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**CONSUMPTIVE AND NON-CONSUMPTIVE EFFECTS OF PREDATORY
FISHES ON LOBSTER IN SOUTHERN MAINE**

BY

Erin B. Wilkinson
B.S. University of Maine, 2008

THESIS

Submitted to the University of New England
In Partial Fulfillment of the
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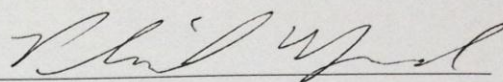
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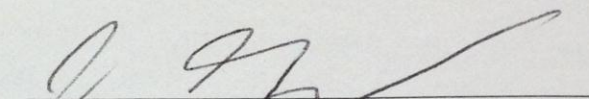
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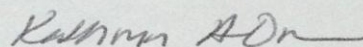
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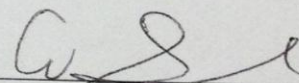
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ABSTRACT

CONSUMPTIVE AND NON-CONSUMPTIVE EFFECTS OF PREDATORY FISHES ON LOBSTER IN SOUTHERN MAINE

By

Erin B. Wilkinson

University of New England, January, 2013

The American lobster, *Homarus americanus*, is an important consumer in the Gulf of Maine benthic community and supports the most valuable fishery in New England. Many fish predators that feed on juvenile lobster are found in the Gulf of Maine, but their abundance has varied over the previous decades. For example, striped bass, *Morone saxatilis*, have recovered from near extinction to become a viable recreational fishery on the east coast, and previous work examining the gut contents of striped bass found that juvenile lobsters were a large component of their diet during the summer in Massachusetts. However, striped bass diet has not been examined extensively in the Gulf of Maine and this raises questions as to how important lobster may be to striped bass diet in southern Maine coastal waters. There are also many management strategies in place to help restore other fish species known to consume juvenile lobster, such as Atlantic cod, to the Gulf of Maine. It has been suggested that the abundance of lobster may be inversely related to the abundance of coastal groundfish in the Gulf of Maine. In addition to consumptive effects through feeding activity these predators may also have non-consumptive effects on their targeted prey species by causing lobster to alter their behaviors. It is unclear what consumptive and non-consumptive effects the

return of these large fish predators may be having on juvenile lobster in the Gulf of Maine.

Chapter 1 examines the food habits of striped bass in Southern Maine coastal waters, with an emphasis on how important lobster is to their diet. Using stomach contents and stable isotope analysis I found that for all sizes of striped bass small pelagic fish species made up the majority of diet, and for large and extra-large fish crustaceans (lobster) were found more often than in the stomachs of smaller fish. Stable isotope analysis revealed that larger striped bass expressed stronger benthic signals of $\delta^{13}\text{C}$, indicating that prey such as lobsters are more important to larger striped bass diet in Southern Maine than stomach contents revealed.

The 2nd chapter presented here examines what sizes of juvenile lobsters are most susceptible to predation, and how juvenile lobster anti-predator response varies among different predators (striped bass, cod, and sea raven). I found that small lobsters (<45mm carapace length) are most susceptible to predation, and observed that the strength of anti-predator responses displayed by lobster varied with predator type. Lobsters reacted to the presence of Atlantic cod or sea raven by decreasing activity levels and increasing shelter use, but did not alter behavior in the presence of striped bass. This varying level of response seems consistent with differences in predator foraging modality.

Taken together, the results of these two studies can be used to increase our understanding of what long term consumptive and non-consumptive effects can be expected for juvenile lobsters in southern Maine if we continue to see the return of large fish to this region

CHAPTER 1

INVESTIGATING FOOD HABITS OF STRIPED BASS (*MORONE SAXATILIS*) IN SOUTHERN MAINE COASTAL WATERS USING STOMACH CONTENT ANALYSIS AND STABLE ISOTOPE ANALYSIS WITH A SPECIAL FOCUS ON LOBSTER (*HOMARUS AMERICANUS*)

ABSTRACT

Striped bass (*Morone saxatilis*), an anadromous coastal predator found throughout eastern North America, have recently recovered in US waters, and may now be contributing to top-down forcing in the Gulf of Maine where they feed during the summer months. Here, we examined the diet of striped bass in the Gulf of Maine using stomach content and stable isotope analysis. Fish were collected via hook-and-line sampling between May and October 2011. Stomach contents revealed that small pelagic fishes (e.g., Atlantic herring, *Clupea harengus* and Atlantic mackerel, *Scomber scombrus*) dominated the diet of medium-sized striped bass (43.4-59.9cm), while benthic prey (i.e., various crustaceans) increased in frequency in diets of large (60.0-74.9cm) and extra-large striped bass (over 75cm). American Lobster, *Homarus americanus*, was found to be an important component of the diet for larger striped bass, and stable isotope analysis revealed that benthic prey items (including lobster) may be more important to the diet of large striped bass than indicated by stomach content analysis alone. My data suggest that striped bass may be targeting juvenile lobster in the Gulf of Maine, and

consequently that the recovery of striped bass populations could negatively affect lobster populations in coastal Maine.

INTRODUCTION

Striped bass, *Morone saxatilis*, is an anadromous fish species found along the Atlantic Coast of the United States (Walter et al, 2003; Grothues et al., 2009) that occupies many inshore marine areas from North Carolina to Canada (Grothues et al. 2009). Portions of the Atlantic coast stocks of striped bass migrate during the spring and summer to feeding grounds in the north, including Saco Bay, within the Gulf of Maine (Nelson et al, 2003; Grothues et al, 2009). The restoration of striped bass along the east coast of the United States is an ongoing success story, and while the species was once commercially extinct, striped bass populations have been rebuilt since 1995 (ASMFC, 2011).

The rebuilding of striped bass populations along the US East coast may have implications for food web structure and function in coastal areas (Harding and Mann, 2003; Rudershausen et al., 2005). Because individual *M. saxatilis* typically migrate 100's of km annually, prey type has been shown to vary widely with location and time of year (Rudershausen et al., 2005). Generally, clupeid fishes, including bay anchovies (*Anchoa mitchilli*), menhaden (*Brevoortia tyrannus*), and Atlantic herring (*Clupea harengus*), dominate the diet of striped bass over 1 year of age (Walter et al, 2003), but decapod crustaceans and shrimp are also prevalent diet items in some regions (Nelson et al, 2003; Walter et al., 2003). In the Gulf of Maine, adult striped bass have been described to consume predominantly Atlantic herring, sand lance (*Ammodytes* sp.) and other fishes, whereas smaller striped bass were described to consume mostly amphipods

and shrimps (Collette and Klein-MacPhee, 2002). Generally, striped bass are able to consume prey from a broad range of size classes (Hartman, 2000; Overton et al., 2008). However, a study examining the importance of prey size in striped bass diet found that prey less than 41mm total length are most vulnerable, even to average sized bass (340mm total length; Hartman 2000).

Many studies of fish diet rely on analysis of stomach contents, which provides a ‘snapshot’ in time of instantaneous feeding habits, but may over- or underestimate actual, average feeding relationships over longer periods (e.g., weeks to months). On the other hand, stable isotope analysis (SIA) of carbon and nitrogen signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively) can provide information on average feeding behavior over time, but lacks taxonomic specificity. Although SIA cannot differentiate among species consumed, it can distinguish among broad prey categories. For example, enriched $\delta^{13}\text{C}$ values (i.e., more positive) in marine fish are indicative of feeding on benthic rather than pelagic prey, which have more negative or depleted $\delta^{13}\text{C}$ signatures in continental shelf ecosystems (Davenport and Bax, 2002; Sherwood and Rose, 2005). Carbon signatures fractionate very little among trophic levels (Vander Zanden and Rasmussen 2001) and are an indication of different carbon fixation mechanisms at the base of the food web. Conversely, $\delta^{15}\text{N}$ signatures indicate trophic position in consumers (Sherwood and Rose, 2005) because this isotope fractionates on average 3.4 delta units per trophic level (Vander Zanden and Rasmussen 2001). Combining stomach content analysis and SIA is common practice in diet studies and can be used to distinguish between short and longer term feeding behaviors.

My purpose was to explore feeding patterns in striped bass in southern Maine waters. I employed both stomach content analysis and SIA to elucidate diet in striped bass of varying sizes with a particular focus on striped bass – lobster interactions. American lobster (*Homarus americanus*) landings are at all-time highs in the Gulf of Maine (ME dept. of Marine Resources, 2012; Steneck & Wilson, 2001), particularly in the eastern region (mid-coast and eastern Maine), but less so in the western portion (i.e., southern Maine, New Hampshire and Massachusetts). Higher predator abundance in the western Gulf, including striped bass and groundfish like cod (*Gadus morhua*) may play a role in regulating lobster populations (Steneck, 1997). A first step in assessing whether striped bass can impact lobsters is to examine the diet of the former. Based on previous diet studies, we hypothesized that striped bass feed primarily on pelagic forage fish while in the Gulf of Maine. Alternatively, given that previous studies in coastal Massachusetts have found that striped bass feed on decapods to varying degrees, we also hypothesized that they would target lobsters in the coastal waters of southern Maine given the current high abundance of this prey resource.

METHODS

Fish Collection and Stomach Content Analysis

A total of 57 striped bass were collected via hook and line sampling from May through October 2011 in Saco Bay, a known habitat for transient striped bass, as well as an important lobster fishing ground. Groups of local sport fishermen and striped bass fishing tournaments were utilized to supplement striped bass samples and contributed 23 fish to the study. Date, capture location, total length (measured from the tip of the snout to tip of the caudal fin; cm) and total weight (g) were recorded for each striped bass

collected. Fish donated to the study were often received with fillets removed so a total weight was not possible for 16 of the 57 fish collected. After capture, fish were kept on ice until the stomach could be removed for later diet analysis, and a small muscle tissue sample (~ 1 g from dorsal section anterior to first fin) could be collected for SIA. All stomach samples donated to the study were immediately frozen until analysis at a later date. If dissections were not possible in the field, fish were frozen until stomach and tissue samples could be removed at a later date. Once removed from fish (or thawed), stomachs were weighed, and then cut open. All contents were emptied from the stomach and an 'empty weight' was obtained. Stomach contents were then individually identified to the lowest taxonomic level possible, and each item was weighed to the nearest 0.1g and measured to the nearest mm using calipers. A subset of prey samples obtained was also retained for stable isotope analysis. Muscle tissue samples and prey samples were frozen at -20°C in 1.5 ml vials until they could be prepared for SIA.

Collected fish ranged in size from 43.4cm to 109.2cm and were categorized into 3 groups based on total length (arbitrarily to ensure relatively equal samples sizes in each group): "medium" (43.4cm -59.9 cm total length), "large" (60.0cm - 74.9 total length), and "extra- large" (over 75cm total length). Prey taxa were categorized into 6 main groups: 1) forage fish (sand lance, mackerel (*Scomber scombrus*), Atlantic herring, and Atlantic silverside (*Menidia menidia*)); 2) un-identified fish and tissue; 3) crabs (*Cancer borealis*, *Cancer irroratus* or *Carcinus maenas*); 4) lobster; 5) shrimp (*Crangon septemspinosa*); and 6) other (isopods, rocks, algae, and worms). Fourteen of the stomachs collected from striped bass were empty and were excluded from stomach content analyses. Frequency of occurrence (FO), percent volumetric contribution (V) and

mean partial fullness index (PFI) were determined for all identifiable prey taxa to assess the relative importance of each type of prey to the diet of striped bass in Southern Maine.

Frequency of occurrence (FO) was calculated as

$$FO = \frac{N_i}{N_{tot}} \times 100$$

where N_i is the total number of stomachs with prey i , and N_{tot} is the total number of stomachs for a particular group of striped bass (e.g. size class). Percent volumetric contribution (V) was calculated as

$$V = \frac{W_i}{W_{tot}} \times 100$$

where W_i is the weight of prey item i (grams) and W_{tot} is the total weight of all prey (grams) consumed by a particular group of striped bass (e.g. size class). PFI is a measure of prey importance in the diet that takes into account variations in predator length (Bowering and Lilly, 1992) and was calculated using the following equation:

$$\text{Mean PFI} = \frac{1}{n} \sum \left(\frac{W_{ij}}{L_j^3} \right) \cdot 10^4$$

where W_{ij} is the weight of prey i from fish j (g), and L_j is the total length of fish j (cm). Mean PFI values were calculated for each prey taxa and each prey group by striped bass size grouping (Table 1).

Relationships between predator size and prey size were examined by dividing prey into “benthic” or “pelagic” prey categories and regressing prey size against striped

bass total length (linear regression). Pelagic prey included forage and unidentifiable fish while benthic prey included lobster, crabs, and shrimp.

To gain rudimentary insight into the possible relationship between diet and energetic fitness, we examined the scaling coefficient from the length – weight relationship (LWR) for striped bass, an indication of body condition in fish (Eastwood and Couture 2002). The LWR, given as:

$$W = a \cdot L^b$$

where W is weight in grams and L is total length in cm (a is a constant), provides an estimate for the allometric scaling coefficient (b) of the average fish in the population. Under optimal conditions, for a species like striped bass with positive allometric growth (i.e., they normally become disproportionately heavier with length), b should be greater than 3 (Froese and Pauly 2012, Wigley et al. 2003). A b value of less than 3 would indicate that larger fish are in poorer condition than smaller individuals and may signal some form of feeding bottleneck (*sensu* Sherwood et al. 2007). Thus, I examined whether b from the LWR was significantly greater than 3 by comparing confidence intervals for b to the value of 3.

Stable Isotope Analysis

Frozen muscle tissue samples and representative prey samples were thawed and dried in a drying oven at 60°C for 48 hours. Samples were then homogenized using a mortar and pestle, weighed (nearest µg), placed in 4 × 6 mm tin capsules, and sent to the Colorado Plateau Stable Isotope Laboratory for analysis. Stable isotope signatures were determined by the analysis of carbon (CO₂) and nitrogen (N₂) produced by combustion

on an elemental analyzer followed by gas chromatograph separation interfaced via continuous flow to an isotope ratio mass spectrometer. Stable isotope signatures are expressed in delta (δ) notation, and defined as parts per thousand (‰) deviations from a standard material. Ten percent of the samples (57 striped bass samples and 57 diet samples) were analyzed in duplicate. The average coefficient of variation for these replicate pairs was 0.4 % for $\delta^{13}\text{C}$ and 1.0 % for $\delta^{15}\text{N}$.

Stable carbon isotope ratios of consumers are influenced by lipid content in samples; higher lipid content results in more depleted (i.e., negative) $\delta^{13}\text{C}$ signatures which do not necessarily reflect trophic relationships. A common method for removing the influence of variable lipid content is to standardize $\delta^{13}\text{C}$ values to carbon/nitrogen ratio (C/N) which is a proxy for lipid content (McConnaughey and McRoy 1979); we applied this correction technique and lipid-corrected $\delta^{13}\text{C}$ values for striped bass samples are hereafter denoted as $\delta^{13}\text{C}'$. There is no value in lipid-correcting the prey items because the carbon signature of prey, regardless of lipid content, is consumed and assimilated.

To determine general feeding trends, mean isotopic values of each size class of striped bass were qualitatively compared to mean isotopic values of individual and broad prey categories. Average prey isotopic signatures for each striped bass size group was back-calculated by assuming a trophic fractionation of +1.0 ‰ for $\delta^{13}\text{C}$ and +3.4 ‰ for $\delta^{15}\text{N}$ (Vander Zanden and Rasmussen, 2001; Minagawa and Wada, 1984). Ontogenetic changes in diet were explored by regressing isotopic signature (both $\delta^{13}\text{C}'$ and $\delta^{15}\text{N}$) against fish length (linear regression). A two source mixing model (Vander Zander and

Vadebonceour, 2002; Sherwood and Rose, 2005) was used to examine the percent reliance on benthic prey for each size class of striped bass using the equation % reliance = $[(\delta^{13}\text{C}_f - \delta^{13}\text{C}_p) - (\delta^{13}\text{C}_b - \delta^{13}\text{C}_p)] * 100$; where $\delta^{13}\text{C}_f$, $\delta^{13}\text{C}_p$, and $\delta^{13}\text{C}_b$ are the mean $\delta^{13}\text{C}$ values for striped bass (medium = -19.51, large = -18.63, extra-large = -18.76), pelagic prey species (-20.83), and benthic prey species (-17.59) respectively. $\delta^{13}\text{C}$ derived trophic designations were determined based on the % reliance of benthic prey: <25% benthic reliance is pelagic; 25-75% benthic reliance is mixed; >75% benthic reliance is benthic (Sherwood and Rose, 2005). This new trophic designation was then compared to previous trophic designations from earlier diet studies.

RESULTS

Stomach Contents

Striped bass ranged in size from 43.4 to 109.2 cm. Most striped bass were classified as medium (43.4-59.9 cm; n=18) and large (60.0-74.9 cm; n=19) while only a few were extra-large (over 75 cm; n=6).

Across all size classes, forage fish and unidentifiable fish made up the majority of *M. saxatilis* diet (FO = 30-45%), but American lobster (*Homarus americanus*) was also a major prey item identified (FO = 0-50%) (table 1). Diet varied among size class; for medium sized fish, forage fish were the dominant prey taxa, but crabs and shrimp also made up a large proportion of the diet, while forage fish and lobster made up the majority of diets in large and extra-large fish (figures 1, 2). Forage fish and unidentifiable fish and shrimp were present in all sizes of striped bass. Although crabs were present in medium and large size striped bass, lobster was only present in fish measuring over 60 cm.

Prey sizes varied with prey type and increased with striped bass size for pelagic prey, but did not vary with striped bass size for benthic prey items. Linear regression indicated a positive relationship between total length of striped bass and pelagic prey size ($r^2=0.12$, $p<0.0001$, $n=83$ (figure 3), but did not change significantly for benthic prey ($r^2=0.00$, $p>0.9$, $n=46$). Consumed lobsters and crabs were, 38 mm (mean carapace length) and 25 mm (mean carapace width), respectively. Shrimp ranged in size from 37 to 53 mm, while forage fish were the largest prey items by size and ranged from 73 to over 120 mm total length.

An allometric scaling coefficient of $3.28 (\pm 0.19)$ was determined for the relationship between length and weight of all striped bass examined ($n = 47$) (figure 4). While this value was not significantly different than 3, it did indicate positive allometric growth which, in turn, does not suggest energetic deficiencies as striped bass grow larger. This qualitative result was not changed by removing the two largest individuals (i.e., greater than 95 cm). With these two exclusions, $b = 3.31 \pm 0.24$ ($n = 45$).

Stable Isotopes

Isotope results for striped bass ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and common prey items ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) contributed to our understanding of which diet items are assimilated into striped bass muscle tissue (figure 6). Values for prey species ranged from very benthic (more positive, enriched in ^{13}C) to more pelagic (more negative, or depleted in ^{13}C). Lipid-corrected carbon isotope values for striped bass were intermediate (neither highly benthic nor highly pelagic, mean $\delta^{13}\text{C}$ = -19.03 ‰) and $\delta^{15}\text{N}$ values (mean striped bass $\delta^{15}\text{N} = 16.00$ ‰) indicated a relatively high trophic position for striped bass compared to

all measured prey (mean prey $\delta^{15}\text{N} = 12.53 \text{ ‰}$). Without taking into account individual and ontogenetic variations, the difference between mean striped bass and mean prey $\delta^{15}\text{N}$ signatures was 3.47 ‰, which agrees well with published trophic fractionation values for $\delta^{15}\text{N}$ (Minagawa and Wada, 1984; Vander Zanden and Rasmussen 2001).

Linear regression showed that as striped bass increase in size they have a more enriched $\delta^{13}\text{C}$ signal ($r^2=0.05$, $p<0.05$, $n=56$; figure 7). No significant relationship existed between $\delta^{15}\text{N}$ and fish length.

The trophic classifications of striped bass did not differ among size groups: all three size categories have been deemed to be pelagic based on previous reports of their feeding habits throughout most of their range (Nemerson & Able, 2003; Walter et al., 2003; Overton et al., 2008; Overton et. al, 2009). However, results from our mixing model showed that all sizes of striped bass in this study rely on benthic prey more heavily and were classified as mixed instead of pelagic (table 2).

DISCUSSION

With the rapid reestablishment of striped bass in northeast US waters over the past two decades, top-down forcing in coastal Gulf of Maine food webs has likely increases during the summer when striped bass migrate to feed. While all three size classes of striped bass considered here consumed a mixed diet of pelagic and benthic prey, feeding preferences of striped bass varied with size. Results also suggested that stomach contents may underestimate the importance of benthic prey to large striped bass. Even though the percent occurrence of benthic prey was consistently low across size classes, stable isotope analysis revealed an increasing reliance on benthic prey as striped

bass grew into the largest sizes. Results from the partial fullness index, a measure of volumetric importance of prey in the diet, suggest that this ontogenetic shift is related to higher predation rates on lobsters, which have a more benthic $\delta^{13}\text{C}$ signature. Thus, results suggest that while all three size classes consume benthic prey, the largest size class of striped bass rely more heavily on this prey type in southern Maine.

Pelagic prey size increased with striped bass total length (figure 3), and this trend has been observed for other groundfish species (Atlantic cod, spiny dogfish, *Squalus acanthias*; Scharf et al., 2000). Although striped bass consumed benthic and pelagic prey across a broad spectrum of sizes, the inclusion of small sized prey may be attributed to handling time associated with larger prey, and variation in predator foraging behavior (Scharf et al., 2000). Previous diet work has found that pelagic clupeid fish species (e.g., bay anchovies, menhaden, etc.) are most important for large striped bass, while invertebrates and shrimp make up the majority of the diet in smaller sized striped bass (Nemerson and Able, 2003; Walter and Austin, 2003; Overton et al., 2009). My findings in the Gulf of Maine are similar to results for striped bass diet in Massachusetts coastal waters around the North shore, Cape Cod bay and Nantucket sound, where diet of large striped bass was also dominated by American lobster and other crustaceans (Nelson et al., 2003). Explanations for the differences found in the diet of striped bass in the Gulf of Maine (including Massachusetts) compared to more southerly locations may be related to the change in availability of prey that striped bass encounter as they migrate to the Gulf of Maine during summer months (Walter et al., 2003; Nelson et al., 2003), and the high abundance of lobster in this region (Steneck and Wilson, 2001).

For fish, length - weight relationships (LWR) can provide insight into overall fitness and health of the animal, but also information on physiological and reproductive conditions (Lizama and Ambrosio, 2002). The scaling coefficient (b) from the LWR was examined here to address whether an ontogenetic shift in diet from mostly pelagic sources to more benthic prey had any effect on physiological condition in striped bass. I assumed that if this shift had a negative impact on striped bass bioenergetics, condition factor would decline with increasing size and b would be less than 3 (i.e., negative allometry). Alternatively, this diet shift may entail no change on striped bass bioenergetics ($b = 3$; isometry) or may have a positive effect ($b > 3$; positive allometry). Results indicated b values not different than 3 and tending towards greater than 3. This suggests, at the very least, that a shift towards more benthic prey for large striped bass in southern Maine waters had no negative effect on bioenergetics and possibly even a slight positive impact.

Striped bass, like all other predators, have higher $\delta^{15}\text{N}$ signatures than their prey. A trophic enrichment factor for $\delta^{15}\text{N}$ of 3.4 ‰ between the average striped bass and the average prey was verified here and agrees very well with published values (Minagawa and Wada, 1984; Vander Zanden and Rasmussen 2001). Typically, for most large marine predators, an increase in size results in a higher percentage of $\delta^{15}\text{N}$ and thus a higher trophic position (Cohen et al., 1993; Sherwood and Rose, 2005; Hussey et al., 2011). Contrary to my expectations, there was not a significant positive relationship between total length and $\delta^{15}\text{N}$ for striped bass. On the other hand, a positive relationship between total length and $\delta^{13}\text{C}$ did exist (figure 7). This result was consistent with stomach content data that revealed lobsters, but not other benthic prey items, to be present only in

the diets of striped bass larger than 65 cm. In other words, an apparent ontogenetic shift in diet for striped bass from less than 65 cm to greater than 65 cm involved a shift in carbon (i.e., pelagic to benthic) but not nitrogen signatures (i.e., trophic position). With the exception of herring, all other pelagic forage fish species have relatively similar $\delta^{15}\text{N}$ values to lobsters, and therefore similar trophic positions (figure 6). Therefore a shift from forage fish to lobsters should not involve a shift in $\delta^{15}\text{N}$ and trophic position. This prediction is notwithstanding any baseline variation in $\delta^{15}\text{N}$ that can result in higher baselines for benthic versus pelagic consumers (Sherwood and Rose 2005). If such baseline variation did exist, it would only decrease trophic position estimates for larger, more benthic striped bass. As such, trophic position would not be expected to increase with size in striped bass.

Results from a two source mixing model (table 2) show that even though striped bass feed mainly on pelagic fishes across much of their range (Walter et al, 2003), their $\delta^{13}\text{C}$ derived trophic designation is 'mixed' in Saco Bay, Maine. Percent reliance on benthic prey increased from medium to large and extra-large fish, and this finding, as well as the classification, are consistent with stomach content results since an increased presence of benthic prey (mostly lobsters) was found in the larger-sized striped bass. Even though medium fish had the lowest percent reliance on benthic prey, they can still be considered 'mixed' feeders as stomach contents did contain some instances of benthic prey (figure 1,2), and the mixing model estimated percent reliance on benthic prey to be 36%. Thus, although previous diet work has found that many small fish species are the most important prey items for the species across much of their range (Nemerson & Able 2003; Walter et al. 2003; Rudershausen et al. 2005; Overton et al. 2008), in coastal

Maine, a trophic designation of 'mixed' is more appropriate and reflects the importance of benthic prey during the summer months in this region.

The return of striped bass to New England waters is a success story for fisheries management in the region. However, we must also consider how the return of this predator species will affect populations of its prey (Hartman and Margraf, 2003). This study used both stomach content and stable isotope data to depict feeding relationships for striped bass while in southern Maine coastal waters and revealed that benthic prey is more important to their diet than has previously been found in other regions (Walter & Austin, 2003; Overton et al. 2008; Overton et al. 2009). My results suggest that juvenile lobsters (<38mm CL) are an important component of diet for larger sized striped bass. Thus, large striped bass may contribute to the natural mortality of lobsters in the Gulf of Maine. It is unclear if further increases in striped bass populations in coastal Maine will eventually negatively impact lobster populations. Juvenile lobsters did not display anti-predator responses when in the presence of striped bass (see Chapter 2), suggesting that lobsters are extremely vulnerable to increased predation by striped bass in the Gulf of Maine. By revealing potential linkages between the dynamics of these two managed species, the results from this study will be of value in predicting future impacts of rebuilt populations of striped bass and other highly transient predator species on resident resources such as lobster and crabs.

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TABLES AND FIGURES

Table 1.1: Frequency of occurrence (FO), percent volumetric contribution (V) and mean partial fullness index (mean PFI) prey items for each size class of striped bass

Prey Taxa	Striper Size Class								
	Medium			Large			Extra-Large		
	FO (%)	V (%)	Mean PFI	FO (%)	V (%)	Mean PFI	FO (%)	V (%)	Mean PFI
Forage Fish									
<i>Ammodytes americanus</i> (sand lance)	38.89	22.65	0.17	42.11	43.32	0.11	16.67	16.67	0.21
<i>Scomber scombrus</i> (mackerel)	16.67	15.64	0.84	10.53	8.07	0.49	16.67	16.67	0.27
<i>Clupea harengus</i> (herring)	0.00	0.00	0.00	5.26	5.04	0.30	0.00	0.00	0.00
<i>Menidia menidia</i> (Atlantic silverside)	5.56	4.40	0.04	0.00	0.00	0.00	0.00	0.00	0.00
Mean	15.28	10.67	0.26	14.47	14.11	0.23	8.33	8.33	0.12
Un Id Fish and Tissue									
<i>Un id fish</i>	22.22	14.58	0.10	10.53	6.29	0.21	33.33	23.04	0.68
<i>Un id tissue</i>	38.89	18.44	0.13	21.05	12.74	0.16	33.33	0.40	0.02
Mean	30.56	16.51	0.12	15.79	9.52	0.19	33.33	11.72	0.35
Crabs									
<i>Cancer</i> spp.	11.11	7.53	0.05	10.53	9.24	0.03	0.00	0.00	0.00
Mean	11.11	7.53	0.05	10.53	9.24	0.03	0.00	0.00	0.00
Lobster									
<i>Homarus americanus</i>	0.00	0.00	0.00	15.79	12.22	0.11	50.00	24.80	0.21
Mean	0.00	0.00	0.00	15.79	12.22	0.11	50.00	24.80	0.21
Shrimp									
<i>Crangon septemspinosa</i>	27.78	7.81	0.01	5.26	0.13	0.01	16.67	16.67	0.03
Mean	27.78	7.81	0.01	5.26	0.13	0.01	16.67	16.67	0.03
Other									
<i>Isopods</i>	5.56	0.76	0.00	5.26	0.34	0.00	0.00	0.00	0.00
<i>Worms</i>	0.00	0.00	0.00	5.26	0.08	0.00	0.00	0.00	0.00
<i>Rocks</i>	0.00	0.00	0.00	5.26	0.04	0.00	0.00	0.00	0.00
<i>Algae</i>	5.56	5.56	0.00	5.26	0.64	0.00	16.67	0.88	0.00
<i>Drift Wood</i>	5.56	0.94	0.00	5.26	0.04	0.00	0.00	0.00	0.00
<i>Shell Fragments</i>	0.00	0.00	0.00	5.26	0.36	0.00	0.00	0.00	0.00
Mean	2.78	1.21	0.00	5.26	0.25	0.00	2.78	0.15	0.00

Table 1.2: Estimate of percent reliance on benthic prey for each size class of striped bass based on stomach contents, and comparison of *a priori* trophic designation and $\delta^{13}\text{C}$ derived trophic designation.

Striper Size Class	Reliance on Benthic Prey (%) ^a	A priori trophic designation ^b	$\delta^{13}\text{C}$ derived trophic designation ^c
Medium	35.55	Pelagic	Mixed
Large	64.99	Pelagic	Mixed
Extra-Large	60.76	Pelagic	Mixed

^a: Percent reliance on benthic prey was determined for each size class of striped bass using the equation % reliance = $[(\delta^{13}\text{C}_f - \delta^{13}\text{C}_p) - (\delta^{13}\text{C}_b - \delta^{13}\text{C}_p)] * 100$; where $\delta^{13}\text{C}_f$, $\delta^{13}\text{C}_p$, and $\delta^{13}\text{C}_b$ are the mean $\delta^{13}\text{C}$ values for striped bass, pelagic prey species, and benthic prey species respectively (Vander Zander and Vadebonceour, 2002).

^b: A priori trophic designation determined based on previous diet work for striped bass

^c: $\delta^{13}\text{C}$ derived trophic designation were determined based on the % reliance of benthic prey: <25% benthic reliance is pelagic; 25-75% benthic reliance is mixed; >75% benthic reliance is benthic (Sherwood and Rose, 2005).

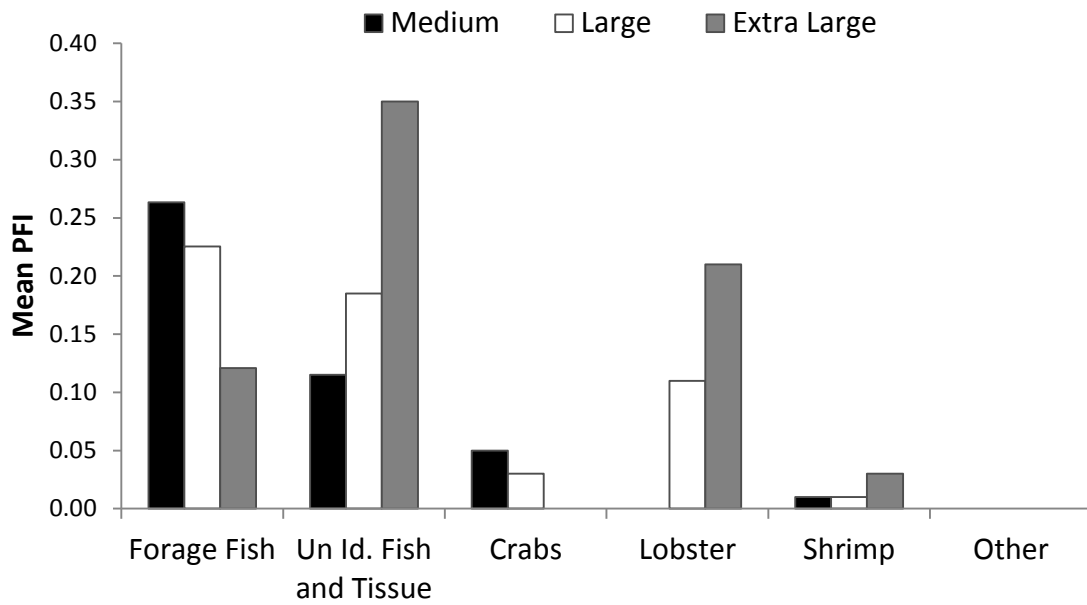


Figure 1.1: Mean PFI for all major prey categories found in medium (n=18) large (n=19) and extra-large (n=6) striped bass.

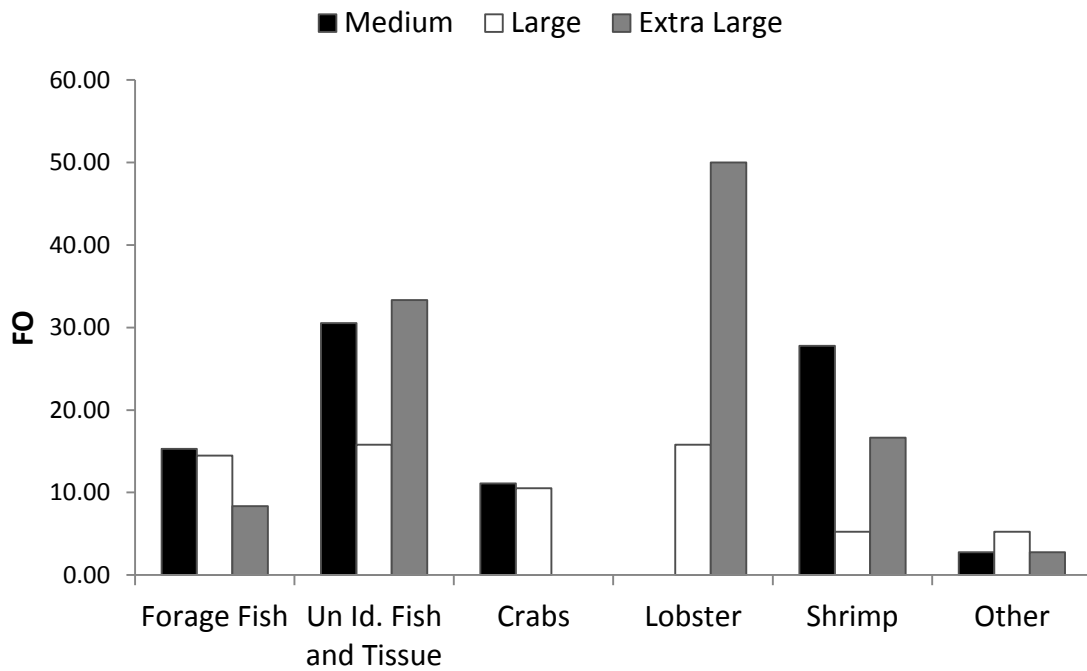


Figure 1.2: Frequency of occurrence (%) for the 6 major prey categories found in medium (n=18) large (n=19) and extra-large (n=6) striped bass

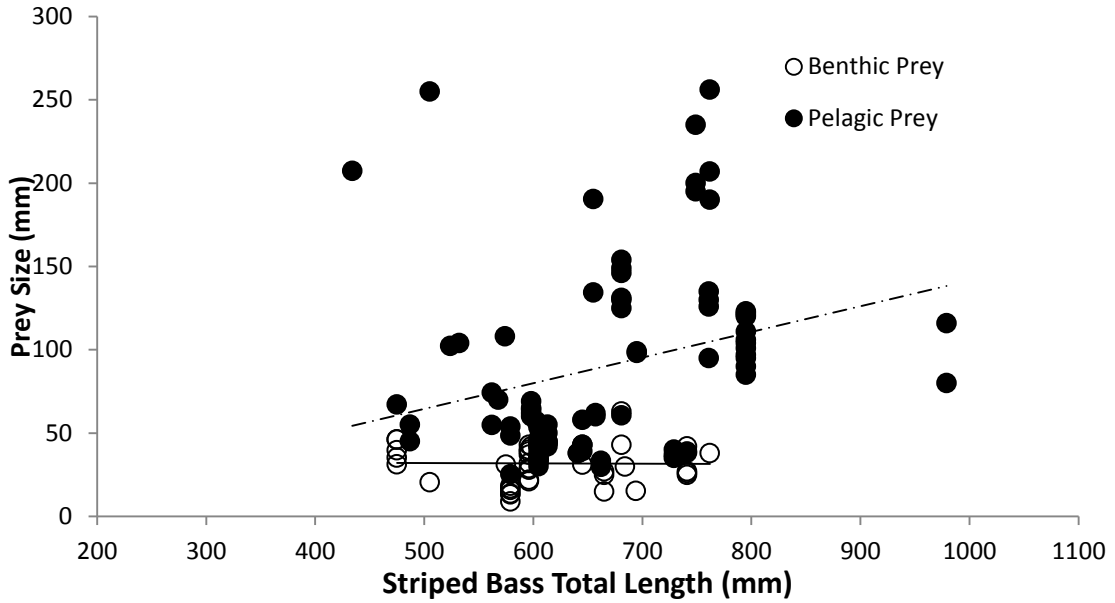


Figure 1.3: Prey size vs. striped bass total length for benthic vs. pelagic prey items; Benthic prey size (solid regression line) = $33.12 - 0.00x$ StripedBassTotalLength; $r^2=0.00$, $p>0.9$, $n=47$); Pelagic prey size (dashed regression line) = $-54.01 + 0.19x$ StripedBassTotalLength; $r^2=0.12$, $p>0.0001$, $n=83$)

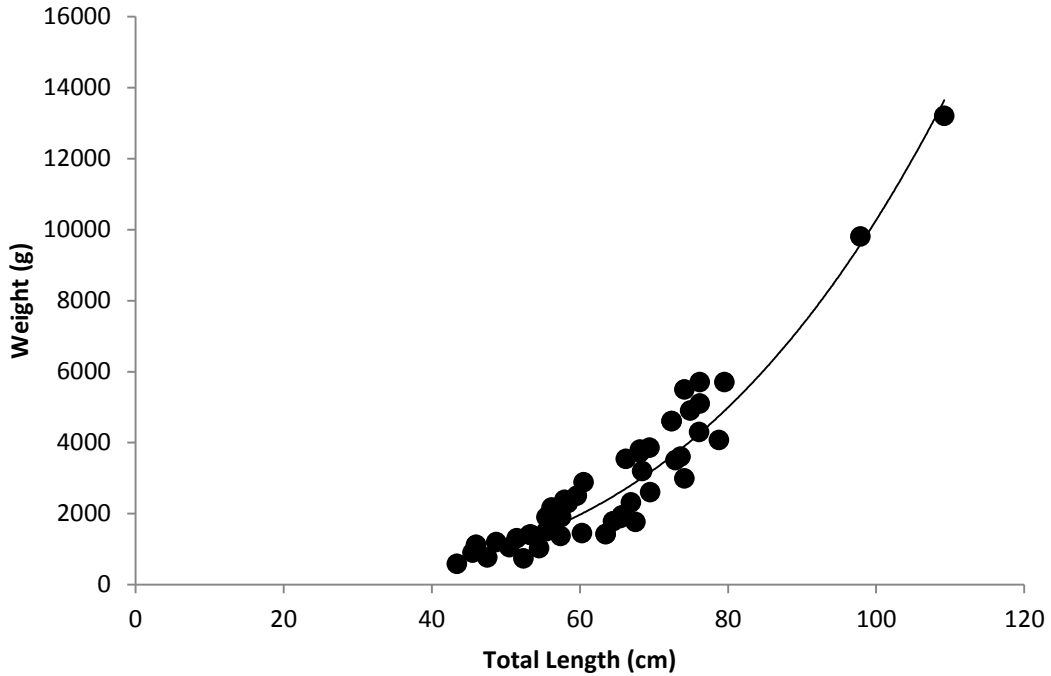


Figure 1.4: Weight length power relationship for striped bass samples. Weight = $0.0035 * \text{total length}^{3.28}$; $R^2=0.8503$, $n=47$

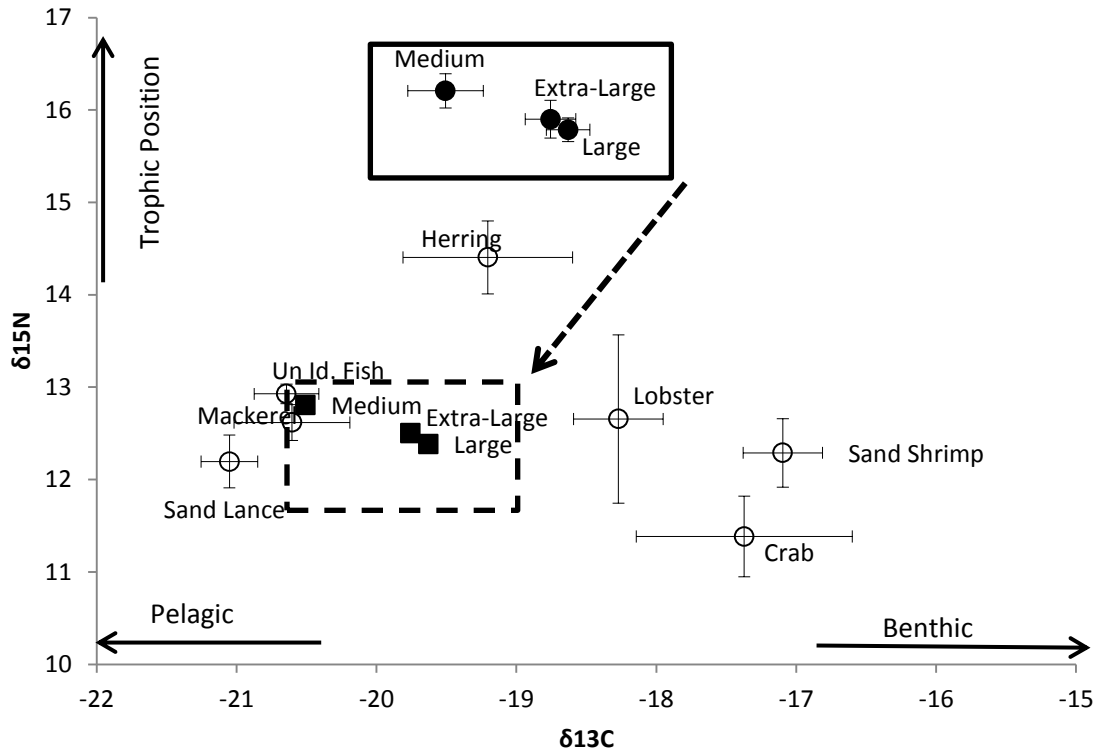


Figure 1.5: Mean $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ for striped bass (solid circles) and common prey species (open circles). Solid box outlines sampled values for striped bass tissue; dotted box outlines theoretical values for striped bass (black squares) after accounting for fractionation of isotope signatures between prey and predator.

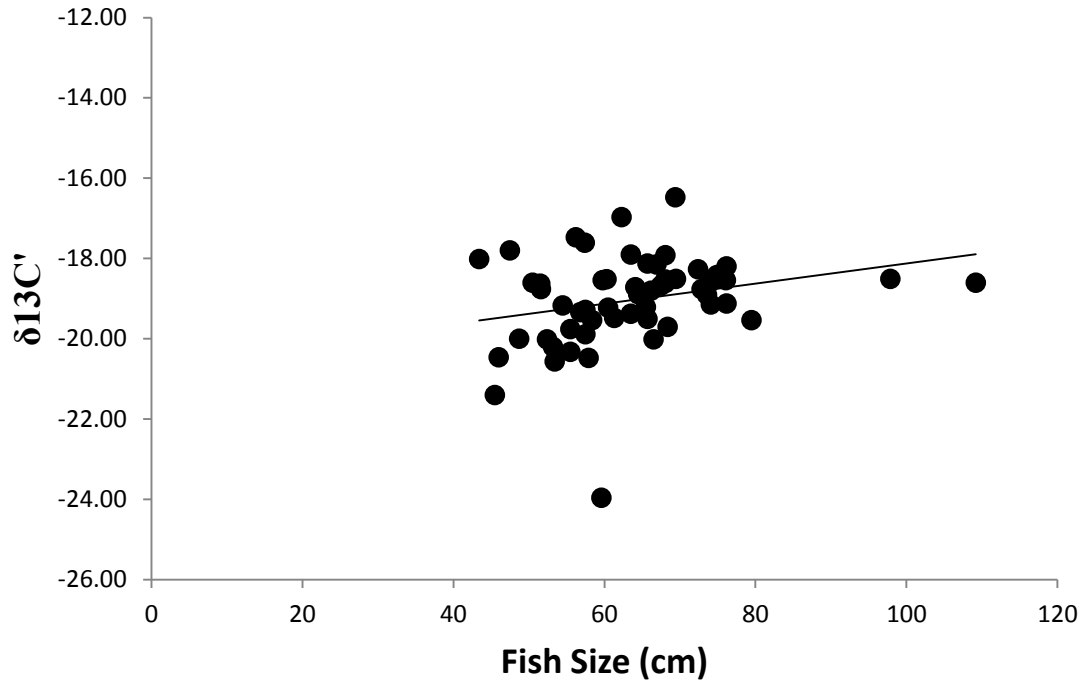


Figure 1.6: $\delta^{13}C'$ vs. Fish Size (cm) for all striped bass samples. $\delta^{13}C' = -20.83 + 0.025 * \text{FishSize}$; $r^2 = 0.05$, $p < 0.05$, $n = 56$

CHAPTER 2

INFLUENCE OF PREDATOR IDENTITY ON THE STRENGTH OF PREDATOR AVOIDANCE RESPONSES IN JUVENILE LOBSTERS

ABSTRACT

Predators affect prey species by capturing and consuming prey, and can also influence population dynamics by triggering predator avoidance responses. The American lobster, *Homarus americanus*, is an important benthic consumer in the Gulf of Maine and supports the most valuable fishery in New England, but is also an important prey item for many fish species. There is substantial interest in restoring large predator fish species to the Gulf of Maine, and these predators may impact lobster populations through consumptive and behavioral effects that are likely to vary with lobster size. We conducted a series of experiments to explore the response of juvenile lobsters to a range of predators. First, lobster tethering experiments were used to examine the susceptibility of juvenile lobsters to predation in Saco Bay, Maine, and revealed that small juvenile lobsters (measuring less than 45mm) are most vulnerable to predation. Second, small juveniles were exposed to three different fish predators separately in experimental mesocosm tanks: (Atlantic striped bass [*Morone saxatilis*], Atlantic cod [*Gadus morhua*] and sea raven [*Hemitripterus americanus*]). Juvenile lobster behavior was quantified by both direct observation and video monitoring. The strength of predator-induced responses from lobsters varied greatly among predator species. Lobsters exposed to striped bass

exhibited no anti-predator response, but in the presence of cod or sea ravens reduced movement and spent more time in shelter. Such behaviorally-induced predator effects can result in less foraging activity, which may translate into reduced lobster growth and reproduction. Understanding such effects is critical for moving toward a multi-species or ecosystem-based management approach.

INTRODUCTION

Predator-prey interactions are important drivers of community structure (Hairston et al. 1960; Paine 1966; Carpenter et al. 1985; Siddon & Witman 2004). Historically, predator-prey interactions were thought to be predominately density-mediated, however, more recent evidence suggests that predators may cause prey to alter their behavior to evade predation (Lima & Dill 1990; Abrams 1995; Werner & Peacor 2003; Trussell et al., 2006). Altered behavior often influences the prey's capacity to forage successfully, and can thus affect prey population dynamics (Werner & Peacor 2003; Schmitz et al. 2004; Trussell et al. 2006; Schmitz 2008). Consequently, overall prey responses represent a trade-off between the risk of being consumed (Lima & Bednekoff 1999) and the cost of anti-predator strategies such as stopping or altering risky feeding behavior or moving to less profitable habitat (Lima & Dill 1990; Werner & Anholt 1993; Abrams 1995; Werner & Peacor 2003; Trussell et al. 2006).

Prey utilize different types of anti-predator strategies depending on predator identity and other risk factors, and predator-specific avoidance strategies likely reflect differences in predator foraging and hunting strategies (Schmitz et al. 2004). Schmitz (2005) classified the following predator foraging modalities: sit-and-wait predators remain in a

fixed location for extended periods of time and ambush a prey species when it moves within close attacking range; sit-and-pursue predators are sedentary, but actively seek a prey species when it is within the immediate location; and active predators are highly mobile and have much larger foraging arenas than the previous two modalities. Schmitz et al. (2004) hypothesized that sit and wait predators emit cues that are more predictable than those from highly mobile pursuit predators because they remain in a fixed location, and consequently should evoke stronger predator-avoidance behaviors in prey. Schmitz (2008) found support for this hypothesis in old grassland fields where active hunting spiders elicit little to no anti-predator response from grasshoppers, but sit-and-wait spiders induce grasshoppers to seek refuge in less desirable, but safer, feeding areas. It is unknown whether predators with different foraging modalities emit different cues or whether the ability of the prey to exploit the cue varies. Further, it is unclear if marine aquatic prey communities respond accordingly to these different types of predators.

The American lobster, *Homarus americanus*, is a decapod crustacean that after settling on the benthos as a small juvenile is predominantly shelter based (Stein & Magnuson 1976; Wahle 1992; Brown 2007; Hovel & Wahle 2010). Many fish predators are known to prey on juvenile American lobster, and size is an important predictor of survival as larger lobsters are less vulnerable to predation (Wahle 1992). Predator-avoidance behaviors in crustaceans generally attenuate with larger body size. Juvenile crustaceans typically respond to fish predators by decreasing their activity levels and remaining sheltered while larger individuals exhibit no change in behavior (crayfish: Stein & Magnuson 1976; American lobster > 40 mm carapace length [CL]: Wahle 1992).

McMahan (2011) found that small adult lobsters (51-83 mm CL, suggesting that the predator cue may not always relay size information (i.e., actual risk).

The American lobster supports one of the most valuable fisheries in New England, and commercial landings continue to increase in many portions of the Gulf of Maine (Steneck & Wilson 2001; Jackson et al. 2001). Although the mechanisms driving the recent uptick in the abundance of adult lobsters are not completely clear, factors affecting the distribution of juveniles and their establishment on the benthos are thought to be predictive of the abundance and distribution of adults (Steneck & Wilson 2001). Many fish, such as striped bass (*Morone saxatilis*) and Atlantic cod (*Gadus morhua*) feed on juvenile lobster (Collette & Kelin-MacPhee 2002), and within the last ten years, the abundances of some large fish species have changed. Atlantic coast migratory stocks of striped bass have increased from under 10 million to over 52 million fish (ASMFC, 2010), and management strategies that have been enacted to restore Atlantic Cod populations. The abundance of lobster may be inversely related to that of coastal groundfish (Steneck 1997). Specifically, lobsters have been under fairly low predation pressure over the past couple of decades when populations of many large predators were in decline (Jackson et al. 2001; Steneck 1997; Witman & Sebens 1992).

I investigated the response of juvenile lobsters to the presence of different predators to better understand the effects large fish predators may have on lobsters in the Gulf of Maine. Specifically, I tested whether the size of juvenile lobsters affects their susceptibility to predation in the field, and then conducted laboratory experiments investigating the anti-predator responses of juvenile lobster to striped bass, Atlantic cod and sea raven (*Hemitripterus americanus*). These three predators were chosen because

they all are currently, or were historically, important predators in the Gulf of Maine that feed on juvenile lobster (Collette & Kelin-MacPhee 2002) and have different foraging modalities. I hypothesized that lobsters would increase the proportion of time sheltered in the presence of fish predators, and that the proportion of time spent sheltered would be greatest in the presence of sea raven, lowest in the presence of striped bass, and intermediate in the presence of cod. In addition, I predicted that the variation in the proportion of time sheltered would reflect differences in predator identity and foraging strategies.

METHODS

Size-Specific Predation Rates

Lobster tether experiments were conducted in August 2011 to determine what sizes of juvenile lobsters are most vulnerable to predation. Juvenile lobsters measuring between 26mm and 58mm carapace length (CL) were collected from rocky intertidal habitats in Biddeford Pool and Cape Elizabeth, Maine, and housed in flowing seawater tanks at the University of New England's Marine Science Center in Biddeford, Maine prior to the inception of the field experiment. One day prior to conducting the tethering experiment, lobsters were removed from the water and bridles made from mono-filament fishing line were tied between the 2nd and 3rd pair of walking legs. Bridles were also affixed to the top of the carapace with cyanoacrylate glue, and a small loop was tied into the bridle between the walking legs for quick attachment to the tether lines. At four areas within Saco Bay, Maine (43°29'24.41N 70°20'26.99W), two tether lines (each with 20 juvenile lobsters) were deployed on sand bottom at 7-14m depths. Tether lines were

stretched and anchored at either end to ensure the line rested on the bottom. All lobsters were re-measured and attached to the tether line just before deployment. Each line was approx. 100 meters long and lobsters were spaced at 5-m intervals. After 24 hours, all tether lines were retrieved, and if a lobster was missing a successful predation event was determined by the existence of a “carapace disk” remaining on the line where the cyanoacrylate glue and bridle had been affixed to the lobster the previous day. Any lobster still attached to the tether line was re-measured and then released.

Lobsters were grouped into 3-mm size classes to examine how survival varied across all sizes of lobster deployed. The percent survival for each size class was determined from the number and sizes of lobsters deployed vs. recovered. Linear regression was then used to determine if lobster survival significantly increased with each 3-mm size group.

Laboratory Behavior Assays

Juvenile lobster behavior was observed under the presence of 3 different predators: striped bass, Atlantic cod and sea raven and a control (no predator) during October and November 2011. Sea ravens are sit-and-pursue predators that are highly sedentary and will remain in rocky areas for long periods of time (Collette & Kelin-MacPhee 2002), but have been observed to ambush and pursue their prey (Martinez 2003). By contrast, Atlantic striped bass are highly active roaming predators and feed in many habitats on a variety of prey types (Walter et al. 2003). Atlantic cod use both sit-and-pursue and active foraging strategies (Sherwood & Grabowski 2010). Striped bass and Atlantic cod were collected via hook and line sampling while the sea ravens were

collected from lobster traps by local lobsterman. All fish were collected from the Gulf of Maine and housed in flowing sea water tanks at the University of New England. Sea Ravens used in trials ranged from 34-44cm total length, cod ranged from 43-63cm total length, and striped bass ranged from 56-75cm total length. Average predator length from all treatments was 50cm. Juvenile lobsters ranging in size from 26mm to 45mm carapace length were collected from rocky intertidal habitats in Biddeford Pool Maine and housed at the University of New England. This lobster size range was used because it corresponded to those sizes of lobster with the lowest survival rates during the tethering experiments. Lobsters and fish predators were starved for at least 48 hours before participating in a trial. Although some of the fish in the present study were too small to consume the juvenile lobsters that were used, other behavior studies with American lobster have used smaller or similar sizes of fish. (Wahle, 1992; Wahle and Steneck, 1992; McMahan, 2011).

Behavior trials were conducted in a large continuous flow through tank at the Marine Mammal Rehabilitation Center at the University of New England. The experimental tank measured 3.5m by 4.8m and was filled to a depth of 1.5m (Figure 1). Four individual cobble shelters were spaced approximately 0.7m apart along the back side of the tank and were constructed using cut sections of 7.6 cm diameter PVC pipe and cobble stones to provide refuge for the lobsters. Prior to the commencement of each trial, four lobsters were measured and allowed to acclimate to the experimental tank for 2 hours. After the acclimation period, 5 dead herring were placed in the center of the tank to encourage the lobsters to feed, and a fish predator was measured and added to the system. Control treatments were initiated in the same manner, only no predator was

placed in the system after the addition of bait. All trials began after the addition of the predator and continued for 13 hours. Natural sunlight from windows provided light during day hours, and red darkroom safe lights were used to illuminate the room during night hours to permit observations and video recording while providing minimal light cues to experimental animals.

Canon R200 camcorders were stationed at two locations on the side of the tank to record lobster movements throughout the trial. In addition to video recordings, direct visual observations were conducted every 10 minutes over the course of a 2 hour period in the middle of the day (between 11:30am and 2pm) and at night (between 7pm and 10pm). During each observation, the number of lobsters in shelter or actively moving around the tank was noted. New lobsters were used for each trial, and all predators were replaced after each trial with the exception of 2 sea raven, which were allowed to recover for 48 hours in a holding tank before use in a second trial. At the completion of each trial, any remaining bait was removed, and the experimental tank was drained, rinsed with fresh water, and refilled. A total of 5 control, 5 striped bass, 5 cod and 5 sea raven trials were conducted.

Laboratory Behavior Assay Analyses

During direct observations, the number of lobsters in shelter or number of lobsters moving at each 10 minute period was used to determine the proportion of lobsters either moving or sheltered in the tank. To supplement the direct observations, video recordings of each trial were reviewed and each individual lobster was tracked for 13 hours. The first 6.5 hours of each video were conducted during daylight hours, while the second 6.5

hours occurred at night. The amount of time lobsters spent in shelter or moving around the tank was determined for each lobster. As only 2 types of behavior were categorized (either in shelter or moving around the tank), once the % of time spent sheltering was determined the % of time out of shelter could be determined as 100 - % time sheltered for each lobster. All percentage data were arc-sin transformed in order to meet the assumption of homogeneity of variances, and a one-way ANOVA was performed using treatment as the factor and percentage of time spent in shelter as the dependent variable, followed by Tukey's post hoc multiple comparisons of the means. Statistical analyses were initially conducted with and without the two trials involving recycled sea ravens. Because excluding those two replicates did not alter the outcome, they were included in the final analysis.

RESULTS

Size-Specific Predation Rates

A total of 159 juvenile lobsters ranging in size from 26 to 58mm carapace length were deployed on the benthos. Of these 159 lobsters, 80 succumbed to predation while the remaining 79 survived the tethering experiments. Lobsters were grouped into 3mm size bins and linear regression showed survival increases with juvenile lobster size ($r^2=0.97$, $p<0.001$, $n=1$; figure 2). Based on this result, the bottom half of the size distribution (< 44mm carapace length) was deemed most susceptible to predation, and these sizes were used in subsequent predator avoidance experiments.

Laboratory Behavior Assays

Lobster behavior varied significantly with both time of day and predator treatment. During the day, there was no significant effect of predator treatment on the amount of time juvenile lobsters spent in shelter (direct observations: ANOVA: $F_{3,19}=1.49$, $p > 0.249$; video observations: ANOVA: $F_{3,73}=0.41$ $p > 0.747$), and all lobsters spent the majority of the trial time in shelter and not moving around the tank. At night, there was a significant effect of predator treatment on the amount of time spent in shelter (direct observations: ANOVA $F_{3,19}=16.77$, $p < 0.001$; video observations: ANOVA $F_{3,73}=7.85$, $p < 0.001$) (Figure 3, 4). At night, control and striped bass treatments did not differ from each other; in addition, cod did not differ from sea raven treatments (Tukey $p > 0.05$ for both direct and video observations). However, control and striped bass treatments differed significantly from cod and sea raven treatments (Tukey $p < 0.05$ for both direct and video observations).

DISCUSSION

Body size is an important factor in determining the outcome of predator-prey interactions and can effect prey survival in a range of species (Costa 2009; Holmes & McCormick 2010). Lobsters are shelter dependent as juveniles, but this dependency relaxes as lobsters become more mobile, body size increases, and they are released from predation pressure (Wahle 1992; Wahle & Steneck 1992). My results confirmed a body-size dependency for the risk of direct predation (Figure 2), and support the idea that lobsters can grow into an effective size refuge.

The tethering experiments gave me insight on the relative risk of early ontogeny predation in a field setting. To understand how lobsters may perceive and respond to the

risk of predation, I conducted a series of experiments exposing juvenile (vulnerable) lobsters to a range of different predators. I found that juvenile lobsters employed varying levels of anti-predator responses depending on predator identity and time of day. During the day, no noticeable difference in antipredator behavior was observable among treatments. This is because lobsters are primarily nocturnal (Karnofsky et al. 1989; Wahle 1992; Scopel et al. 2009) and in this experiment, spent the majority of their time in artificial refuge habitat during the day.

When lobsters were more active (i.e., night), I observed major differences in their behavior among treatments and controls. It should be noted that these experiments were not designed to tease apart which cues may be driving lobster responses to predators. The fact that lobsters responded to all three predator species when encountered at short range (< 1m, typically exhibiting an aggressive claw display; data not analyzed) suggests that lobsters have a refined ability to detect predators in close proximity. This may involve visual, tactile, sound or olfactory cues. Visual and tactile cues are likely more developed for close-up encounters. For example, Gherardi et al. (2010) showed that lobsters use sight to evaluate risk from conspecifics during agonistic interactions. However, it is well known that lobsters exploit scent cues to detect and evade predators (Wahle 1992), presumably at distances greater than could be detected by other cues. Response to olfactory cues from predators involves increased shelter seeking behavior (Wahle 1992; Spainer et al. 1998) as opposed to more acute and proximal “fight and flight” type responses. In fact, previous experiments have shown that juvenile lobsters increase shelter use when exposed only to water from tanks housing predators (Wahle 1992, Grabowski, unpublished data). For the remainder of this discussion, I assume that

olfaction is the primary mechanism by which juvenile lobsters detected the presence of the predators that induced greater shelter use in our experiments.

Differences in the strength of anti-predator responses in juvenile lobsters at night (i.e., sheltering) are largely consistent with my predictions regarding the effects of predator identity and foraging modality on prey behavior. Lobsters significantly increased shelter use in the presence of cod and sea ravens, compared to controls, but did not alter their behavior for striped bass. Given that all predators are likely to emit a scent cue (e.g., kairomones) and that my experimental setting was probably small enough so that this cue would become widely dispersed throughout the tank, the difference in response to the three predators was likely due to differences in the ability of lobsters to either perceive the scent or in their ability to assess the relative risk associated with the scent (note that by ‘assess’ I imply an evolved or adapted response). Due to their foraging strategy (sitting and waiting and/or slowly browsing near the bottom), cod and sea raven may remain within the same location for an extended period. Thus, any olfactory cue emitted will dissipate out from one location (Bouskila 2001; Schmitz et al. 2004) and likely trigger a “proximal warning” signal in lobsters before a predator is within striking range. In other words, lobsters may “recognize” the scent of a cod or sea raven as an imminent danger that can be avoided by seeking shelter. Previous work has indicated that the American lobster also responds to other sit-and-pursue predators such as the sculpin (*Myoxocephalus aeneus*) by increasing time spent in shelter (Wahle 1992). Similar decreases in foraging, increases in shelter use, or shifts in habitat usage have been demonstrated in response to other aquatic and terrestrial sit-and-pursue predators (Grabowski 2004, Schmitz 2008). It should be noted that cod also employ active cruising

while foraging (similar to striped bass), although this behavior may be more associated with offshore migrants (Rose 1993) and less so with inshore resident “ecotypes” (Sherwood and Grabowski 2010). For this study, cod were captured at a specific inshore location where animals may be highly sedentary like sea raven (similar to the cod studied by Lindholm and Auster [2007]) in the western Gulf of Maine).

Unlike cod and sea raven, striped bass use a highly active foraging strategy. They are transient to the Gulf of Maine (summer months only in southern Maine), primarily occupy the pelagic zone well off the bottom and feed on pelagic forage fish, lobsters and other crustaceans (Walter et. al. 2003; Grothues et al. 2009), and may be absent from the Gulf of Maine entirely for extended periods of time (years or decades) due to contractions in their population (e.g., most recent stock decline; ASMFC 2010). Thus in southern Maine, lobsters may not recognize the scent of striped bass as a meaningful risk due to a lack of familiarity, even though lobsters are prevalent in the diet of striped bass here and elsewhere in the Gulf of Maine (Nelson et al. 2006; see Chapter 1). Lobsters also may not recognize the scent of a striped bass because they are incapable of effectively avoiding this predator since the time between arrival of scent and the actual predator is too short to undertake any meaningful evasive action. In other words, lobsters may not have evolved a response because they are consumed before they can respond to the scent of a striped bass. There is likely little benefit to seeking shelter, and consequently reducing time spent foraging, even if a lobster does recognize the scent and survive an encounter since a highly active predator such as the striped bass has likely moved on to another location.

Upon smelling a cod or sea raven, on the other hand, the lobsters increased refuge use at the cost of time spent foraging. These less mobile fish predators forage in a fixed area and on the bottom thereby posing a more imminent and localized risk, so that seeking shelter in response to the detection of their scent cues likely enhances lobster survivorship. Future experiments with a wider range of predator and prey species could be used to test whether predator foraging modality is a general indicator of shelter seeking behavior in prey such as lobsters, and to isolate the effects of visual vs. chemosensory predator cues. Also, it would be informative to conduct similar experiments with lobsters further south in their range where encounters with striped bass may be more frequent and evenly spaced throughout the year.

Predators can influence community structure and ecosystem functioning via non-consumptive effects (Werner & Peacor 2003; Schmitz 2005). However, the strength of these non-consumptive effects likely varies with predator identity, foraging modality and time of day. Reduced lobster activity levels could lead to reduced foraging success, growth and reproductive effort, and ultimately mortality, which likely would have population level implications. Juvenile lobsters may be especially vulnerable to predation from striped bass, as they did not show a strong anti-predator response to this species. Studies examining striped bass diet have found that the American lobster is an important component of the diet of striped bass in New England especially in summer (Nelson et al. 2003; see Chapter 1). However, further work is needed to determine the effects of striped bass on lobster population dynamics in coastal Maine and other overlapping portions of their ranges. With the return of striped bass, and other large predators, to Southern Maine, efforts to parse whether these predators have consumptive

and non-consumptive effects on lobsters will assist efforts to study and manage these species. In particular, exploring all aspects of these species' interactions is crucial so that we may continue to restore large predatory fish populations to southern Maine without adversely affecting lobster populations and associated fisheries.

Acknowledgments

I thank Keith Matassa and the University of New England's Marine Animal Rehabilitation Center staff for the use of its tanks and resources as well as Curt Brown, Jay Turnure, Troy Thibeau, Tim Arienti, Shaun Gill, Caitlyn Little and Meagan Sims. Funding was provided by the University of New England and the National Science Foundation.

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FIGURES

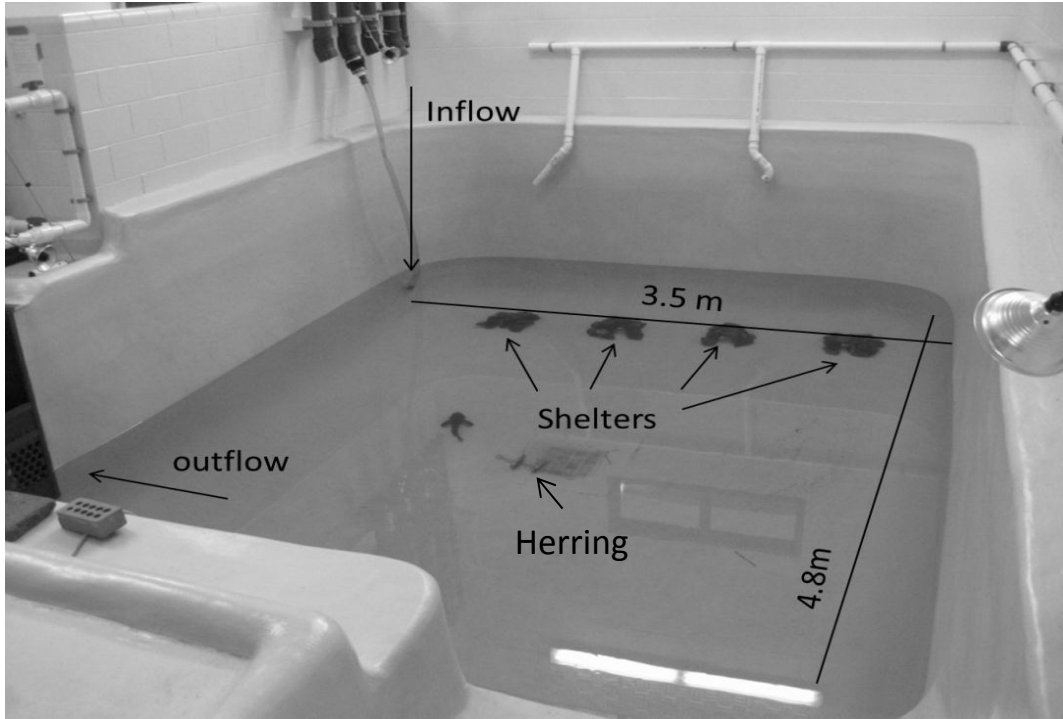


Figure 2.1:Picture of Mesocosm tank design

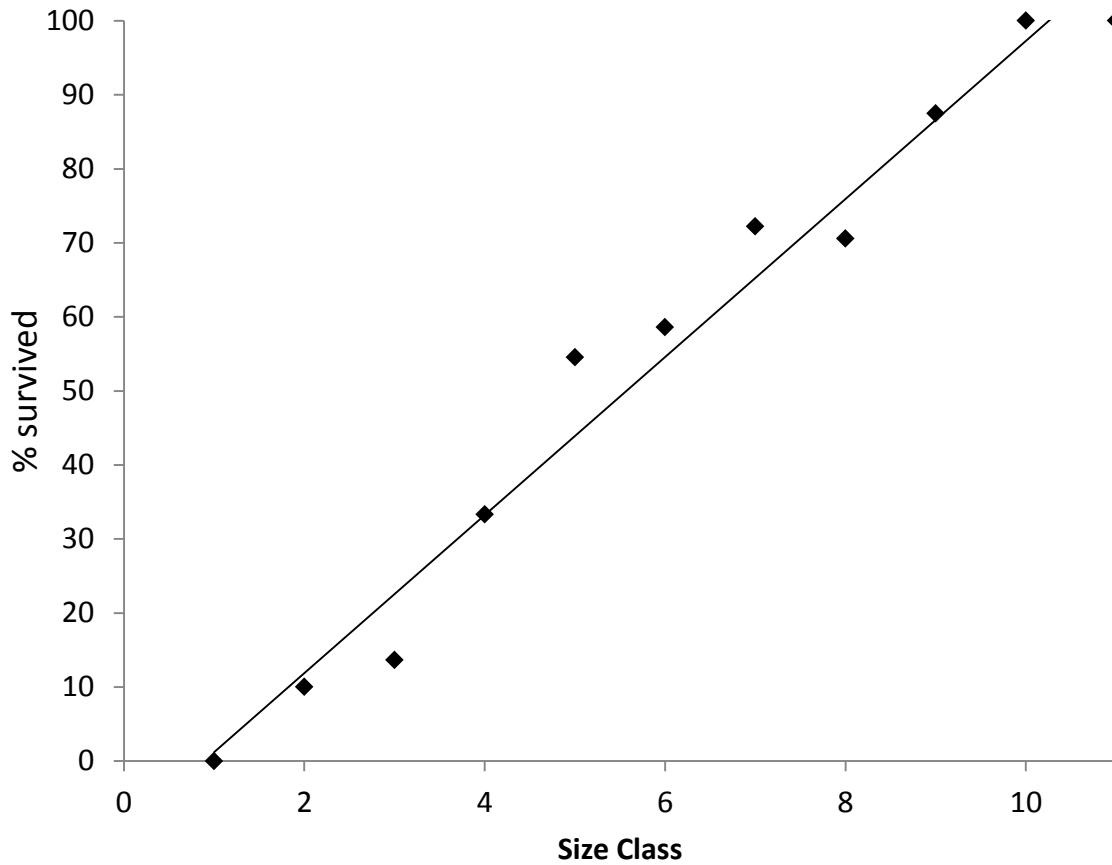


Figure 2.2: % of lobsters survived during tethering experiments. Size Class represent the following lobster sizes (carapace length): 1= 26-28mm; 2=29-31mm; 3=32-34mm; 4=35-37mm; 5=38-40mm; 6=41-43mm; 7=44-46mm; 8=47-49mm; 9=50-52mm; 10=53-55mm; 11=56-58mm. Total number of lobsters deployed per carapace group is indicated above each point on the graph. ($r^2=0.9719$, $p < 0.001$, $n=11$)

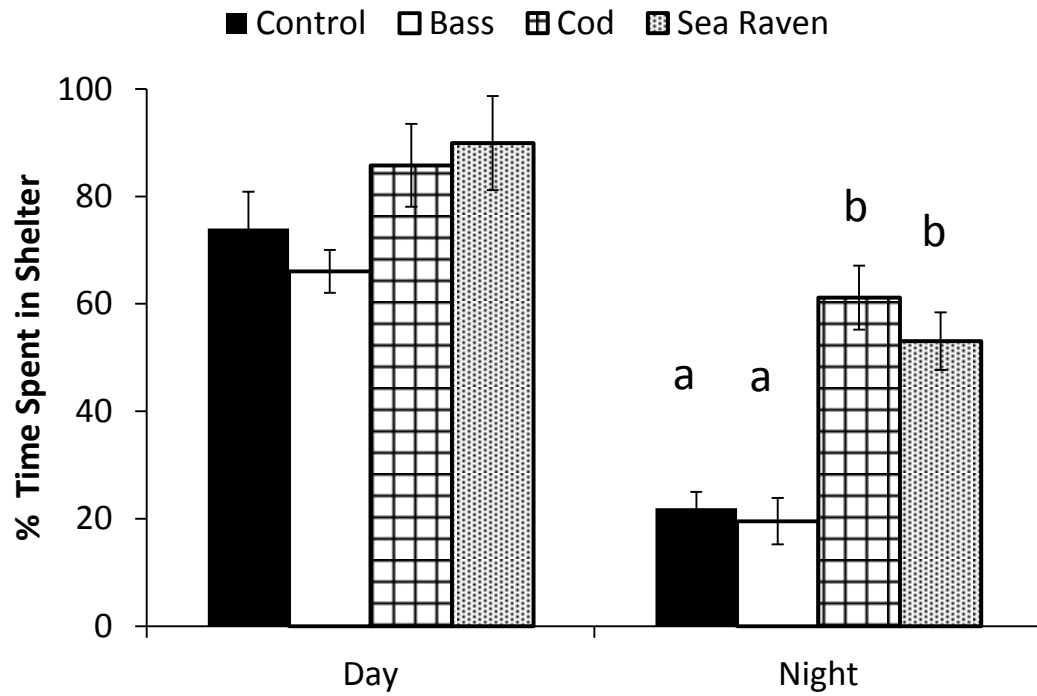


Figure 2.3: % of time lobsters spent in shelter during the day and night as assessed via direct observation. N=5 control, 5 striped bass, 5 cod, and 5 sea raven trials. Treatment means in the night period that did not differ from one another share a letter. Error bars represent standard error of the mean.

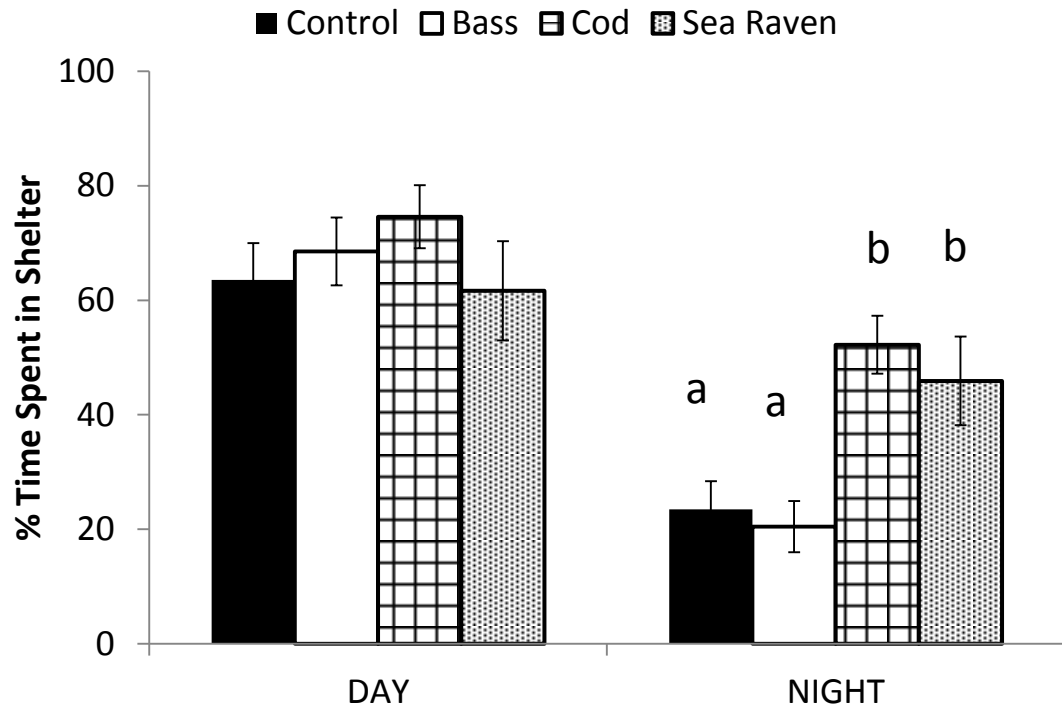


Figure 2.4: % of time lobsters spent in shelter during the day and night as assessed via video observation. N=5 control, 5 striped bass, 5 cod, and 5 sea raven trials. Treatment means in the night period that did not differ from one another share a letter. Error bars represent standard error of the mean

APPENDIX

Institutional Animal Care and Use Committee
Renee LeClair, Chair

Biddeford Campus

11 Hills Beach Road
Biddeford, ME 04005
(207)602-2244 T
(207)602-5905 F

Portland Campus

716 Stevens Avenue
Portland, ME 04103

IACUC Protocol Number: UNE-20110616WILKE

TO: Erin Wilkinson

FROM: Renee LeClair, Ph.D.

DATE: October 19, 2011

RE: Protocol Amendment Approval

Notice of IACUC Review - APPROVAL

Your October 18, 2011 amendment to the protocol entitled "**Lobster and Striped Bass Interactions in Southern Maine**" has been reviewed by the UNE Institutional Animal Care and Use Committee (IACUC). Your project amendment has been approved with the following conditions:

1. You are approved to conduct this research only during the period of approval cited below.
2. You will conduct the research according to the plan and protocol you submitted.
3. You will immediately inform the IACUC of any injuries or near injuries to researchers or animal handlers that occur in the course of your animal care or use.
4. You will immediately inform the IACUC of any adverse events that arise in the course of your research including but not limited to animal illness or unexpected animal death.
5. You will immediately request approval from the IACUC for any proposed changes in your research. You will not initiate any changes until they have been reviewed and approved by the IACUC.
6. If your research is anticipated to continue after **6/15/2012**, you must submit a continuing review form at least 30 days prior to this date. A complete *de novo* review is required on a triennial basis at least 60 days prior to the expiration date of **6/15/14**.

7. You are reminded that the IACUC requires animals that would otherwise experience severe or chronic pain or distress that cannot be relieved will be painlessly killed at the end of the procedure or, if appropriate, during the procedure.
8. You will follow all IACUC approved euthanasia procedures.
9. You will follow all IACUC approved procedures for the disposal of carcasses.
10. You will notify the IACUC if you terminate the study before completing it, or upon concluding it.

General Safety Requirements:

1. Accidents, injuries or illness resulting from the use of toxic, biological, or radioactive substances must be reported to the IACUC and the UNE Environmental Health and Safety department immediately.
2. Any injuries or near injuries to researchers or animal handlers that occur in the course of your animal care or use must also be immediately reported to the IACUC.
3. Appropriate protective equipment and procedures for use and handling of toxic, biological, or radioactive substances must be maintained at all times.
4. Appropriate ABSL's and/or BSL's will be maintained at all times, including the use of appropriate biosafety cabinets.

The University appreciates your efforts to conduct research in compliance with the federal and state regulations that have been established to ensure the protection of animal subjects in research, teaching and testing.

The IACUC wishes you well with your research. Please feel to contact William Harrison, Director of Research Integrity, if you have any questions about the IACUC process or continuing review procedures at 602-2244, or by email at wharrison@une.edu

Approval Period: 06/16/2011-06/15/2014

Continuing Review required before: 06/15/2012

Complete *de novo* Review required before: 06/15/2014

Sincerely,



Renee LeClair, Ph.D.
IACUC Chair



PAUL R. LEPAGE
GOVERNOR

STATE OF MAINE
DEPARTMENT OF
MARINE RESOURCES
MARINE RESOURCES LABORATORY
P.O. BOX 8, 194 MCKOWN POINT RD
W. BOOTHBAY HARBOR, MAINE 04575-0008

PATRICK KELIHER
ACTING COMMISSIONER

October 21, 2011
SPECIAL LICENSE NUMBER 2011-60-00
Amendment #4

Acting under the authority vested in the Commissioner of Marine Resources by virtue of 12 M.R.S. §6074, I hereby issue subject to renewal a Special License to **ERIN WILKINSON**, student at the University of New England (UNE), 11 Hills Beach Road, Biddeford, Maine 04005-9599. This Special License exempts said ERIN WILKINSON, while conducting a research study to examine the diet of striped bass and the relationship between lobsters and striped bass to determine the extent striped bass are consuming lobster, if lobster still constitutes a significant portion of the striped bass diet in Saco Bay. The exemptions include those portions of Marine Resources laws and regulations pertaining to 12 M.R.S. §6431, which makes it unlawful to take, transport, or possess lobsters less than legal size; §6432 method of take; and Chapter 42.02 pertaining to size and bag limits for striped bass. This Special License is issued subject to the following conditions:

1. **Who: UNE: Erin Wilkinson**, Dr. Phil Yund, Shaun Gill, Tim Arienti; GRMI: Curtis Brown Jr. , Graham Sherwood , Jonathan Grabowski; Vessels (owner UNE): 23' R/V LLYR (ME 125J) and 18' vessel (ME 16EJK), *CFVS inspections expire 02-08-12 Vessel (owner GMRI) 22' ME162VB/O.N. SCG22508A909, CFVS inspections expire 07-31-13
2. **What:** A. Striped bass stomach content analysis, B. Striped bass stable isotope analysis, C. Lobster tether experiments, and D. Lobster laboratory behavior study
3. **Species and Quantities:** A. ~50 striped bass from each category: under 20 inches and 26-40 inches (100 total); B. Legal size striped bass (20-26 inches and over 40 inches) caught by recreational fishermen and who donate the tissue and liver samples; C. 20 striped bass that may be caught during the lobster tethering study (A & C total 120 illegal size striped bass) plus fish caught in the lobster tether no longer alive will be taken for analysis; and D. 320 sub legal lobsters from 160 in the size ranges under 45 mm carapace length and 160 between 45 and 60 mm. After 24 hours survivors are released alive. An additional 80 lobsters will be used in the laboratory study and released alive where collected. Up to 7 sea raven and 7 cod, each 45-60cm in length, will be captured and released alive at the conclusion of the behavior study.
4. **How:** Illegal size striped bass will be collected using hook and line and the UNE vessels listed or shore. Sublegal lobsters will be collected by divers (snorkeling). Tethering work will be completed by tethering ~80 lobsters on ground lines attached to a buoy line that conforms to the ATRWR Plan, soak time is 24 hours, then removed. Video cameras will be mounted inside a trap modified to not be able to fish, with a tethered lobster affixed to the end of the trap. Four trips/80 lobsters/trip = 320 total.
5. **When:** Collection of striped bass late May through October. Lobster tether experiments, 2 trips in July and 2 trips in Sept or Oct
6. **Where:** Striped Bass: collected from the Saco River, Saco Bay (Saco Maine) or Casco Bay (Portland Maine)
Fishing will take place off of the University of New England vessels or from shore where public access is permitted or permit holder has permission of the land owner.
Lobsters will be collected from nursery habitats inshore within Saco and Casco Bays.
Lobsters used for tethering will be held at the UNE Marine Science Center until used in the field.
Animals kept for the behavior study will be kept at the UNE Marine Science Center.
Any lobsters surviving the tethering experiments will be released back into the same area they were collected from (i.e. rocky inshore bays and coves within Saco and Casco Bay).
All striped bass caught on tether lines that are still alive will be released at the location it was caught.
7. **Conditions:** Marine Patrol Division I, west of Port Clyde, tel. (207) 633-9595, or the local Marine Patrol Officer, shall be contacted at least 24 hours prior to the start up of collecting activities and make arrangements as to the necessary frequency to contact them to provide the Special License (SL) number, location(s), dates of all activities, and name(s) of persons participating in the field work on this SL.
 - No marine organism authorized under this SL shall be used for human consumption.
 - A report shall be provided to the Department by the end of the year and study.
 - *This SL is contingent upon current USCG commercial fishing safety inspections for vessels used for this SL.
 - Additional conditions may be added at the discretion of the Commissioner.
 - Any infraction of these conditions or any violation of any Marine Resources laws shall be grounds for the immediate revocation of this Special License.

This Special License expires on December 31, 2011.

LINDA MERCER
ADMINISTRATIVE OFFICER, AS AUTHORIZED BY 12 M.R.S. §6023

cc: Marine Patrol Division I, Gail Wippelhauser, Mike Brown

<http://www.Maine.gov/dmr>

PHONE: (207) 633-9500

FAX: (207) 633-9579