



Influence of predator identity on the strength of predator avoidance responses in lobsters



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ABSTRACT

The American lobster, *Homarus americanus*, is an important benthic consumer in the Gulf of Maine and supports an extremely valuable fishery in New England and eastern Canada. Meanwhile, there is substantial interest in restoring large predator fish species to the Gulf of Maine, and these predators may impact lobster populations both by consuming them and by inducing them to alter their behavior. Lobster tethering experiments were used to examine the susceptibility of a range of lobster size classes to predation in Saco Bay, Maine. The most susceptible sizes of lobsters were then exposed to three different fish predators (Atlantic striped bass *Morone saxatilis*, Atlantic cod *Gadus morhua*, and sea raven *Hemitripterus americanus*) separately in experimental mesocosm tanks. Juvenile lobsters moved less and spent more time in shelter when in the presence of cod or sea raven. By contrast, striped bass did not induce lobsters to alter their behavior. Striped bass are highly mobile, active pursuit predators, which are thought to induce weaker behavioral responses in prey than sit-and-pursue predators like sea ravens. Thus, differences in lobster sheltering behavior corresponded with differences in predator foraging behavior. These predator-induced changes in behavior can result in less foraging activity, which may translate into reduced lobster growth and reproduction. Efforts to model marine communities and ecosystems will benefit from a more holistic understanding of whether predators induced prey to modify their foraging behavior and habitat usage.

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1. Introduction

Predator–prey interactions are important drivers of community structure (Carpenter et al., 1985; Hairston et al., 1960; Paine, 1966; Sih et al., 1998). Predator–prey interactions are either driven by consumptive effects or when predators induce prey to alter their behavior to avoid being consumed (Abrams, 1995; Lima and Dill, 1990; Trussell et al., 2006; Werner and Peacor, 2003). When predators evoke changes in prey behavior, these effects often negatively impact prey foraging rates, and consequently can influence prey population dynamics (Schmitz, 2008; Schmitz et al., 2004; Trussell et al., 2006; Werner and Peacor, 2003). Thus, tradeoffs exist between the risk of being consumed and the cost of anti-predator strategies such as stopping or altering risky feeding behavior and moving to resource-poor habitats that provide refuge (Abrams, 1995; Lima and Bednekoff, 1999; Lima and Dill, 1990; Trussell et al., 2006; Werner and Anholt, 1993; Werner and Peacor, 2003).

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). Sit-and-wait predators remain in a fixed location for extended periods of time and ambush a prey species when it moves into the area; sit-and-pursue predators are sedentary, but actively seek a prey species when it is in the area; 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, and consequently should evoke stronger predator-avoidance behaviors in prey. Schmitz (2008) found that hunting spiders elicit little to no anti-predator response from grasshoppers, but sit-and-wait spiders induce grasshoppers to seek refuge in areas with lower predation risk but poorer food quality. It is less clear if marine aquatic prey communities respond accordingly to these different types of predators.

We experimentally examined the effects of different predators on juvenile lobster (*Homarus americanus*) behavior to enhance our understanding of how predator foraging modality influences prey behavior in temperate coastal marine ecosystems. Specifically, we tested if the size of juvenile lobsters affects their susceptibility to predation in the field, and then conducted laboratory experiments investigating the anti-predator responses of susceptible sizes of juvenile lobster to striped

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bass (*Morone saxatilis*), Atlantic cod (*Gadus morhua*) 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 and Klein-MacPhee, 2002) and have different foraging modalities. We hypothesized that lobsters would spend more time sheltered in the presence of these fish predators. Furthermore, we predicted that the level of response would be strongest in the presence of sea raven, weakest in the presence of striped bass, intermediate in the presence of cod, and that the variation in response would reflect differences in predator identity and foraging strategies.

2. Methods

2.1. Study system

The American lobster is a decapod crustacean that is predominantly shelter-based after settling on the benthos as a small juvenile (Brown, 2007; Hovel and Wahle, 2010; Stein and Magnuson, 1976; Wahle, 1992). 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 less change in behavior, though often still respond to the threat of predation (crayfish: Stein and Magnuson, 1976; American lobster: Wahle, 1992; McMahan et al., 2013).

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 despite having been heavily fished for over a century (Jackson et al., 2001; Steneck and Wilson, 2001). Although the mechanisms driving the recent uptick in the abundance of adult lobsters are not completely clear, it has been suggested that factors affecting the distribution of juveniles and their establishment on the benthos are predictive of the abundance and distribution of adults (Steneck and Wilson, 2001). Many fish such as striped bass and Atlantic cod feed on juvenile lobster (Collette and Klein-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 (Atlantic States Marine Fisheries Commission, 2010), and there are also currently management strategies aimed at rebuilding Atlantic cod populations. It has been suggested that the abundance of lobster may be inversely related to that of coastal groundfish (Steneck, 1997). Specifically, lobsters were 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 and Sebens, 1992). Meanwhile, lobsters and striped bass populations in coastal Maine have both been increasing over the past couple of decades, suggesting that striped bass may not be an important predator of lobster. Yet Steneck and Wilson (2001) found the weakest increases in juvenile lobsters in southern Maine, which coincides with the largest striped bass populations in coastal Maine. Furthermore, several studies have documented that juvenile lobsters are important dietary component of adult striped bass (Nelson et al., 2003; Wilkinson, 2013).

2.2. Size-specific predation rates

To quantify the relative predation risk that juvenile lobsters of varying size are exposed to in southern Maine, we conducted lobster tether experiments in August 2011. Tethering has been used in several previous studies to examine predation risk for lobsters and other crustaceans (Aronson and Heck, 1995; Herrnkind and Butler, 1986; Hovel and Lipcius, 2001; Wahle and Steneck, 1992; Wahle et al., 2013; Witman and Sebens, 1992). Mills et al. (2008) exposed potential biases

associated with tethering artifacts that potentially limit the utility of these types of data for comparing lobster survival across sites without site-specific correction factors. Without developing site- and size-specific correction factors to account for increased lobster vulnerability associated with being tethered, our results cannot be used to make inferences about absolute lobster predation rates. Wahle et al. (2013) examined how body-size and location affect vulnerability to predation using tethered juvenile lobsters and conducted video surveillance in the field to examine potential artifacts associated with tethering (Peterson and Black, 1994). Although this study acknowledged that tethering may artificially alter the vulnerability of tethered prey to specific types of predators (i.e., those with different foraging modalities), it revealed that tethering can be used effectively to examine how specific traits such as body-size mediate the relative predation risk of motile species such as lobsters. Here we tethered lobsters varying widely in size within Saco Bay to assess relative risk and identify the size classes that are most vulnerable to predation.

Juvenile (26–58 mm carapace length [CL]) lobsters 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 pairs 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°29'24.41 N 70°20'26.99 W), two tether lines (each with 20 juvenile lobsters) were deployed on sand bottom at 7–14 m 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 approximately 100 m long and lobsters were spaced at 5-m intervals. After 24 h, 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.

2.3. Laboratory behavior assays

Juvenile lobsters were exposed to 3 different predators separately during laboratory assays conducted in October and November 2011 to quantify their effects on lobster behavior: striped bass *M. saxatilis*, Atlantic cod *G. morhua*, and sea raven *H. americanus*. We also quantified lobster behavior without any predators present to provide a control that we compared to the predator trials. Sea ravens are sit-and-pursue predators that are highly sedentary and will remain in rocky areas for long periods of time (Collette and Klein-MacPhee, 2002), and have been observed to ambush and slowly pursue their prey (Martinez, 2003). By contrast, Atlantic striped bass are highly mobile and thus have a large foraging arena that encompasses many habitats and variety of prey types (Walter et al., 2003). Atlantic cod use both sit-and-pursue and active foraging strategies (Sherwood and Grabowski, 2010).

Striped bass and cod were collected via hook and line sampling while the sea ravens were collected from local lobsterman after being caught in lobster traps. 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 to 44 cm total length, cod ranged from 43 to 63 cm total length, and striped bass ranged from 56 to 75 cm total length. While the sea ravens used in this study were substantially smaller than either the cod or striped bass, the sea raven has the largest gape width relative to its size of these three species (Collette and Klein-MacPhee, 2002). Thus, the size-ranges used for each predator species in this study included individuals that are capable

of consuming juvenile lobsters. Furthermore, similar-sized fish predators have been used in other studies examining their effects on lobster behavior (McMahan et al., 2013; Wahle, 1992; Wahle and Steneck, 1992).

Juvenile lobsters ranging in size from 26 mm to 45 mm 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 the sizes of lobster with the lowest survival rates during the tethering experiments. Lobsters and fish predators were starved for at least 48 h before being used in a trial.

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 3.5 m by 4.8 m and was filled to a depth of 1.5 m (Fig. 1). Four individual cobble shelters were spaced approximately 0.7 m 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 beginning each trial, four lobsters were measured and allowed to acclimate to the experimental tank for 2 h. 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 h. 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. New lobsters were used for each trial, and all predators were replaced after each trial with the exception of 2 sea ravens, which were allowed to recover for 48 h in a holding tank before being used 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.

2.4. Statistical analyses

For the survival assays in the field, lobsters were grouped into 3-mm size classes to examine how survival varied across all sizes of lobster deployed. Percent surviving for all sizes was determined using the number and sizes of all lobsters deployed. Linear regression was then used to determine if lobster survival significantly increased with lobster size.

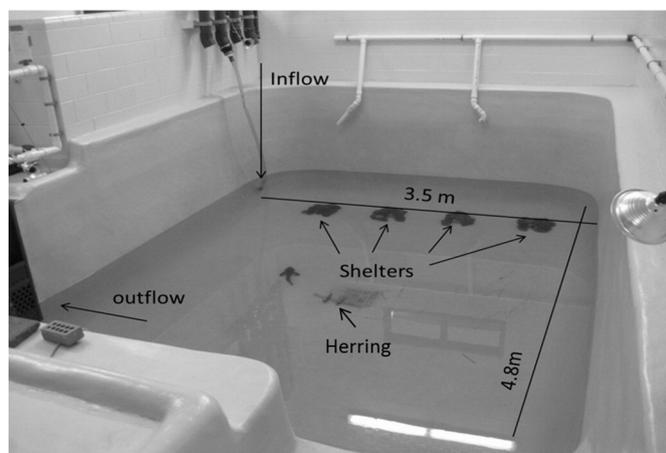


Fig. 1. Picture of mesocosm tank design.

For the behavioral assays conducted in the lab, video recordings of each trial were reviewed and each individual lobster was tracked for 13 h. The first 6.5 h of each video were conducted during daylight hours, while the second 6.5 h occurred at night. For each lobster, the proportion of its time spent in vs. out of shelter was quantified during both the day and night. As only 2 types of behavior were categorized, once the % of time spent sheltering was determined, the % of time outside of shelter was determined as $100 - \% \text{ of time sheltered}$ for each lobster. All percentage data were arc-sin transformed in order to meet the assumption of homogeneity of variances. Separate one-way ANOVA's were performed with the video assay results during the day and night using predator treatment as the factor and percentage of time spent in shelter as the dependent variable. For significant ANOVAs, Tukey's post hoc tests were used to determine if lobster behavior during any of the predator treatments differed from each other or that of the predator-free control. Statistical analyses were initially conducted with vs. without the two trials involving reused sea ravens. Because excluding those two replicates did not alter the outcome, they were included in the final analyses.

3. Results

3.1. Size-specific lobster survival rates

A total of 159 juvenile lobsters ranging in size from 26 to 58 mm carapace length were deployed on the benthos, and 80 were consumed by predators. Lobsters were grouped into 3 mm size bins and linear regression revealed that survival increased significantly with juvenile lobster size ($r^2 = 0.97$, $p < 0.001$, $n = 11$). Because survival increased linearly with size, we selected 60% survival (corresponding to 44 mm carapace length) as the maximum lobster size for our behavior experiments (Fig. 2).

3.2. Laboratory behavior assays

The diurnal cycle influenced lobster behavior. During the day, there was no significant effect of predator treatment on the amount of time juvenile lobsters spent in shelter (ANOVA: $F_{3,73} = 0.41$, $p > 0.747$; Fig. 3). All lobsters spent the majority of the trial time in shelter and not moving around the tank. Meanwhile, there was a significant effect of predators at night on the amount of time spent in shelter (ANOVA: $F_{3,73} = 7.85$, $p < 0.001$; Fig. 3). At night, control and striped bass

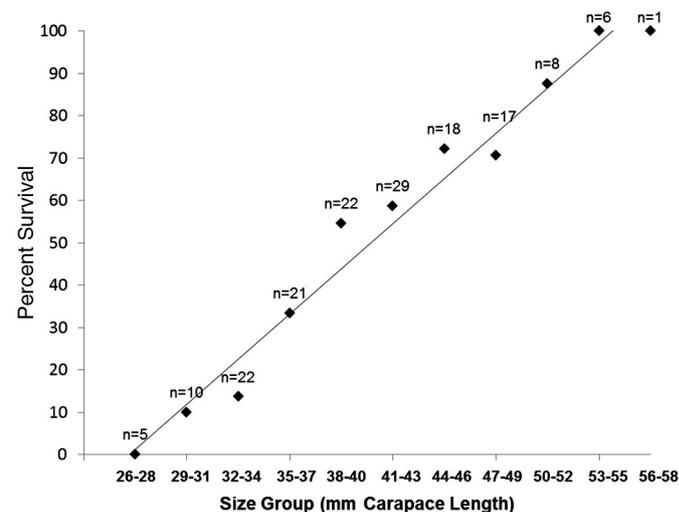


Fig. 2. Lobster survival during tethering experiments conducted in Saco Bay, Maine in 2011. Lobsters were grouped by size using carapace length in 3 mm increments. The total number of lobsters deployed per carapace group is indicated above each point on the graph. Percent survival = $-9.4382 + (10.67 \times \text{Size})$; $r^2 = 0.9719$, $p < 0.001$, $n = 11$.

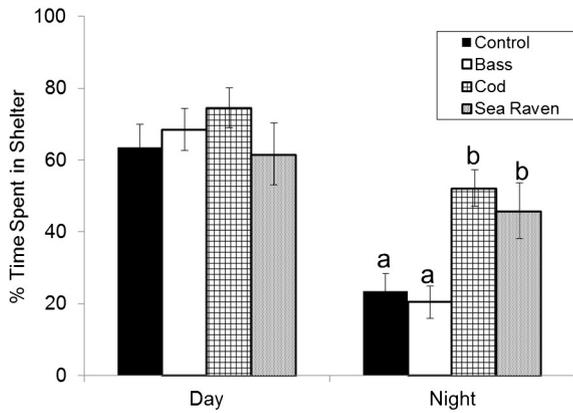


Fig. 3. Percent of time lobsters spent in shelter during the day and at night. Tukey's post hoc results are represented with letters above the error bars for treatments at night (bars with different letters above them are significantly different at $P < 0.05$). Error bars represent standard error of the mean ($N = 5$).

treatments did not differ from each other (Tukey: $p > 0.05$), but both of these treatments differed significantly from the cod and sea raven treatments (Tukey: $p < 0.05$; Fig. 3). The proportion of time that lobsters spent in shelter did not differ between the cod and sea raven treatments (Tukey $p > 0.05$). We observed only one successful predation event, in which a sea raven consumed a lobster.

4. Discussion

Body size has been found to mediate many ecological and biological processes (Costa, 2009; Holmes and McCormick, 2010). Our tethering assays revealed that lobster risk from predation in southern Maine is highly size dependent, which is largely consistent with previous work examining the susceptibility of juvenile lobsters to predation (Wahle, 1992; Wahle and Steneck, 1992; Wahle et al., 2013). Wahle et al. (2013) found that tethered lobster survival was non-linear in Maine, with survival exponentially increasing for smaller (< 25 mm CL) juvenile lobsters. We did not tether lobsters < 26 mm CL. Meanwhile, they found that survival of larger (> 25 mm CL) juvenile lobsters in Maine increased linearly with body size. In addition, they estimated that 50% survival occurred at ~ 39 mm CL, which agrees closely with the 50% mortality at ~ 41 mm CL documented in our study. While we acknowledge that tethering likely results in elevated predation rates (e.g., Mills et al., 2008), collectively these studies suggest that the relative predation risk for lobsters is highly size-dependent and quickly decreases with size in coastal Maine.

Juvenile lobsters displayed varying levels of anti-predator responses that depended on both time of day and predator identity. During the day, no noticeable difference in sheltering behavior was observed among treatments likely because American lobsters are primarily nocturnal (Karnofsky et al., 1989; Scopel et al., 2009; Wahle, 1992) and spent the majority of their time in refuge habitat during the day. We found that lobsters reacted to all three predator species when encountered (i.e., < 1 m distance between predator and lobster; personal observation). This reaction typically involved an aggressive claw display, but lasted only a few seconds, and was consistent across predator treatments. Following such displays, lobsters typically returned to the activity that they were engaged in prior to the encounter.

It is likely that portions of the tank were saturated with olfactory cues from the predator, and olfactory cues may have been stronger in some areas than in others due to the flow dynamics of the tank or the movement behavior of the predators. Previous work has demonstrated that the American lobster is capable of responding to chemosensory cues from predators (Spanier et al., 1998; Wahle, 1992). Because juvenile lobsters in our study reacted similarly during close encounters with all predators, we postulate that the longer-term anti-predator

behaviors documented here are likely a response to scent cues. However, both visual and scent cues were present in the tank, and our experiment was not designed to distinguish between them. Further research aimed at quantifying the relative importance of olfactory vs. visual cues of predators on prey behavior would address the exact mechanism by which predators induce lobsters to alter their behavior. It is also unclear if lobsters respond to sea ravens and cod but not striped bass because they recognize each species or because the two species that induced defenses release more chemosensory or visual cues. Yet our results suggest that cod and sea ravens have a larger sphere of influence on lobster behavior than do striped bass (Turner and Montgomery, 2003).

Differences in the strength of anti-predator responses in juvenile lobsters at night are largely consistent with our predictions regarding the effects of predator identity and foraging modality on prey behavior. All predators are likely to constantly emit olfactory cues that can be dispersed by advection and diffusion. Because of this cue dispersal, prey (such as a foraging lobster) will typically encounter the olfactory cues from sit-and-wait or sit-and-pursue predators before encountering the actual predator (Schmitz et al., 2004). Thus, the strong anti-predator response of lobsters to sea ravens likely represents an evolved response to a reliable cue associated with the sit-and-pursue style of predation. Selection has favored investing resources to develop a response to sit-and-pursue style predators, as the presence of an olfactory cue from these predators is an indication that the chance of a subsequent encounter is high (Bouskila, 2001; Schmitz et al., 2004). Previous work has indicated that the American lobster also responds to other sit-and-pursue predators such as the sculpin (*Myoxocephalus aeneus*) by increasing the time spent in shelter (Wahle, 1992). The European Spiny lobster also responds to sit-and-wait (octopus) and sit-and-pursue (eel) predators by using anti-predator behaviors such as tail flipping and "alert" posturing, where the lobster attempts to avoid consumption by orienting the body and antennae toward the predator (Buscaino et al., 2011). Similar decreases in foraging, increases in shelter use, or shifts in habitat usage have been demonstrated in response to terrestrial sit-and-pursue predators (Schmitz, 2008).

Striped bass, as active predators, are fast moving, do not remain in one location and have a broad foraging arena; they feed throughout the water column on both benthic and pelagic prey types (Walter et al., 2003). Unlike a sit-and-wait predator, active predators are present in a given area for only a brief period, and any olfactory cues emitted likely disperse more slowly than the predator moves. Consequently, such cues are not likely to be detected by the prey until after the predator has already arrived at the prey's location or left the vicinity (Schmitz et al., 2004). Thus, if prey detect an olfactory cue from an active predator, it is likely not very indicative of actual risk because the predator has either already encountered the prey or moved to another location. Because active predators provide a cue that cannot be effectively exploited by the prey, and cue detection is disconnected from actual risk, there is no selective pressure for prey to modify behavior in the predator's presence (Bertness, 1981; Freeman and Hamer, 2009; Large et al., 2012; Smee and Weissburg, 2008). Therefore, it is likely that lobsters did not respond to striped bass because they have not evolved a response to this predator as it would be energetically costly and lack an associated fitness benefit (Bouskila, 2001; Preisser et al., 2007; Schmitz et al., 2004). Our results are similar to those from terrestrial systems where prey also do not respond to active predators (Schmitz, 2008; Schmitz et al., 2004).

Atlantic cod, as neither a solely sit-and-pursue nor an active predator, caused very strong anti-predator responses in juvenile lobsters. As a very mobile species with the ability to feed on many prey types, cod might be expected to provide scent cues that are difficult to exploit, resulting in a weak prey response similar to that seen with active predators. However, the response witnessed here was similar to that observed with a sit-and-pursue predator. Cod populations in the Gulf of Maine can be divided into transient and locally resident individuals

(Lindholm et al., 2007; Morris and Green, 2002; Neat et al., 2006; Sherwood and Grabowski, 2010). In areas where resident cod exist, they are presumably less mobile than transient cod. Consequently, the cue provided by locally resident cod is likely to mimic that of a sit-and-pursue predator, providing a more reliable cue for prey species to detect (Large and Smee, 2010; Large et al., 2012; Schoeppner and Relyea, 2005; Turner, 2008). Therefore, potential prey would likely detect any olfactory cue from resident cod prior to an encounter, so that evolution of an anti-predator response would potentially reduce the likelihood of prey being consumed.

While we conducted our study in a large (~20 m²) mesocosm, as with any mesocosm or cage experiment, it is possible that locally elevated levels of predator cues may have saturated the experimental arena. However, we were interested in investigating the relative response of lobsters to each of the three species rather than quantifying the absolute sphere of influence. Cue dispersal is likely influenced by many environmental variables such as turbidity, hydrodynamic regime, bottom topography, and habitat complexity, and each of these factors would potentially alter the relative strength of lobster behavioral responses (Weissburg and Zimmer-Faust, 1993, 1994). In our study, species identity was important and influenced the relative strength of induced sheltering behavior in lobsters. Furthermore, our finding that cod increased lobster use of shelter habitat agrees with McMahan et al. (2013), which found that cod induce lobsters to seek refuge in cobble habitat in a large (~20,000 m²), semi-enclosed bay.

Predators can influence community structure and ecosystem functioning via non-consumptive effects (Schmitz, 2005; Schmitz et al., 2008; Werner and Peacor, 2003). However, the strength of these non-consumptive effects likely differs with predator identity, foraging modality, prey size, and time of day. Reduced lobster activity levels could lead to reduced foraging success, growth and reproductive effort, which likely would have population-level implications (McMahan et al., 2013). Juvenile lobsters may be especially vulnerable to predation from striped bass, as they did not alter their behavior and seek refuge in the presence of this species. Studies examining striped bass foraging patterns have found that the American lobster is an important component of its diet in New England, especially in summer (Nelson et al., 2003; Wilkinson, 2013). Furthermore, examining whether a wide range of other active and sit-and-pursue predator fish species induce lobster sheltering behavior will help determine if predator foraging modality is an effective general predictor of lobster anti-predator responses. 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 with the development of lobster population models that incorporate behavioral interactions. Exploring all aspects of these species interactions is crucial so that we may more fully understand the consequences of restoring large predatory fish populations in coastal Maine on lobster stocks and their associated fisheries.

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