, mature fish are now recruiting to NMA. Meanwhile, small, immature fish (i.e., those that can be outcompeted by larger fish) appear to continue further north to ME, where conspecific density is lower, but habitat may be suboptimal (i.e., colder temperature and less diverse prey availability).

Collectively, my results suggest that demographic patterns and life-history strategies of range expanding sea bass differ from more centralized populations, and that important stock metrics, such as growth and maturity, vary over relatively short distances. Previous black sea bass stock assessment reviews explicitly called for the incorporation of spatial structure within the northern stock due to concern that incomplete mixing was occurring (NEFSC 2016). In response, the most recent sea bass stock assessment incorporated a spatial divide at the Hudson Canyon and found that the two-area model better represented overall population dynamics (NEFSC 2016). However, my results suggest that latitudinal heterogeneity exists in sea bass populations north of the Hudson Canyon divide. Furthermore, the poleward range expansion of black sea bass is predicted to continue as additional warming occurs along the U.S. Northeast Continental Shelf (Kleisner 2016, 2017), which could result in further divergence of life-history
traits of range expanding sea bass away from more centralized populations. I recommend that future assessments target GOM sea bass to build upon these initial findings and enhance our understanding of the biology and population dynamics of sea bass in their newly expanded range. Finally, these findings apply more broadly to the global redistribution of species that is currently underway and expected to intensify (Pecl et al. 2017), and emphasize the need to incorporate alternative assessment and management approaches to range shifting species.

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### Tables

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Table 2.1. Parameter estimates and standard error (SE) for von Bertalanffy growth curves of sea bass from southern Massachusetts (SMA), all regions combined, and from the 2016 Black Sea Bass Stock Assessment (NEFSC 2016).
Figures

Figure 2.1. Cumulative length frequency distribution of black sea bass collected in Maine (blue), northern Massachusetts (gray) and southern Massachusetts (red) for A) all capture methods combined, and B) trap caught fish only.
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Figure 2.12. Age-at-maturity for black sea bass in Maine (blue), northern Massachusetts (gray), southern Massachusetts (red) and all regions combined (black).
Chapter 3: Nonconsumptive effects of a range expanding predator (black sea bass, *Centropristis striata*) on juvenile American lobster (*Homarus americanus*) population dynamics

Abstract

Distribution shifts poleward are a widespread response to climate change and can result in altered community composition and interactions among species that previously were geographically isolated. The novel communities and species interactions that may arise during range shifts provide an opportunity to study fundamental ecological processes, as well as address potential conservation issues. Black sea bass (*Centropristis striata*) historically ranged from the Gulf of Mexico to Cape Cod, but recently have expanded north into the Gulf of Maine. Very little is known about the impact of this range expansion on benthic community structure throughout the coastal waters of the Gulf of Maine. To investigate the effects of sea bass on the behavior of juvenile American lobsters (*Homarus americanus*), I manipulated the presence of sea bass olfactory cues and observed shelter use and foraging behavior of lobsters from three regions in the Gulf of Maine with different contact histories with sea bass. Sea bass presence increased shelter usage and reduced foraging in lobsters, but contact history influenced the strength of these behavioral responses. Lobsters with no previous contact with sea bass did not significantly increase shelter usage or decrease movement in their presence, but there was a significant reduction in their foraging rate on mussels. This observed reduction in consumption indicates that naïve lobsters recognize novel predators, but the ineffective anti-predator responses exhibited support the ‘naïve prey’ hypothesis. Meanwhile, lobsters with the longest contact history with sea bass significantly increased shelter usage when sea bass were present; however, they exhibited limited movement and foraging behavior in both the absence and presence of sea bass. Finally, lobsters with a short contact history with sea bass exhibited increased shelter
usage, reduced movement, and reduced mussel consumption in the presence of sea bass, revealing that juvenile lobsters quickly adapt anti-predator defenses to avoid this novel threat.

Overall, my results suggest that prey contact history to novel predators mediates the strength of NCEs, and consequently influences geographic patterns in predator-prey dynamics.

**Introduction**

Range shifts have become a widespread response to recent climate-induced warming (e.g., Parmesan & Yohe, 2003, Perry et al. 2005, Poloczanska et al., 2013), often resulting in altered community composition and interactions among species that do not share an evolutionary history (Hobbs et al 2006, Williams and Jackson 2007, Walther 2010). In particular, distribution shifts can significantly impact predator-prey dynamics by altering local species abundance, generating new interspecific interactions, or eliminating historic interactions (reviewed in: Harley et al. 2006, Kordas et al. 2011, Doney et al. 2012). Observing and forecasting how distribution shifts alter community interactions and trophic pathways is critical to robust management and conservation efforts given that current rates of climate change are predicted to intensify (Peters et al. 2013, García Molinos et al. 2015).

The importance of predation in regulating the structure and function of ecological communities has been well established over the past several decades (e.g., Hairston et al. 1960, Paine 1980, Sih et al. 1985, Werner and Peacor 2003). Predators can impact prey populations by consuming individuals (Hairston et al. 1960, Paine 1980, Estes et al. 1998) and/or by inducing behavioral, morphological or physiological responses (Lima 1998a, Trussell et al. 2002, Werner and Peacor 2003, Schmitz et al. 2004). These latter responses, termed nonconsumptive effects (NCEs), may have an equal or larger impact on community structure than consumptive effects (Peacor and Werner 2001, Preisser et al. 2005, Peckarsky et al. 2008, Schmitz et al. 2008). For
instance, behavioral avoidance of predators can potentially impact prey habitat use, foraging rates, energy allocation and ultimately population dynamics (e.g., Schmitz et al. 1997, Grabowski 2004, Schmitz et al. 2004, Preisser and Bolnick 2008). The strength of NCEs can be context dependent, and is influenced by both biotic and abiotic processes. For instance, Kimbro et al. (2013) found that the magnitude and direction of NCEs varied with both latitude and habitat. Understanding the factors that drive regional variation in the strength of NCEs will enhance efforts to predict how species interactions and community structure change across ecosystems.

Species invasions and distribution shifts present a unique opportunity to explore predator-prey dynamics across biogeographic gradients of contact history. The ability of prey to recognize novel predator cues will likely determine the strength of both consumptive effects (CEs) and NCEs by non-native predators. The ‘naïve prey’ hypothesis (Diamond and Case 1986) suggests that a lack of evolutionary history between predators and prey may result in ineffective antipredator defenses (Cox and Lima 2006, Freeman and Byers 2006, Sih et al. 2010). Banks and Dickman (2007) proposed that the impact of an alien predator on prey populations depends on the type of naiveté that prey exhibit: (1) Prey may not recognize a predator and fail to adopt anti-predator defenses, (2) they may recognize a predator but adopt ineffective anti-predator defenses, or (3) they may recognize a predator and adopt appropriate anti-predator defenses (Banks and Dickman 2007). Furthermore, Sih et al. (2010) hypothesized that non-native predators have the greatest impact if the community they invade has prey, predators and competitors that are similar to their native habitat, whereas the invaded community is entirely naïve to the new predator. Yet, some prey species have been found to respond effectively to novel predators (Sih et al. 2010, Kimbro et al. 2013, Ferrari et al. 2015), including greater plasticity in antipredator defenses in
areas where the threat of predation is more variable in space and time (Trussell 2000, Trussell and Nicklin 2002).

Many marine species in the Northwest Atlantic are exhibiting poleward distribution shifts (Nye et al. 2009, Pinsky et al. 2013, Bell et al. 2015, Hare et al. 2016). This phenomenon is particularly evident in the Gulf of Maine (GOM) where sea surface temperatures are rising faster than 99% of the rest of the world’s oceans (Pershing et al. 2015). The northern stock of black sea bass historically ranged from Cape Hatteras to Cape Cod; however, in recent years, the center of stock biomass has shifted poleward (Bell et al. 2015, Kleisner et al. 2016) and range boundary populations have expanded into the GOM. The GOM is a low diversity system, making it likely that species introductions and range shifts will be ecologically disruptive. Indeed, a rapid increase in abundance of sea bass may have significant impacts on community structure, partly because adult black sea bass are aggressive and territorial (Nelson et al. 2003), which may influence predator-prey and competitive dynamics.

Of particular concern is the impact of sea bass on crustacean populations in the GOM. In their native range, sea bass have a diet comprised of greater than 50% decapod crustaceans (i.e., south of Cape Cod; Garrison and Link 2000) and American lobsters, *Homerus americanus*, an ecologically and economically important species, have also been found in the stomachs of sea bass collected in the GOM (Chapter 2). Furthermore, Selden et al. (2016) found that a recent contraction in the southern range limit of lobsters was correlated with the northern expansion of sea bass. Because predatory fish induce strong NCEs in juvenile lobster populations, such as increased shelter usage and reduced foraging (Wahle 1992, Spanier et al. 1998, McMahan et al. 2013, Wilkinson et al. 2015), the expansion of this aggressive fish predator into the GOM could have substantial ecological and socioeconomic impacts.
The recent poleward shift of sea bass has increased their extent of geographic overlap with lobsters at the southern end of their distribution. Sea bass were historically rare in the southern GOM, and it is only in the recent decade that their abundance has rapidly increased. In southern and midcoast Maine, sea bass have been regularly captured by fishers since the warm water temperature anomaly of 2012 (Chapters 2 and 4, Mills et al. 2013). However, sea bass have not been reported via fisheries dependent or independent surveys conducted north of Penobscot Bay in Maine (also referred to as “Downeast” Maine), and fishers surveyed in this region had not encountered sea bass as of 2015 (Chapter 4). Therefore, latitudinal variation in contact history with sea bass exists in the GOM.

To examine the potential NCEs of sea bass on juvenile lobster behavior, I exposed juvenile lobsters to the presence and absence of water-borne sea bass risk cues and observed the behavior (shelter use and foraging) of lobsters from three regions in the GOM that differ in their contact history with sea bass. I hypothesized that the presence of sea bass would induce lobsters to increase shelter usage and decrease foraging, and that this response would be stronger for lobsters having a longer contact history with sea bass.

**Methods**

In the summer of 2015, I conducted a mesocosm experiment at Northeastern University’s Marine Science Center (MSC) in Nahant, Massachusetts, USA, to test how the presence/absence of black sea bass risk cues influences juvenile lobster habitat use and foraging from three regions in the GOM that have different contact histories for these two species. I manipulated the presence of sea bass olfactory cues and quantified the amount of time lobsters spent in shelter, the number of trips made to a prey plot, the time spent handling prey, and the total number of prey consumed.
Collection and maintenance:

Juvenile American lobsters were collected by hand from the intertidal-subtidal interface in northern Massachusetts (MA) (Marblehead, MA), midcoast Maine (Mid) (Harpwell, ME) and downeast Maine (DE) (Beals Island, ME) in July 2015 (Figure 3.1). Thirty lobsters, ranging from 25 to 40 mm CL, were collected in each location. All lobsters were in the intermolt stage and had no visible signs of injury (i.e., missing appendages). After capture, each lobster was carefully wrapped in a paper towel soaked with sea water, and then placed in a cooler to prevent thermal stress. Lobsters were immediately transported to the MSC and placed in individual 2.54 x 1.27 cm rubber coated mesh wire cages housed within 2 m-diameter x 1 m deep (3.1 m² area) flow-through tanks. Tanks were located outside, and therefore exposed to ambient light, temperature and weather. All lobsters were allowed to acclimate to these conditions and fed twice per week for a minimum of two weeks prior to the beginning of experiments. Each lobster was fed the same species, and approximately the same amount (10-15 g) at each feeding event. Their diet alternated between blue mussels (Mytilus edulis) and fish (species varied depending on what was available but included herring (Clupea harengus) and mackerel (Scomber scombrus)). Lobsters were deprived of food for 72 h prior to the start of the experiments. Water temperature was recorded hourly using an Onset® data logger deployed in the lobster storage tank and ranged from 11.3 to 22.3°C. This range of temperatures is similar to what juveniles experience at the intertidal-subtidal interface in the summer and early fall in the GOM (McMahan et al. 2016). No mortality was observed during storage or experiments.

Black sea bass were collected by hook and line in Boston Harbor on 20 July 2016. Sea bass ranged in size from 29.5 to 36.0 cm total length. These fish were returned to the MSC in a live well and immediately transferred to a 2 m-diameter (3.1 m² area) x 1 m deep flow-through
tank. Fish were allowed to acclimate for two weeks prior to the beginning of the experiments. During this time, survival and behavior were monitored daily. Sea bass rapidly acclimated to the storage tank and no mortality was observed. Fish were fed three times per week leading up to the start of the experiments. Their diet was based on gut content results from fish captured in the same region (Chapter 2), and included small crabs, squid, fish and bivalves. Although lobsters have also been found in the diet of sea bass, I specifically avoided this diet item to ensure that experimental lobsters were reacting to the scent of the predator, rather than an alarm cue of conspecifics in the predator’s feces. Sea bass were deprived of food for 24 h prior to the start of the experiments. Water temperature was recorded hourly using an Onset® data logger deployed in the sea bass storage tank and ranged from 12.8 to 22.7ºC.

Experimental design:

During experiments, lobsters were placed in mesocosms that sat within the larger flow-through tanks (Figure 3.2). Mesocosms consisted of a 48-cm diameter plastic mesh fish basket coated in 5 mm Vexar® to prevent appendages from getting caught in the basket mesh. The bottom of each basket was coated in a 2.54 cm layer of pea gravel. I also secured a shelter (12.7 cm length of 2.54 cm diameter PVC pipe) to the bottom of the basket with a cable tie. Two flat rocks (roughly 12 cm diameter) were also placed over the PVC pipe to add additional structure to the shelter. A prey plot was placed opposite of the shelter, and consisted of 10 blue mussels (ranging in length from 7 to 12.5 mm) that were super glued to a 7.6 x 15.2 cm ceramic tile. I firmly secured mussels to the tile to prevent lobsters from removing them and returning them to the shelter. Hence, lobsters that consumed mussels were forced to do so at the prey patch. During experiments, each mesocosm was placed in a flow-through tank in a depth of water that left 6 cm at the top of the basket exposed. This ensured that lobsters could not escape the mesocosm, but
also allowed the top of the mesocosm to remain unobstructed during video recording. At the end of each trial, mesocosms were removed from the tanks, thoroughly rinsed with fresh water, and left exposed to direct sunlight for six days to ensure sea bass cues were absent before being reused.

My experimental design crossed two fixed factors: Sea Bass Predation Risk (present, absent) and Region (MA, Mid and DE). For each combination, there were six replicates (i.e., replicate runs; n = 36). One replicate was run each week, and the study lasted 58 days (between late July and the end of September). Lobsters were added to mesocosms and allowed to acclimate for 2 h prior to experiments beginning. After the acclimation period, tanks housing experimental treatments received an additional fish basket containing a live sea bass. These baskets were sealed at the top with Vexar®, ensuring sea bass could not escape. This approach prevented direct predation, and also prevented lobsters from being exposed to visual cues. Experiments began at approximately 1800 hrs and ran for 18 h. During this time, juvenile lobster behavior was monitored with Sony Handycam® Camcorders (DCR-SR100) that were equipped with a 30-gigabyte hard drive and outfitted with a 0.5X lens in order to increase (~2X) the camera’s field of view. Illumination was provided by 15-W red-coated incandescent bulbs mounted on the side of each tank. The entire mesocosm could be observed in the focal view of the video camera. At the conclusion of each experiment, lobsters and sea bass were moved to new storage tanks (to ensure they were not reused in replicate treatments), prey plots were removed, and mussels were counted. There was no significant difference in lobster size among regions (ANOVA, \( F_{2,32} = 1.45, p = 0.25 \)) or treatments (ANOVA, \( F_{1,32} = 0.53, p = 0.47 \)).

**Data Analysis:**
Two randomly selected 30-min segments of video were analyzed for each trial, and the duration of specific activities and behaviors was measured. The first video segment was selected between 2000-2300 hrs and the second was selected between 0200-0500 hrs. Video segments were selected from the evening hours because lobsters are nocturnal (Wilkinson et al. 2015). Behaviors analyzed included time spent in the shelter, the number of trips made to the prey plot, and the time spent handling prey. Time spent in the shelter was defined as any period when the lobster was completely enclosed within the shelter. A trip to the prey plot consisted of the lobster leaving its shelter and traveling directly to the prey plot. Time spent handling prey included any use of the lobsters’ chela or maxillipeds to grasp or manipulate mussels. The total number of prey consumed during the 18 h experiment was quantified when prey plots were removed at the conclusion of the experiment.

The Shapiro-Wilks test for normality was conducted on all behavioral data prior to analyses. All data were non-normal and were analyzed using Generalized Linear Models (GLMs) with a Poisson distribution using the ‘stats’ package in R (R Core Team 2017). GLMs were checked for overdispersion, and those showing evidence of overdispersion (time spent in shelter) were refit using a negative binomial distribution (‘MASS’ package). Predation risk, region (MA, Mid, DE) and their interaction were included as fixed effects in all GLMs. The significance of main effects and their interaction was tested using type II Wald’s $\chi^2$-tests. Post-hoc multiple comparison analyses were conducted using the glht function in the ‘multcomp’ package, which conducts simultaneous tests and confidence intervals for GLMs (Bretz et al. 2010, Hothorn et al. 2008).
Results

Both region and predator presence influenced lobster shelter use and foraging behavior. The amount of time juvenile lobsters spent in shelter significantly increased in the presence of sea bass ($\chi^2 = 30.1, p < 0.001$; Figure 3.3). There was also a strong trend suggesting that the effects of sea bass on lobster shelter use varied among the three regions (predation risk x region interaction: $\chi^2 = 5.63, p = 0.06$). Sea bass presence increased the time spent in shelter from 6.3% to 84.9% for MA lobsters and from 7.0% to 97.8% for Mid lobsters (Tukey’s HSD, $p < 0.05$, respectively). By contrast, time spent in shelter increased from 11.1% to 36.8% for DE lobsters but this trend was not significant (Tukey’s HSD, $p > 0.05$). In addition, DE lobsters spent significantly less time in shelter than Mid lobsters when sea bass were present (Tukey’s HSD, $p < 0.05$).

There was also a strong interaction between the effects of sea bass predation risk and region on the number of trips that lobsters made to prey plots (predation risk x region interaction: $\chi^2 = 12.74, p = 0.002$; Figure 3.4). Sea bass presence reduced the number of trips made to the prey plot by 63.4% for MA lobsters and by 79.7% for Mid lobsters (Tukey’s HSD, $p < 0.05$, respectively), but predation risk did not significantly affect the number of trips made to the prey patch for DE lobsters (Tukey’s HSD, $p > 0.05$). In addition, Mid lobsters made 44.4% more trips to the prey plot than MA lobsters when sea bass were absent (Tukey’s HSD, $p < 0.05$), and DE lobsters made 62.1% more trips to the prey plot than MA and Mid lobsters when sea bass were present (Tukey’s HSD, $p < 0.05$, respectively).

There was a strong interaction between the effects of sea bass predation risk and region on the time that lobsters spent handling prey (predation risk x region interaction: $\chi^2 = 8.48, p = 0.014$; Figure 3.5). The presence of sea bass significantly decreased the amount of time that Mid
lobsters spent handling prey from 15.3% to 4.2% (Tukey’s HSD, $p < 0.05$), whereas, there was no effect of predation risk on the amount of time that MA and DE lobsters spent handling prey (Tukey’s HSD, $p > 0.05$). In addition, Mid and DE lobsters spent significantly more time (15.3% and 14.2%, respectively) handling prey than MA (2.7%) lobsters when sea bass were absent (Tukey’s HSD, $p < 0.05$), and DE lobsters spent more time (10.4%) handling prey than MA lobsters (2%) when sea bass were present, although this trend was not significant (Tukey’s HSD, $p = 0.10$).

The total amount of prey that lobsters consumed was significantly reduced by the presence of sea bass ($\chi^2 = 19.44$, $p < 0.001$; Figure 3.6). Mid and DE lobsters consumed 68.1% and 73.2% fewer mussels, respectively, in the presence of sea bass (Tukey’s HSD, $p < 0.05$). MA lobsters consumed an average of 0.67 mussels when sea bass were absent, and no mussels when sea bass were present. There was also a significant effect of region on the number of mussels consumed ($\chi^2 = 25.95$, $p < 0.001$). Mid and DE lobsters consumed significantly more mussels than MA lobsters (87.8% and 78.9%, respectively; Tukey’s HSD, $p < 0.05$).

**Discussion**

The nonconsumptive effects (NCEs) of predators on prey foraging can strongly influence community structure and ecosystem function (e.g., Schmitz et al. 2004, 2008, Preisser et al. 2005, Peckarsky et al. 2008). Here, I showed that the NCEs of a predator undergoing range expansion on juvenile lobsters vary across a broad geographic range. I found that the presence of sea bass predation risk increased shelter use and reduced foraging in juvenile lobsters, but risk effects on these behaviors depended on geographic variation in the contact history between sea bass and lobsters. NCEs were weakest where lobsters had no contact history with sea bass, which is consistent with the ‘naïve-prey’ hypothesis. In contrast, NCEs were strongest at the leading
edge of the sea bass range expansion, indicating that despite recent contact with a novel predator, prey have the capacity to express anti-predator defenses.

Massachusetts (MA) lobsters have the longest contact history with sea bass, but contrary to my expectations, sea bass presence did not affect the amount of time that lobsters spent handling prey or the number of prey they consumed. Indeed, even in the absence of predation risk juvenile lobsters from MA foraged infrequently, suggesting that reduced movement and foraging may be advantageous in this region. I suspect that such canalized behaviors may reflect the high background level of predation risk typically experienced by MA lobsters. In the southern GOM, lobsters are exposed to a greater diversity and abundance of fish predators compared to the northern GOM. Many predatory fish, such as tautog and scup, are absent or rare in Maine (Wahle et al. 2013, MDMF 2015, MDMR 2015), and the abundance of sea bass and striped bass is low compared to Massachusetts (Chapter 1, MDMF 2015, MDMR 2015). Furthermore, Wahle et al. (2013) found that predation intensity on tethered lobsters was greater in southern New England than in Maine. Hence, when faced with the tradeoff between foraging success and predation risk (Lima and Dill 1990, Lima 1998b), lobsters exposed to greater predation intensity may favor risk-avoidance behavior. The strong risk-avoidance behavior exhibited by MA lobsters, even in the absence of predators, suggests that increased sea bass abundance due to range-shifting may not alter lobster foraging behaviors, and thus population dynamics, in this region. Indeed, the high level of predation pressure already experienced by lobsters in southern New England and the southern GOM may be one factor influencing the drastic differences in lobster stock abundance between these areas and coastal Maine (Wahle et al. 2013, ASMFC 2015).
Despite the relatively brief time in which these populations have geographically overlapped, lobsters from midcoast Maine (Mid) recognized and responded to sea bass as they would to native fish predators, such as sculpin and Atlantic cod (Wahle 1992, McMahan et al. 2013, Wilkinson et al. 2015). Furthermore, Downeast (DE) lobsters consumed significantly fewer mussels in the presence versus absence of sea bass, indicating that they too were able to recognize and respond to a novel predator. This finding supports the life-dinner hypothesis, which predicts that prey rapidly adapt anti-predator defenses because they are experiencing greater selective forces than predators (i.e., a prey losing its life is worse than a predator losing its dinner; Brodie and Brodie 1999).

Recognition of novel predators may arise through neophobia, a generalized fear response to any novel stimuli (Greenberg 1990, Brown et al. 2013, Ferrari et al. 2015). The presence of neophobia in populations can depend upon the background level of risk prey experience in the environment (Ferrari et al. 2015). Specifically, prey from high-risk environments tend to exhibit neophobic responses to novel predator cues, but prey from low risk environments do not (Brown et al. 2013, Brown et al. 2014, Chivers et al. 2014, Ferrari et al. 2015). Downeast Maine is a relatively low risk environment compared to the southern GOM, and therefore lobsters from DE may not exhibit a strong response to novel predators. We found DE lobsters exhibited weak responses to the threat of predation in the majority of behaviors measured, but strongly responded in reducing their consumption of mussels, suggesting that perhaps some level of neophobia is occurring. However, the amount of time that they spent in shelter, number of trips to the prey patch, and time spent handling prey were not significantly affected by the presence of sea bass. Therefore, despite recognizing a novel predator, DE lobsters still exhibited ineffective predator avoidance responses, as predicted by the ‘naïve prey’ hypothesis (Banks and Dickman...
Furthermore, the lack of a strong response in predator avoidance behavior agrees with Sih et al. (2010) in suggesting that CEs may be stronger than NCEs for naïve prey.

In addition, I found that the presence of sea bass induced a trophic cascade, as evidenced by the reduced consumption of mussels by both Mid and DE lobsters. These findings demonstrate the importance of NCEs in driving marine trophic cascades at the edge of predator species’ ranges. Furthermore, reduced foraging and resource consumption by lobsters may lead to reduced growth, and ultimately impact overall fitness (e.g., Lima and Dill 1990, Werner and Anholt 1993, Lima 1998a, Trussell et al. 2006). Combined with the evidence that consumptive predation of lobsters by sea bass is also occurring (Chapter 2), it is likely that the northern range expansion of sea bass is impacting lobster population dynamics and benthic community structure in midcoast Maine and other newly expanded areas.

The variation in how Mid and DE lobsters responded to sea bass presence may be driven by differences in the potential adaptive ways that prey utilize to cope with novel predators. Sih et al. (2010) illustrated several scenarios for how naive prey can respond to non-native predators. For example, if prey use specific cues to identify native predators, then they will only respond to a novel predator if it provides a similar cue. If the cues are different, then the effectiveness of the response will depend on the ability of the prey to recognize general cues, such as conspecific alarm cues, to gauge risk. Prey that use specific cues may ignore a novel predator or exhibit ineffective defenses, and consequently suffer consumptive predation (Sih et al. 2010). Wilkinson et al. (2015) found that lobsters do not respond behaviorally to all fish predators, but rather avoid specific fish predators that they recognize to be a high-risk threat. Confronted with a novel predator, lobsters may not respond effectively, such as I found with lobsters from DE Maine. However, some prey species can smell the diet of their predators and can learn to recognize the
chemical cue of a novel predator after a single exposure to an individual that has ingested a
Therefore, lobsters with even a brief exposure history to sea bass may have learned to recognize
them as predators, as evidenced by the strong predator avoidance behavior exhibited by Mid
lobsters. Further investigation into the effects of predators across a range of contact histories, and
the mechanisms underlying the ability of prey to recognize novel predators, would greatly
enhance in our understanding of the relative importance of the CEs and NCEs of non-native
predators and their role in driving community structure.

Predation plays an important role in shaping communities (e.g., Hairston et al. 1960,
Paine 1980, Sih et al. 1985, Werner and Peacor 2003); however, wide spread climate-induced
distribution shifts have begun to alter traditional food webs and trophic interactions (reviewed in:
intensification of current rates of climate change (Peters et al. 2013, IPCC 2014, García Molinos
et al. 2015) will likely drive more species to shift their distribution to avoid thermal stress. As
predators shift into new environments, the relative importance of CEs and NCEs will depend on
the ability of prey to recognize novel predators, the speed at which they adapt anti-predator
defenses, and the effectiveness of those defenses. Observing CEs and NCEs across species’
native and newly expanded ranges, as well as areas where expansion is predicted to occur, will
reveal important insights on how range expansions will affect community structure.
Understanding species-specific responses to distribution shifts, as well as broader ecosystem
impacts, will be crucial to effective management and conservation efforts.
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Figure 3.1. Location of juvenile *Homarus americanus* collection sites in northern Massachusetts (MA) (42º30’37”N, 70º50’34”W), midcoast Maine (Mid) (43º48’35”N, 69º42’56”W) and downeast Maine (DE) (44º30’17”N, 67º36’12”W).
Figure 3.2. Image of mesocosm set-up used in *Homarus americanus* behavioral experiments.
Figure 3.3. Average percent of time spent in shelter for juvenile *Homarus americanus* from three regions in the absence (white bars) and presence (gray bars) of black sea bass olfactory cues. Error bars indicate ± 1 standard error. Letters indicate significant differences from post-hoc multiple comparison analyses (Tukey’s HSD, *p* < 0.05).
Figure 3.4. Average number of trips made to the prey patch for juvenile *Homarus americanus* from three regions in the absence (white bars) and presence (gray bars) of black sea bass olfactory cues. Error bars indicate ± 1 standard error. Letters indicate significant differences from post-hoc multiple comparison analyses (Tukey’s HSD, \( p < 0.05 \)).
Figure 3.5. Average percent of time spent handling prey for juvenile *Homarus americanus* from three regions in the absence (white bars) and presence (gray bars) of black sea bass olfactory cues. Error bars indicate ± 1 standard error. Letters indicate significant differences from post-hoc multiple comparison analyses (Tukey’s HSD, $p < 0.05$).
Figure 3.6. Average number of prey consumed for juvenile *Homarus americanus* from three regions in the absence (white bars) and presence (gray bars) of black sea bass olfactory cues. Error bars indicate ±1 standard error. Letters indicate significant differences from post-hoc multiple comparison analyses (Tukey’s HSD, $p < 0.05$).
Chapter 4: Fishers’ observations and perceptions of the northern range expansion of black sea bass (*Centropristis striata*)

Abstract

Many commercially important marine species are undergoing climate-driven distribution shifts, which is a concern for coastal communities that depend on fisheries resources. Management often struggles to keep pace with rapidly shifting species, particularly when data are unavailable in their newly expanded range. Black sea bass (*Centropristis striata*) have recently expanded their range into the Gulf of Maine. I surveyed commercial lobster fishers in Maine and Massachusetts to document their observations and perceptions of the northern range expansion of black sea bass. Fishers reported historic trends of sea bass bycatch in their lobster traps, including distribution, abundance and habitat information. Overall, 73.3% of fishers reported sea bass being most abundant between 2012-2015, and 56% of fishers believed increased sea bass abundance was due to an increase in water temperature. 48% of fishers believed that sea bass eat lobsters; however, 57% of fishers believed that sea bass becoming more abundant would be ‘somewhat’ or ‘very beneficial,’ indicating an optimistic viewpoint of the northern range expansion. However, 67% of fishers in Massachusetts reported that they were not satisfied with current sea bass management, and many specifically called for higher quotas now that sea bass are more abundant. These results provide baseline trends of sea bass distribution and abundance in the Gulf of Maine along with lobster fisher perceptions that may aid in ongoing assessment and management efforts. Furthermore, these findings indicate that fishers support expanding the sea bass fishery in its newly expanded range, but also identify areas where communication between fishers and managers could be strengthened to enhance the management of this new resource.
Introduction

Global change is driving a poleward shift in the distribution of many commercially important marine species (Perry et al. 2005, Nye et al. 2009, Pinsky et al. 2013, Cheung et al. 2013), which is a concern for coastal communities and stakeholders who rely on fisheries resources (Pinsky and Fogarty 2012). Recently, efforts to project future range shifts and theorize potential outcomes have accelerated (Hare et al. 2010, Madin et al. 2012, Cheung et al. 2010, Pinsky and Fogarty 2012, Kleisner et al. 2017), yet the ecological and socioeconomic implications of range shifts are still not well understood. In this study, I surveyed the American lobster fishery to examine the socio-ecological implications of the northern range expansion of black sea bass, *Centropristis striata*, into the Gulf of Maine (GOM).

A challenge to adaptively managing species’ range shifts is that there is often little information about them in their newly expanded range. However, fishers’ observations have become a critical component of establishing historic trends of species’ distribution and abundance (e.g., Saenz-Arroyo 2005, Azzurro et al. 2011, Thornton and Scheer 2012) and may be incredibly valuable for documenting species’ range expansions. In particular, older fishers may be a vital source of information on historical changes when long-term data sets are unavailable (Johannes et al. 2000, Saenz-Arroyo 2005). Furthermore, the use of fishers’ observations to improve resource management has gained traction in recent years, particularly in rapidly changing ecosystems (Thornton and Scheer 2012, Beaudreau and Levin 2014).

The potential socioeconomic implications of range shifts are diverse, and likely perceived differently across stakeholder groups (Madin et al. 2012, Pinsky and Fogarty 2012). Species shifting away from traditional fishing grounds likely is of great concern among fishers who will have to travel further to access the resource, or lose access entirely (Pinsky and Fogarty 2012).
Conversely, when species expand their ranges and inhabit new areas, fishers are potentially presented with a new opportunity, but only if they are able to harvest that biomass. Perceptions of shifting species may be further complicated by ecological interactions. For example, *Centrostephanus rodgersii* is a range expanding urchin in Tasmania that could potentially represent an emerging economic opportunity for fishers. However, *C. rodgersii* converts productive kelp beds into urchin barrens, which negatively impacts the commercially important abalone and rock lobster fisheries (Johnson et al. 2011), and therefore threatens the livelihood of those fishers.

Quantifying and allocating newly available resources sustainably and fairly among different user groups is exceptionally challenging. Resource managers have struggled to keep pace with rapidly shifting species distributions in New England and other regions globally where coastal seawater temperatures are rising rapidly (Pershing et al. 2015). Considering the socioeconomic complexities of range expansions before they occur, as well as the perceptions of local stakeholders, will be the first step in executing effective responses and mitigating potential impacts. Determining how fishers perceive range shifts and identifying their harvesting preferences and concerns will help coastal managers adapt to these shifts.

Black sea bass are a commercially and recreationally important species along the east coast of the United States and Gulf of Mexico. The northern stock historically ranged from Cape Hatteras to the GOM, but sea bass were rarely found north of Cape Cod (DeWitt et al. 1981, Drohan et al. 2007). However, the center of stock biomass has shifted poleward in recent years (Bell et al. 2015). This shift was first noted in the GOM by recreational and commercial fishers. During a 2012 warm water temperature anomaly in the northwest Atlantic (Mills *et al*. 2013),
commercial lobster fishers reported sea bass bycatch in traps as far north as midcoast Maine (McMahan unpublished data).

Traditional fisheries independent trawl surveys rarely detect sea bass in the GOM, likely because sea bass prefer structured habitat such as cobble-ledge bottom (Peterson et al. 2003, Drohan et al. 2007) that is not conducive to sampling with otter trawls. However, sea bass are commonly caught as bycatch in lobster traps. Indeed, anecdotal reports from lobster fishers were the only evidence that sea bass existed in Maine and New Hampshire until very recently (MDMR 2000-2015). The tendency for sea bass to enter lobster traps is not surprising, given that the majority of commercial sea bass harvest occurs in traps in their native range (Rudershausen et al. 2008). The Northeast Data Poor Stocks Working Group has even suggested using fish traps as an alternative survey gear for measuring sea bass distribution and abundance (Shepherd 2008). Although fishers’ observations do not meet the rigorous criteria for inclusion in stock assessment models, they can provide a historic baseline of sea bass distribution and abundance in the GOM from which to compare current and future observations.

The socio-economic implications of the northern range expansion of black sea bass remain unclear. While this range expansion presents a new opportunity, it has also been a source of contention for commercial and recreational fishers in areas of the western GOM where black sea bass abundances have rapidly increased. This tension has given rise to a political debate at both state and federal levels, with some federal officials demanding greater responsiveness to quota allocations. Anecdotal evidence suggests that fishers’ perceptions are divided between those that believe that sea bass pose a threat to the lobster industry (i.e., the most lucrative fishery in the U.S. (NMFS 2015)) vs. those that think that sea bass offer a new or enhanced economic opportunity. Further complicating this matter is that black sea bass management
efforts are not keeping pace with this rapidly shifting species (Pinsky and Fogarty 2012). For instance, commercial quotas remain low in Rhode Island and Massachusetts, despite black sea bass having become so abundant that they are considered a nuisance species in these areas (W. Lister, personal communication).

This study documents the observations and perceptions of commercial lobster fishers in Maine (ME) and Massachusetts (MA). MA allows both commercial and recreational harvest of sea bass, while ME has only recently implemented recreational harvest regulations. Therefore, commercial lobster fishers are the only type of fisher who have historically observed sea bass in both states. I conducted a mail survey of commercial lobster license holders in ME and MA and assessed: 1) fisher perceptions of sea bass range expansion, 2) fisher observations of sea bass and 3) fisher perceptions of current sea bass management efforts. Given that sea bass have a diet comprised of greater than 50% decapod crustaceans in their native range (Garrison and Link 2000), I hypothesized that lobster fishers would perceive the range expansion of sea bass as a threat to their livelihood. Alternatively, I hypothesized that MA lobster fishers may already benefit from the recreational or commercial harvest of sea bass, and therefore may perceive the range expansion as a benefit. In addition, I hypothesized that MA lobster fishers would not be satisfied with current sea bass regulations due to low quotas and a limited harvest season.

Methods

Survey design and data collection:

I conducted a survey of commercial lobster license holders in Maine and Massachusetts to better understand their attitudes, perceptions and observations of the northern range expansion of black sea bass. Commercial lobster fishers frequently catch sea bass as bycatch in their traps, and are the only type of fisher that is currently landing sea bass in both Maine and
Massachusetts. At the time of the survey, Maine did not permit recreational or commercial harvest of sea bass.

License holder information was obtained from the Maine Department of Marine Resources and the Massachusetts Division of Marine Fisheries in April of 2015. The survey population included 4,419 lobster fishers from Maine and 1,292 from Massachusetts. Demographic data (e.g., sex, age, race) was not included. Fishers were partitioned into regions within each state corresponding to their license management zone. These included Massachusetts state waters south of Cape Cod (southern MA, SMA), Massachusetts state waters north of Cape Cod (northern MA, NMA), Maine state waters between the New Hampshire border and Small Point (southern Maine, SME), Maine state waters between Small Point and Cape Rosier (midcoast Maine, MME) and Maine state waters from Cape Rosier to the Canadian border (northern Maine, NME (Figure 4.1)). Within each region, 300 mailed surveys were distributed to a random sample of fishers in June of 2015. Each survey included a cover letter that explained the purpose of the study and asked participants to respond to a survey approximately 15 minutes in length. All survey methods were approved by Northeastern University’s Institutional Review Board (IRB # 13-11-25). Five $50 gift certificates to Cabelas were raffled as an incentive.

Survey questions were divided into three categories: fisher classification, sea bass observations, and attitudes and perceptions on sea bass range expansion and management (Table 4.1). Each category contained both ordered response variables and open-ended questions. Fisher classification questions documented a fisher’s management zone, number of years spent fishing, number of traps fished, and the percent contribution of commercial lobster fishing to their household income. Observational questions documented the frequency of sea bass sightings, year of first sea bass sighting, depth and bottom type where sea bass are most typically caught,
seasonal abundance of sea bass, sea bass diet, and observations of other species that have increased in abundance in recent years. The attitude and perception portion of the survey was designed to measure if and why fishers believe sea bass abundance is changing, how they would prefer abundance to change, and their level of concern regarding the impact of the sea bass range expansion on native species, local fisheries, their personal livelihood, and their community’s economy. Fishers from MA were also asked about their views on current sea bass management efforts.

Data analysis:

Classification and regression tree analyses were used to determine the strongest predictors of fishers’ observations and perceptions. Potential predictors included region, possession of a commercial black sea bass permit, the number of years spent lobster fishing, and the percent of income earned from lobster fishing. There was a strong correlation ($r^2 = 0.70$) between percent of earned income and number of traps fished; therefore, the number of traps fished was not used as a predictor. Fishers’ perceptions of sea bass were also used as predictors in some analyses, including if fishers thought sea bass ate lobsters, and their perceptions on the impact of sea bass on local fisheries and their livelihood. All classification and regression trees were pruned using complexity parameters that minimized cross-validated error. The ‘rpart’ package in R was used for all tree-based analyses (R Core Team 2017). Covariance and correlation matrices were constructed for the types of prey fishers reported sea bass eating, as well as for fishers’ responses to a four-part question regarding the impact of sea bass on native species, local fisheries, their livelihood, and their community’s economy. The year of fishers’ first sea bass sighting and the year when sea bass were most abundant were compared among
region using separate generalized linear models (GLMs). The ‘stats’ package in R was used for all GLMs. Nonresponses and responses of “do not know” were not considered in analyses.

**Results**

A total of 124 fishers completed my mailed survey (overall response rate: 11.1%), with 60 from ME (ME response rate: 10%) and 64 from MA (MA response rate: 10.7%). Due to the low response rate from NME (n = 9), and the reported absence of sea bass in this area, NME was removed prior to analysis.

Overall, 63% (n = 72) of fishers rated sea bass as having become ‘more’ or ‘much more’ abundant in recent years. Fishers who held a commercial black sea bass permit tended to rate sea bass as having become ‘much more’ abundant (56% n = 10), while fishers who did not hold a commercial sea bass permit tended to rate them as having become ‘more’ abundant if they had spent 36 years or less fishing (47%, n = 25), and tended to rate abundance as having stayed the same if they had spent more than 36 years fishing (39%, n = 17 (Figure 4.2)). Only 9% (n = 8) of fishers rated sea bass as being ‘less’ or ‘much less’ abundant. Overall, 56% (n = 48) of fishers referenced warming ocean temperatures as the reason why sea bass have increased in abundance; however, regional variation existed in this response. Fishers from SMA predominantly referenced that factors other than temperature were responsible for the increase in abundance (e.g., fewer predators, more prey, lower commercial quotas (67%, n = 12)), while fishers from NMA, SME and MME predominantly referenced warming temperature (62%, n = 41 (Figure 4.3)).

There were significant regional differences in the average year in which sea bass were first sighted (GLM, p = 0.003). Sea bass sightings were reported significantly earlier in SMA (average year = 1982) compared to NMA (average year = 1996; Tukey’s HSD, p = 0.02), SME
(average year = 1999; Tukey’s HSD, p = 0.002), and MME (average year = 1996; Tukey’s HSD, p = 0.02). A similar regional divide occurred for the habitat where fishers reported catching sea bass. Overall, 52% (n = 57) of fishers reported catching sea bass in structured habitat only. However, 65% (n = 13) of fishers from SMA reported catching sea bass in both structured (e.g., rocky or reef habitat) and non-structured habitat (e.g., sand, mud, gravel), while 56% (n = 50) of fishers from NMA, SME and MME reported catching sea bass in structured habitat only. The depth at which fishers reported catching sea bass varied greatly among region. Overall, 64.5% (n = 71) of fishers reported catching sea bass between 0-60 ft, and 23.4% (n = 26) reported catching them between 0-30 ft.

Whether sea bass fishers held a commercial black sea bass permit was the greatest predictor of the number of sea bass that they caught annually. When fishers holding a commercial sea bass permit were removed from the analysis, region was the strongest predictor. Fishers in SMA and NMA caught more fish annually (annual average = 625) than fishers in SME and MME (annual average = 48). Furthermore, fishers in SMA and NMA who had a lower income dependency on the lobster fishery reported catching more sea bass. There was no significant difference among region for the year fishers reported seeing the greatest abundance of sea bass (GLM, p > 0.05). Overall, 73.3% (n = 52) of fishers reported that sea bass were most abundant between 2012-2015 (Figure 4.4). When comparing the average number of sea bass fishers caught in a typical year to the average number in the year they were most abundant, catch increased by 30.5% for SMA fishers, 15.8% for NMA fishers, 62.1% for SME fishers, and 38.4% for MME fishers.

Fishers most frequently reported that sea bass eat crabs, lobsters and fish, although several other prey groups were also named (Figure 4.5). Prey types reported did not significantly
covary \( r^2 = 0.01 - 0.1 \). Overall, 48\% (n = 34) of fishers believed that sea bass eat lobsters. Classification tree analysis revealed that fishers who had spent less than 14 years fishing did not believe sea bass ate lobsters (100\%, n = 7). Fishers who had spent more than 14 years fishing and whose income from lobstering was greater than 99\% also tended to believe sea bass do not eat lobsters (61\%, n = 11), while those whose income from lobstering was less than 99\% tended to believe they do eat lobsters (59\%, n = 27). Overall, 50\% (n = 55) of fishers rated that they would like sea bass abundance to stay the same. However, 44\% (n = 33) of fishers who believed sea bass were not eating lobsters wanted to see them become ‘more’ or ‘much more’ abundant, while only 26\% (n = 19) of fishers who believed sea bass were eating lobsters wanted to see them become ‘more’ or ‘much more’ abundant.

Fishers expressed modest concerns about potential impacts from sea bass expanding its range. For instance, 57\% (n = 59) of fishers rated that an increase in sea bass abundance would ‘somewhat’ impact native species abundance, and 55\% (n = 58) rated that it would ‘somewhat’ impact their state’s fisheries. However, 61\% (n = 64) of fishers rated that an increase in sea bass abundance would have no impact on their personal livelihood, and 51\% (n = 53) rated that it would have no impact on their community’s economy. Between 10-15\% (n = 10-16) of fishers responded that an increase in sea bass abundance would ‘very much’ impact the above factors. The greatest predictor of the perception that sea bass would impact native species abundance was experience. Fishers who had spent 41 or more years fishing predominantly thought sea bass would have no impact on native species (59\%, n = 13), while those who had fished for less than 41 years tended to think there would be some impact (64\%, n = 52). There was a high degree of correlation among fishers’ responses to the impact of sea bass on native species, local fisheries, their personal livelihood and their community’s economy \( r^2 = 0.40-0.76 \). For instance, fishers
who thought that sea bass would have a large impact on native species’ abundances also tended to think that they would largely impact local fisheries, their personal livelihood and their community’s economy, and vice versa for those who thought sea bass would have little or no impact.

Overall, 57% (n = 45) of fishers rated that sea bass becoming more abundant would be ‘somewhat’ or ‘very beneficial’ (Figure 4.6). This response was most influenced by whether fishers believed sea bass consumed lobsters. 75.5% (n = 31) of fishers who did not believe that sea bass consume lobsters rated that an increase in abundance would be ‘somewhat/very beneficial’, and only 5% (n = 2) rated that it would be ‘somewhat/very harmful’. In contrast, only 37% (n = 14) of fishers who believe sea bass consume lobsters rated that an increase would be ‘somewhat/very beneficial’, while 39% (n = 15) rated that it would be ‘somewhat/very harmful’.

Fishers reported observing numerous species that were once rare but are now more abundant (Table 4.2). Most notably, 14.6% of fishers observed an increase in scup abundance, and 18.3% observed an increase in green crab abundance. The strongest predictor of fishers’ level of concern about rare species increasing in abundance was whether they believed sea bass eat lobsters. Fishers who do not believe sea bass eat lobsters tended to rate that they were ‘not concerned’ about rare species increasing in abundance (44%, n = 20), while of the fishers who do believe sea bass eat lobsters, only 18% (n = 7) were ‘not concerned’.

Finally, 67% (n = 28) of fishers in MA (i.e., SMA and NMA) were not satisfied with current black sea bass regulations (Figure 4.7). Regionally, 84% (n = 16) of fishers from SMA were not satisfied with current regulations, whereas satisfaction for fishers from NMA varied with experience. Those who had fished for less than 34 years tended to be satisfied with
regulations (62% n = 8), and those who had fished for more than 34 years tended to not be satisfied (70%, n = 7). The majority of fishers unsatisfied with management specifically referenced wanting to see an increase in quota (82%, n = 23).

**Discussion**

Species undergoing rapid range shifts can be challenging to assess and manage, particularly when there is little information about them in their newly expanded range (Link et al. 2011, Pinsky and Fogarty 2012, Madin et al. 2012). However, the observations amassed by fishers throughout their lifetime is of a scale and quality not typically accessible by biological surveys, and may aid in filling critical gaps in scientific knowledge. This information can also be used to identify socioeconomic impacts and areas where future research and mitigation are needed. My survey of commercial lobster fishers in ME and MA revealed previously undocumented trends in black sea bass distribution and abundance, which may provide a baseline for future assessments. I also found that fishers’ perceptions of the northern range expansion were influenced by whether they perceive that sea bass will impact their livelihood.

The majority of commercial lobster fishers in ME and MA reported observing an increase in sea bass abundance in recent years. However, there were fishers who reported that sea bass abundance had not changed, and these surprisingly tended to be fishers with more than 36 years of experience. The majority of these fishers were also from ME, and some had reported catching sea bass in the 1970s and 80s. This finding suggests that sea bass may have intermittently occurred in this area prior to the northern range expansion. However, the majority of respondents in ME and MA observed an increase in abundance during and after 2012, coinciding with the 2012 warm water temperature anomaly in the Northwest Atlantic (Mills et al. 2013). These observations provide historic information on the distribution and abundance of sea bass in the
GOM that was previously unavailable from scientific surveys, and are also an indication of the geographic extent of the northern range expansion.

Fishers within the GOM (i.e., NMA, SME and MME) predominantly believed the recent increase in sea bass abundance was due to increased water temperature. The GOM is warming at a faster rate than 99% of the world’s oceans (Pershing et al. 2015), and my findings demonstrate that fishers are aware that this environmental change is altering patterns of species distribution and abundance. This finding may prove useful when faced with traditional barriers of communicating the impacts of climate change on fisheries resources (Nursey-Bray et al. 2012). Concerns over the impacts of rapidly warming water temperature appear to be common among fishers, regardless of if they believe in climate change (Nursey-Bray et al. 2012, Frusher et al. 2014, Musinguzi et al. 2016). Identifying such areas of concern may aid in opening a dialog among industry, scientists and managers regarding the current and future impacts of environmental change on fisheries resources, which will be crucial for effective adaptation of fisheries management measures associated with these changes (Leith et al. 2013). The tendency of SMA fishers to not reference warming water as the major driver of changes in sea bass abundance is also noteworthy, and suggests that factors other than temperature may be more impactful in this area. For instance, several respondents referenced either an increase in prey, a decrease in predators, or both as the primary reason why sea bass abundance has changed, although none referenced specific species. Further investigation into the ecological changes fishers have observed in this area, and their perceptions of the resulting impacts, is warranted.

Fishers in NMA and SME reported catching as many as 1,000 sea bass annually, indicating that sea bass are much more abundant in these areas than previously documented in fisheries independent trawl surveys (MDMR 2000-2015, MDMF 2016, NEFSC 2016). One
respondent from SMA replied that “offshore lobstermen throw back thousands of pounds a trip” and another from NMA responded that they “discard hundreds of fish a day.” Fishers also reported catching sea bass primarily in structured habitat in the GOM, but in both structured and non-structured habitat south of Cape Cod. This difference likely indicates regional variation in habitat usage or availability, rather than differences in targeted trapping areas, as fishers in southern New England and the GOM target both structured and non-structured habitat (Saila et al. 2002). Furthermore, fishers from all regions reported catching sea bass in relatively shallow water. These observations may provide evidence as to why trawl surveys rarely find sea bass in the GOM, despite fishers reporting hundreds to thousands of sea bass caught as bycatch each year in some areas. Therefore, my stakeholder survey results support previous conclusions that trawl surveys may not provide an accurate measure of sea bass abundance (Shepherd 2008).

The additional species that fishers most frequently reported as increasing in abundance were scup (*Stenotomus chrysops*) and green crabs (*Carcinus maenas*). Recent research corroborates these observations with evidence that the center of scup stock biomass has shifted northward (Bell et al. 2015), and green crab abundance is positively correlated with temperature (Congleton et al. 2006, Beal 2013). Many of the other species observations listed are also supported in scientific literature. Overall, these results demonstrate consistency between fishers’ observations and scientific knowledge.

Although almost half of the respondents believe that sea bass eat lobsters and they will impact native species’ abundances, the majority of fishers still believed that an increase in sea bass abundance would be beneficial. This finding suggests that fishers are more optimistic about the potential to harvest this new resource as opposed to primarily being concerned about potential negative impacts that sea bass could have on the lobster industry. The economic
diversity of marine resources in the GOM has drastically declined in the past 20 years, particularly in ME, where fishers are almost entirely dependent on the lobster fishery (Steneck et al. 2011). In their native range, sea bass are a highly sought-after game fish and support lucrative recreational and commercial fisheries. Thus, the establishment of sea bass fisheries in the northern GOM could provide a much-needed economic opportunity, and ultimately benefit the region. However, there were some respondents who believed sea bass were a threat to the lobster industry and that an increase in abundance would be harmful. The potential net economic benefit of sea bass abundances increasing in the GOM has yet to be determined; however, documenting fishers’ concerns and perceptions is an important first step to building adaptive strategies to climate change impacts, which should include maximizing economic opportunities and minimizing potential threats (Metcalf et al. 2014).

The expansion or establishment of sea bass fisheries in the GOM will depend upon accurate population assessments and timely management decisions. I found that many fishers in MA, particularly in SMA where sea bass are most abundant, were dissatisfied with current management efforts and specifically referenced wanting higher quotas and a longer season. Despite the clear increase in abundance that fishers have observed, increased quotas have not been allocated, in part because sea bass are a data poor species, and very little is known about them in their newly expanded range. Although reduced pressure on newly arrived species may ultimately hasten the establishment of viable fisheries (Pinsky and Fogarty 2012), fishers are frustrated that they cannot currently benefit from the increase in sea bass abundance. Meanwhile, managers are unable to accommodate higher quotas with the data that is available to them. The frustration with management documented in this study is indicative of the disconnect between fishers and managers that pervades in many fisheries. Efforts to incorporate fishers’ observations
into management decisions, as well as targeted efforts to assess stocks in newly expanded areas, could help bridge this divide and increase stakeholder buy-in to local management policies.

The projected continuation and intensification of current ocean warming trends (Peters et al. 2013, IPCC 2014, García Molinos et al. 2015) is expected to result in major changes to the distribution and abundance of marine species in the Northwest Atlantic (Kleisner et al. 2017), which may have far reaching socioeconomic consequences for coastal communities. The ability of fishers to adapt to, and the successful management of, changing resources will require collaboration among fishers, managers, scientists and other stakeholders. My study showed that fishers observations and perceptions can fill critical gaps in scientific and socioeconomic knowledge, and emphasizes the need to incorporate this information into ongoing assessment and management efforts when possible.

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Table 4.1. Summary of survey questions.

<table>
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<tr>
<th>Question Categories</th>
<th>Fisher type (permit)</th>
<th>State of residence</th>
<th>Fishing zone</th>
<th># of years fishing</th>
<th># of traps fished</th>
<th>Income from commercial harvest of lobsters</th>
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<tr>
<th><strong>Observations</strong></th>
<th>Frequency of sea bass sightings</th>
<th>First year of sea bass sightings</th>
<th>Depth and bottom type where seas bass are caught</th>
<th>Seasonal abundance of sea bass</th>
<th>Other species changing in abundance</th>
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<table>
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<th><strong>Perceptions</strong></th>
<th>Greatest factors influencing changes in sea bass abundance</th>
<th>Sea bass diet</th>
<th>Impact of increased sea bass abundance on: native species, fisheries, personal livelihood, community economy, overall</th>
<th>Satisfaction with current sea bass management</th>
<th>Proposed changes to current sea bass management</th>
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<td>Massachusetts</td>
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<td>n</td>
<td>%</td>
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Table 4.2. Summary of species fishers listed as having increased in abundance.
Figure 4.1. Location of commercial lobster fisher survey regions in downeast Maine (NME), midcoast Maine (MME), southern Maine (SME), Massachusetts north of Cape Cod (NMA) and Massachusetts south of Cape Cod (SMA).
Figure 4.2. Classification tree of black sea bass abundance. Variables support fishers’ observations of changes in sea bass abundance. Numbers in pie charts correspond with percent response in each category.
Figure 4.3. Classification tree of reasons for changes in black sea bass abundance. Variables support fishers’ perceptions of why black sea bass abundance has changed. Temp = temperature, other = other reasons for change (e.g., fewer predators, more prey, low quota). Numbers in pie charts correspond with percent response in each category.
Figure 4.4. Cumulative frequency histogram of fishers’ observations of the year in which black sea bass were most abundant for all regions combined.
Figure 4.5. Bar plot of the species fishers believe black sea bass eat in midcoast Maine (MME), southern Maine (SME), Massachusetts north of Cape Cod (NMA) and Massachusetts south of Cape Cod (SMA).
Figure 4.6. Classification tree of the impact of black sea bass abundance. Variables support fishers’ perceptions of the overall impact of black sea bass becoming more abundant. Numbers in pie charts correspond with percent response in each category.
Figure 4.7. Classification tree of satisfaction with current black sea bass management. Variables support Massachusetts fishers’ opinions of current management. Numbers in pie charts correspond with percent response in each category.