

# Nonconsumptive effects of a range-expanding predator on juvenile lobster (*Homarus americanus*) population dynamics

MARISSA D. McMAHAN<sup>1,2,†</sup> AND JONATHAN H. GRABOWSKI<sup>1</sup>

<sup>1</sup>Marine Science Center, Northeastern University, 430 Nahant Rd, Nahant, Massachusetts 01908 USA

<sup>2</sup>Manomet, 14 Maine Street, Brunswick, Maine 04011 USA

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

**Key words:** American lobster; black sea bass; Gulf of Maine; naïve prey; nonconsumptive effects; novel predator; range expansion.

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† **E-mail:** mcmahan@manomet.org

## INTRODUCTION

The importance of predation in regulating the structure and function of ecological communities has been well established over the past several decades (Hairston et al. 1960, Paine 1980, Sih et al. 1985, Werner and Peacor 2003). Predators

can impact prey populations by consuming individuals (Hairston et al. 1960, Paine 1980, Estes et al. 1998) and/or by inducing behavioral, morphological, or physiological responses (Lima 1998a, Trussell et al. 2002, Werner and Peacor 2003, Schmitz et al. 2004). These latter responses, termed nonconsumptive effects (NCEs), may

have an equal or larger impact on community structure than consumptive effects (CEs; Peacor and Werner 2001, Preisser et al. 2005, Peckarsky et al. 2008, Schmitz et al. 2008). For instance, behavioral avoidance of predators can potentially impact prey habitat use, foraging rates, energy allocation, and ultimately population dynamics (Schmitz et al. 1997, 2004, Grabowski 2004, Preisser and Bolnick 2008). The strength of NCEs can be context dependent and is influenced by both biotic and abiotic processes (Werner and Peacor 2003, Watson and Estes 2011, Kimbro et al. 2014, Matassa and Trussell 2015). For instance, Kimbro et al. (2014) found that the magnitude and direction of NCEs varied with both latitude and habitat. Understanding the factors that drive regional variation in the strength of NCEs across biogeographic gradients will enhance efforts to predict how species interactions and community structure change across ecosystems.

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

Species invasions and distribution shifts present a unique opportunity to explore predator–prey dynamics across biogeographic gradients of contact history. The ability of prey to recognize novel predator cues will likely determine the strength of both CEs and NCEs by non-native predators. The naive prey hypothesis (Diamond and Case 1986) suggests that a lack of evolutionary history between predators and prey may result in ineffective anti-predator defenses (Cox

and Lima 2006, Freeman and Byers 2006, Sih et al. 2010). Banks and Dickman (2007) proposed that the impact of an alien predator on prey populations depends on the type of naiveté that prey exhibit: (1) Prey may not recognize a predator and fail to adopt anti-predator defenses, (2) they may recognize a predator but adopt ineffective anti-predator defenses, or (3) they may recognize a predator and adopt appropriate anti-predator defenses. Furthermore, Sih et al. (2010) hypothesized that non-native predators have the greatest impact if the community they invade has prey, predators, and competitors that are similar to their native habitat, whereas the invaded community is entirely naïve to the new predator. Yet, some prey species have been found to respond effectively to novel predators (Sih et al. 2010, Kimbro et al. 2014, Ferrari et al. 2015), including greater plasticity in anti-predator defenses when the threat of predation is more variable in space and time (Trussell 2000, Trussell and Nicklin 2002).

Many marine species in the Northwest Atlantic are exhibiting poleward distribution shifts (Nye et al. 2009, Pinsky et al. 2013, Hare et al. 2016). This phenomenon is particularly evident in the Gulf of Maine (GOM) where sea surface temperatures are rising faster than 99% of the rest of the world's oceans (Pershing et al. 2015). For instance, the northern stock of black sea bass historically ranged from Cape Hatteras to Cape Cod, but the center of stock biomass has shifted poleward in recent years (Bell et al. 2015), and range boundary populations have expanded into the GOM. The GOM is a low diversity system (Steneck 1997, Witman et al. 2004), making it likely that species introductions and range shifts will be ecologically disruptive. Indeed, a rapid increase in the abundance of sea bass may significantly alter community structure, partly because adult black sea bass are aggressive and territorial (Nelson et al. 2003), which may influence predator–prey and competitive interactions.

Of particular concern is the impact of sea bass on crustacean populations in the GOM. In their native range, sea bass have a diet comprised of >50% decapod crustaceans (i.e., south of Cape Cod; Garrison and Link 2000). Furthermore, American lobsters, *Homarus americanus*, an ecologically and economically important species, have been found in roughly 12% of the stomachs

of sea bass collected in the GOM (McMahan 2017). Meanwhile, Selden et al. (2016) found that a recent contraction in the southern range limit of lobsters was correlated with the northern expansion of sea bass. Both active (e.g., cod) and ambush (e.g., sculpin and sea raven) native fish predators can induce strong NCEs in juvenile lobster populations, such as increased shelter usage and reduced foraging (Wahle 1992, Spanier et al. 1998, McMahan et al. 2013, Wilkinson et al. 2015). However, novel fish predators may not cause strong predator avoidance responses in juvenile American lobsters, and therefore, they could be more susceptible to predation (Sih et al. 2010). The potential for sea bass to induce NCEs and/or CE in lobster populations suggests that their expansion into the GOM could have substantial ecological and socioeconomic impacts.

The recent poleward shift of sea bass has increased their extent of geographic overlap with lobsters at the southern end of the lobster's distribution. Sea bass were historically rare in the southern GOM, and it is only in the past two decades that their abundance has rapidly increased. In southern and midcoast Maine, sea bass have been regularly captured by fishers since the warm water temperature anomaly of 2012 (McMahan 2017). However, sea bass have not been reported via fisheries dependent or independent surveys conducted north of Penobscot Bay in Maine (also referred to as "Downeast" Maine), and fishers surveyed in this region had not encountered sea bass as of 2015 (McMahan 2017). Therefore, latitudinal variation in potential lobster contact history with sea bass exists in the GOM.

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

## METHODS

In the summer of 2015, we conducted a laboratory experiment at Northeastern University's

Marine Science Center (MSC) in Nahant, Massachusetts, USA, to test how black sea bass risk cues influence habitat use and foraging of juvenile lobsters from three regions in the GOM with different potential sea bass contact histories. In particular, we manipulated the presence of sea bass olfactory cues and quantified the amount of time lobsters spent in shelter, the number of trips made to a prey plot, the time spent handling prey, and the total number of prey consumed. Collectively, these prey response variables were used to assess the degree to which prior potential contact history between the two species influences how lobsters respond to this new predator.

### *Collection and maintenance*

Juvenile American lobsters were collected by hand from the intertidal–subtidal interface in northern Massachusetts (MA) in Marblehead, midcoast Maine (Mid) in Harpswell, and downeast Maine (DE) on Beals Island in July 2015 (Fig. 1). McMahan (2017) has frequently observed sea bass foraging at 3 m depth during SCUBA surveys conducted in Maine and Massachusetts, so it is likely that lobsters in the intertidal–subtidal zone are exposed to sea bass predation at high tide. Thirty lobsters, ranging from 25 to 40 mm CL, were collected in each location. Lobsters within this size range are approximately 2–4 yr of age (Tang et al. 2015). All lobsters were in the intermolt stage and had no visible signs of injury (i.e., missing appendages). After capture, each lobster was carefully wrapped in a paper towel soaked with sea water and then placed in a cooler to prevent thermal stress. Lobsters were immediately transported to the MSC and placed in individual 12 × 12 cm rubber-coated mesh wire cages housed within a 2 m diameter × 1 m deep (3.1 m<sup>2</sup> area) flow-through tank where they were housed for two weeks prior to the onset of the experiment while being acclimated. All tanks used to house animals and conduct experiments were located outside and therefore exposed to ambient light, temperature, and weather. All lobsters were acclimated to these conditions and fed twice per week prior to the beginning of the experiment. Each lobster was fed the same species and approximately the same amount (10–15 g) at each feeding event. Their diet alternated between blue mussels (*Mytilus edulis*) and fish (species

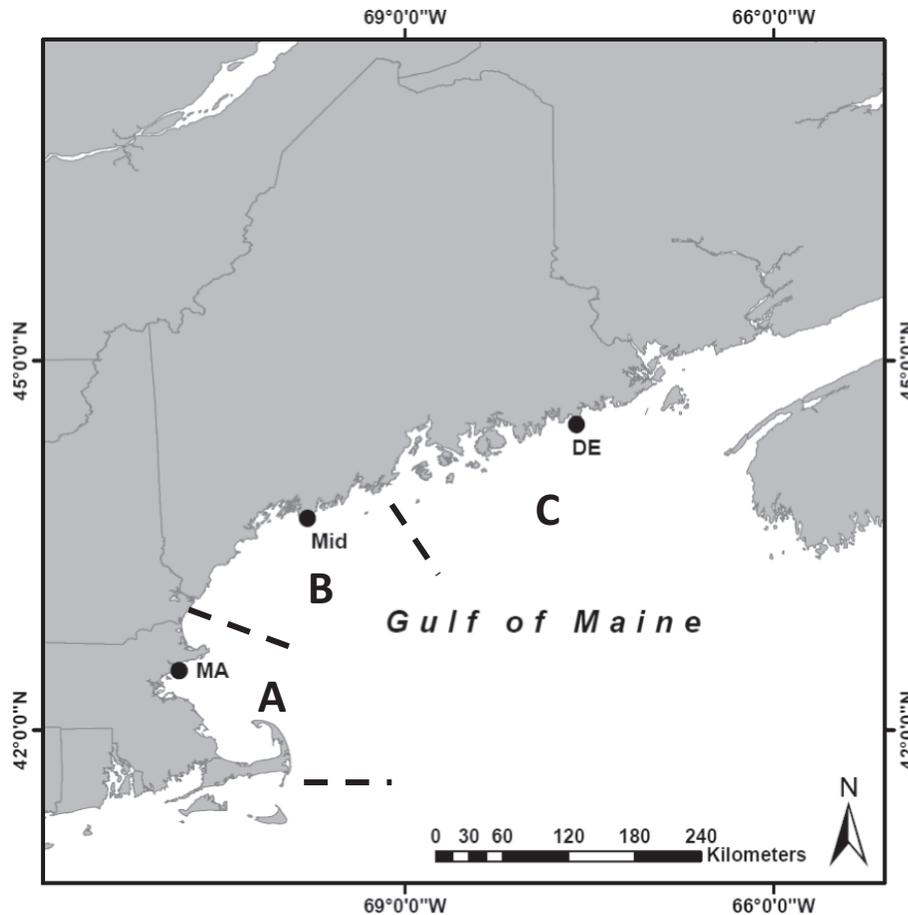


Fig. 1. Location of juvenile *Homarus americanus* collection sites in northern Massachusetts (MA; 42°30'37" N, 70°50'34" W, size range = 29.7–36.2 mm CL) where sea bass have rapidly increased in abundance in the past two decades (Zone A, delineated by dashed lines), midcoast Maine (Mid; 43°48'35" N, 69°42'56" W, size range = 29.0–35.2 mm CL) where sea bass have been regularly sighted by fishermen since 2012 (Zone B, delineated by dashed lines), and downeast Maine (DE; 44°30'17" N, 67°36'12" W, size range = 28.8–35.8 mm CL) where sea bass have not been encountered (Zone C). Distribution and abundance data come from scuba surveys, specimen collection, and fisher surveys conducted from 2013 to 2016 (McMahan 2017).

varied depending on what was available but included herring (*Clupea harengus*) and mackerel (*Scomber scombrus*). Lobsters were deprived of food for 72 h prior to the start of the experiment. Water temperature was recorded hourly using Onset data loggers deployed in the lobster storage tank and treatment tanks and ranged from 11.3 to 22.3°C ( $n = 1881$ , mean  $\pm$  SE = 17.6  $\pm$  0.05°C). This range of temperatures is similar to what juvenile lobsters experience at the intertidal–subtidal interface (i.e., where experimental lobsters were collected) in the summer and early fall in the GOM (McMahan et al. 2016). Lobsters

likely experienced different thermal histories across the geographic range targeted; however, all lobsters experienced the same range of acclimation temperatures over the two-week acclimation period. No mortality was observed during storage or experimental runs.

Twenty black sea bass were collected by hook and line in Boston Harbor on 20 July 2016. Sea bass ranged in size from 29.5 to 36.0 cm total length. These fish were returned to the MSC in a live well and immediately transferred to a 2 m diameter  $\times$  1 m deep (3.1 m<sup>2</sup> area) flow-through tank. Fish were allowed to acclimate for two

weeks prior to the beginning of the experiments. During this time, survival and behavior were monitored daily. Sea bass rapidly acclimated to the storage tank and no mortality was observed. Fish were fed three times per week leading up to the start of the experiments. Their diet was based on gut content results from fish captured in the same region (McMahan 2017) and included small crabs, squid, fish, and bivalves. Although lobsters have also been found in the diet of sea bass, we specifically avoided this diet item to ensure that experimental lobsters were reacting to the scent of the predator, rather than an alarm cue of conspecifics in the predator's feces (Chivers et al. 1996, Wisenden 2000, Brown 2003, Smee and Weissburg 2006). Sea bass were deprived of food for 24 h prior to the start of the experiments. A total of 18 sea bass were used for experiments. Individual sea bass were not reused in replicate treatments. Water temperature was recorded hourly using an Onset data logger deployed in the sea bass storage tank and experimental treatment tanks and ranged from 12.8° to 22.7°C ( $n = 1850$ , mean  $\pm$  SE =  $17.7 \pm 0.04^\circ\text{C}$ ), which is well within the range of temperatures at which

sea bass have been reported being caught in the wild (e.g., 6–29°C; Mercer 1989).

#### Experimental design

During the experimental trials, lobsters were placed in experimental units that sat within individual 2 m diameter  $\times$  1 m deep (3.1 m<sup>2</sup> area) flow-through tanks (Fig. 2). Experimental units consisted of a 48 cm diameter plastic mesh fish basket coated in 5-mm Vexar to prevent appendages from getting caught in the basket mesh. The bottom of each basket was coated in a 2.54-cm layer of pea gravel. We also secured a shelter (12.7 cm length of 2.54-cm diameter PVC pipe) to the bottom of the basket with a cable tie. Two flat rocks (roughly 12 cm diameter) were then placed over the PVC pipe to add additional structure to the shelter. A prey patch was placed opposite of the shelter and consisted of 10 blue mussels (*Mytilus edulis*), ranging in length from 7 to 12.5 mm, that were superglued to a 7.6  $\times$  15.2 cm ceramic tile. We firmly secured mussels to the tile to prevent lobsters from removing them and returning them to the shelter. Hence, lobsters that consumed mussels were



Fig. 2. Image of experimental unit setup used in *Homarus americanus* behavioral experiments. (A) PVC pipe and rock shelter. (B) Prey patch consisting of 10 blue mussels (*Mytilus edulis*) superglued to a ceramic tile.

forced to do so at the prey patch. During experiments, each unit was placed in a flow-through tank such that 6 cm at the top of the basket emerged from the water. This approach ensured that lobsters could not escape the unit, but also allowed the top of the unit to remain unobstructed during video recording. At the end of each trial, experimental units were removed from the tanks, thoroughly rinsed with fresh water, and left exposed to direct sunlight for six days to ensure sea bass cues were absent before being reused.

The experimental design crossed two fixed factors: Sea Bass Predation Risk (present and absent) and Potential Contact History (i.e., region: MA, Mid and DE). For each treatment combination, there were six replicates (i.e., replicate runs;  $N = 36$ ). One replicate of each of the six treatment combinations was run each week, and the entire study lasted 58 days (between late July and the end of September). Lobsters were added to experimental units and allowed to acclimate for 2 h prior to experiments beginning. After the acclimation period, tanks housing experimental treatments received an additional fish basket containing a live sea bass that was placed on the opposite side of the tank from the lobster unit. These baskets were sealed at the top with Vexar, ensuring that sea bass could not escape. This approach prevented direct predation and also prevented lobsters from being exposed to visual cues from the predator. Previous studies have shown that crustaceans sense and respond to olfactory cues released by predators (Wahle 1992, Appelberg et al. 1993, Spanier et al. 1998), but may not respond to visual stimuli without an accompanying odor (Appelberg et al. 1993). Control treatments did not receive an additional basket (i.e., the tank only contained the experimental unit).

Experiments began at approximately 18:00 and ran for 18 h. During this time, juvenile lobster behavior was monitored with Sony Handycam Camcorders (DCR-SR100) that were equipped with a 30-gigabyte hard drive and outfitted with a  $0.5\times$  lens in order to increase ( $\sim 2\times$ ) the camera's field of view (Video S1). Illumination was provided by 15-W red-coated incandescent bulbs mounted on the side of each tank. The entire experimental unit could be observed in the field of view of the video camera. At the

conclusion of each experiment, lobsters and sea bass were moved to new storage tanks (to ensure they were not reused in replicate treatments), prey plots were removed, and mussels were counted. There was no significant difference in lobster size among regions (ANOVA,  $F_{2,32} = 1.45$ ,  $P = 0.25$ ) or treatments (ANOVA,  $F_{1,32} = 0.53$ ,  $P = 0.47$ ).

#### Data analysis

Two randomly selected 30-min segments of video were analyzed for each trial, and the duration of specific activities and behaviors was measured. The first video segment was selected between 20:00 and 23:00 hours, and the second was selected between 02:00 and 05:00 hours. Video segments were selected from the evening hours because lobsters are nocturnal (Wilkinson et al. 2015). Behaviors analyzed included time spent in the shelter, the number of trips made to the prey plot, and the time spent handling prey. Time spent in the shelter was defined as any period when the lobster was completely enclosed within the shelter. A trip to the prey plot consisted of the lobster leaving its shelter and traveling directly to the prey plot mussels (see Video S1 for an example of this behavior). Time spent handling prey included any use of the lobsters' chela or maxillipeds to grasp or manipulate. The total number of prey consumed during the 18-h experiment was quantified when prey plots were removed at the conclusion of the experiment.

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

## RESULTS

Both potential contact history (i.e., region: MA, Mid, and DE) and predator presence influenced lobster shelter use and foraging behavior. The amount of time that juvenile lobsters spent in shelter significantly increased in the presence of sea bass ( $\chi^2 = 30.1$ ,  $P < 0.001$ ; Fig. 3A). There was also a strong trend suggesting that the effects of sea bass on lobster shelter use varied among the three potential contact histories (predation risk  $\times$  potential contact history interaction:  $\chi^2 = 5.63$ ,  $P = 0.06$ ). Sea bass presence significantly increased the time spent in shelter for MA and Mid lobsters (Tukey's HSD,  $P = 0.001$  and  $P < 0.001$ , respectively), but only slightly increased the time spent in shelter for DE lobsters, and this trend was not significant (Tukey's HSD,  $P = 0.81$ ). In addition, DE lobsters spent significantly less time in shelter than Mid lobsters when sea bass were present (Tukey's HSD,  $P = 0.02$ ).

There was also a strong interaction between the effects of sea bass predation risk and potential contact history on the number of times that lobsters visited prey plots (predation risk  $\times$  potential contact history interaction:  $\chi^2 = 12.74$ ,  $P = 0.002$ ; Fig. 3B). Sea bass presence significantly reduced the number of trips made to the prey plot for MA and Mid lobsters (Tukey's HSD,  $P = 0.04$  and  $P < 0.001$ , respectively), but predation risk did not significantly affect the number of trips made to the prey patch for DE lobsters (Tukey's HSD,  $P = 0.97$ ). In addition, Mid lobsters made significantly more trips to the prey plot than MA lobsters when sea bass were absent (Tukey's HSD,  $P = 0.03$ ), and DE lobsters made significantly more trips to the prey plot than MA and Mid lobsters when sea bass were present (Tukey's HSD,  $P = 0.04$  for both comparisons).

Similar to the results for lobster shelter use and the number of times that they visited the prey patch, there was a strong interaction between the effects of sea bass predation risk and potential contact history on the time that lobsters spent handling prey (predation risk  $\times$  potential contact history interaction:  $\chi^2 = 8.48$ ,  $P = 0.014$ ; Fig. 3C). The presence of sea bass significantly decreased the amount of time that Mid lobsters spent handling prey (Tukey's HSD,  $P = 0.03$ ), whereas

there was no effect of predation risk on the amount of time that MA and DE lobsters spent handling prey (Tukey's HSD,  $P = 0.99$  and  $P = 0.63$ , respectively). In addition, Mid and DE lobsters spent significantly more time handling prey than MA lobsters when sea bass were absent (Tukey's HSD,  $P < 0.001$  and  $P = 0.01$ , respectively), and DE lobsters spent slightly more time handling prey than MA lobsters when sea bass were present, although this trend was not significant (Tukey's HSD,  $P = 0.10$ ).

Unlike our previous results, lobster consumption of prey varied with potential contact history and predation risk independently (predation risk  $\times$  potential contact history interaction:  $\chi^2 = 2.08$ ,  $P = 0.35$ ). The total amount of prey that lobsters consumed was significantly reduced by the presence of sea bass ( $\chi^2 = 19.44$ ,  $P < 0.001$ ; Fig. 3D). Mid and DE lobsters both consumed significantly fewer mussels in the presence of sea bass (Tukey's HSD,  $P = 0.03$  and  $P = 0.01$ ), while MA lobsters consumed very few mussels when sea bass were absent, and no mussels when sea bass were present. There was also a significant effect of potential contact history on the number of mussels consumed ( $\chi^2 = 25.95$ ,  $P < 0.001$ ), with Mid and DE lobsters consuming significantly more mussels than MA lobsters (Tukey's HSD,  $P = 0.005$  and  $P = 0.01$ , respectively).

## DISCUSSION

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

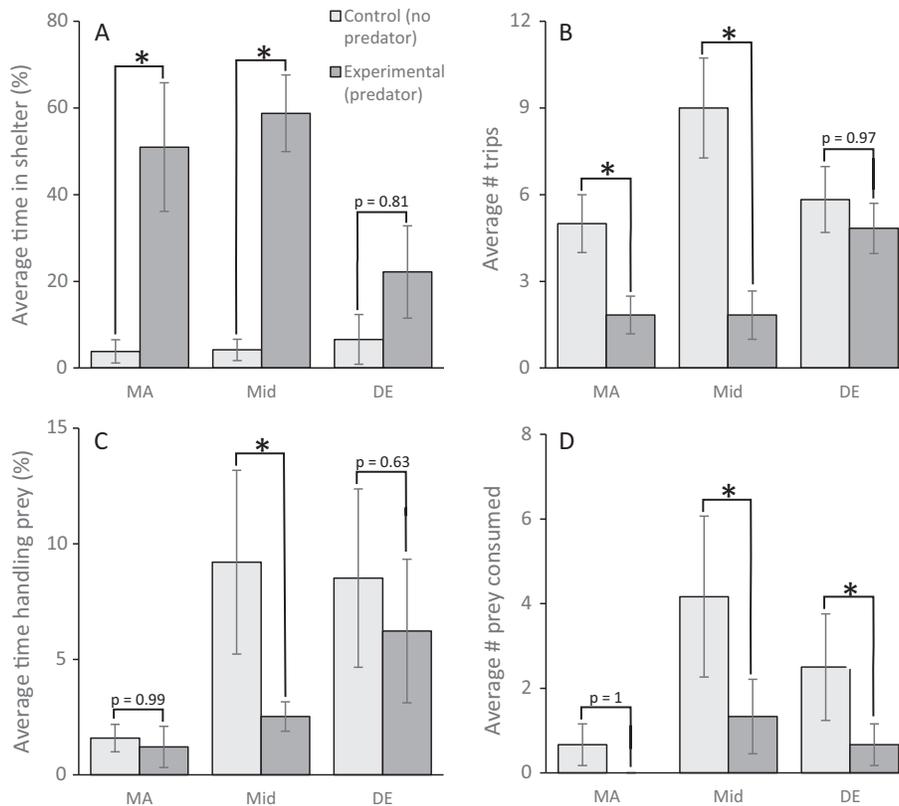


Fig. 3. Average (A) percent of time spent in shelter, (B) number of trips made to the prey patch, (C) percent of time spent handling prey, and (D) number of prey consumed for juvenile *Homarus americanus* from three potential contact history regions in the absence (light gray bars) and presence (dark gray bars) of black sea bass olfactory cues. Error bars indicate  $\pm 1$  standard error. Asterisks indicate significant differences from post hoc multiple comparison analyses of predation risk within regions.

Massachusetts (MA) lobsters have the longest potential contact history with sea bass, but contrary to our expectations, sea bass presence did not affect the amount of time that MA lobsters spent handling prey or the number of prey they consumed. Indeed, even in the absence of predation risk, juvenile lobsters from MA spent very little time trying to dislodge or consume mussels from the prey tile, whereas Mid and DE control lobsters spent more time handling and consuming prey, suggesting that reduced movement and foraging may be advantageous in MA. Such canalized behaviors may reflect the high background level of predation risk typically experienced by MA lobsters. In the southern GOM, lobsters are exposed to a greater diversity and abundance of fish predators compared to the northern GOM; many predatory fish, such as

tautog and scup, are absent or rare in Maine (Wahle et al. 2013, MDMF 2015, MDMR 2015), and the abundance of sea bass and striped bass is low compared to Massachusetts (McMahan and Grabowski unpublished data, MDMF 2015, MDMR 2015). Furthermore, Wahle et al. (2013) found that predation intensity on tethered lobsters was greater in southern New England than in Maine. Hence, when faced with the tradeoff between foraging success and predation risk (Lima and Dill 1990, Lima 1998b), lobsters exposed to greater predation intensity may favor risk-avoidance behavior. The strong risk-avoidance behavior exhibited by MA lobsters, even in the absence of predators, suggests that increased sea bass abundance due to range-shifting may not alter lobster foraging behaviors, and thus population dynamics, in this region. Indeed, the

high level of predation pressure already experienced by lobsters in southern New England and the southern GOM may be one factor influencing the drastic differences in lobster stock abundance between these areas and coastal Maine (Wahle et al. 2013, ASMFC 2015).

Despite the relatively brief time in which these populations have geographically overlapped, lobsters from midcoast Maine (Mid) recognized and responded to sea bass similarly to how they have responded to native fish predators, such as sculpin and Atlantic cod (i.e., reduced movement and foraging; Wahle 1992, McMahan et al. 2013, Wilkinson et al. 2015). Furthermore, Downeast (DE) lobsters consumed significantly fewer mussels in the presence versus absence of sea bass, indicating that they too were able to recognize and respond to a novel predator. This finding supports the life-dinner hypothesis, which predicts that prey rapidly adapt anti-predator defenses because they are experiencing greater selective forces than predators (i.e., a prey losing its life is worse than a predator losing its dinner; Dawkins and Krebs 1979, Brodie and Brodie 1999, Scales et al. 2009). For instance, Scales et al. (2009) found that the evolution of muscle composition in lizards was driven by predator escape behavior rather than foraging mode, likely because selection for survival against predatory attacks is stronger than for incremental gains in foraging efficiency.

Recognition of novel predators may arise through neophobia, a generalized fear response to any novel stimuli (Greenberg 1990, Brown et al. 2013, Ferrari et al. 2015). The presence of neophobia in populations can depend upon the background level of risk prey experience in the environment (Ferrari et al. 2015). Specifically, prey from high-risk environments tend to exhibit neophobic responses to novel predator cues, but prey from low-risk environments do not (Brown et al. 2013, 2014, Chivers et al. 2014, Ferrari et al. 2015). Downeast Maine is a relatively low-risk environment compared to the southern GOM, and therefore, lobsters from DE may not exhibit a strong response to novel predators. We found DE lobsters exhibited weak responses to the threat of predation in the majority of behaviors measured, but strongly responded in reducing their consumption of mussels, suggesting that perhaps some level of neophobia is occurring.

However, the amount of time that they spent in shelter, number of trips to the prey patch, and time spent handling prey were not significantly affected by the presence of sea bass. Therefore, despite potentially recognizing a novel predator, DE lobsters still may be exposing themselves to predation risk. Additional experimental work directly comparing DE lobster responses to black sea bass vs. native predators would help determine if they are in fact behaving like naive prey (Banks and Dickman 2007, Sih et al. 2010). The lack of a strong response in predator avoidance behavior generally agrees with Sih et al. (2010) in suggesting that CEs may be stronger than NCEs for naive prey.

The presence of sea bass induced a trophic cascade, as evidenced by the reduced consumption of mussels by both Mid and DE lobsters. These findings demonstrate the importance of NCEs in driving marine trophic cascades at the edge of predator species' ranges. Furthermore, reduced foraging and resource consumption by lobsters may lead to reduced growth and ultimately impact overall fitness (Lima and Dill 1990, Werner and Anholt 1993, Lima 1998a, Trussell et al. 2006). Combined with the evidence that black sea bass are also consuming lobsters (McMahan 2017), it is possible that the northern range expansion of sea bass may be impacting lobster population dynamics in midcoast Maine and other newly expanded areas.

The variation in how Mid and DE lobsters responded to sea bass presence may be driven by differences in the potential adaptive mechanisms that prey utilize to cope with novel predators. Sih et al. (2010) illustrated several scenarios for how naive prey can respond to non-native predators. For example, if prey use specific cues to identify native predators, then they will only respond to a novel predator if it provides a similar cue. If the cues are different, then the effectiveness of the response will depend on the ability of the prey to recognize general cues, such as conspecific alarm cues, to gauge risk. Prey that use specific cues may ignore a novel predator or exhibit ineffective defenses and consequently be consumed (Sih et al. 2010). Wilkinson et al. (2015) found that lobsters do not respond behaviorally to all fish predators, but rather avoid specific fish predators that they recognize to be a high-risk threat. Confronted with a novel predator, lobsters may not

respond effectively, such as the lobsters from DE Maine. However, some prey species can smell the diet of their predators and can learn to recognize the chemical cue of a novel predator after a single exposure to an individual that has ingested a conspecific (Chivers et al. 1996, Wisenden 2000, Brown 2003, Smee and Weissburg 2006). Therefore, lobsters with even a brief contact history to sea bass may have learned to recognize them as predators, as evidenced by the strong predator avoidance behavior exhibited by Mid lobsters. In otter–urchin–algae ecosystems along the west coast of Vancouver Island, Canada, the reestablishment of otters results in both direct predation on urchins and urchin avoidance of damaged tests from conspecifics, which collectively promote localized patches of algae (Watson and Estes 2011). Further investigation into the effects of predators across a range of potential contact histories, and the mechanisms underlying the ability of prey to recognize novel predators, would greatly enhance our understanding of the relative importance of the CEs and NCEs of non-native predators and their role in driving community structure.

Predation is a fundamental driver of community structure (Hairston et al. 1960, Paine 1980, Sih et al. 1985, Werner and Peacor 2003); however, widespread climate-induced distribution shifts have begun to alter traditional food webs and trophic interactions (e.g., Harley et al. 2006, Kordas et al. 2011, Doney et al. 2012). The expected intensification of current rates of climate change (Peters et al. 2013, IPCC 2014, García Molinos et al. 2015) will likely drive more species to shift their distribution to avoid thermal stress. As predators shift into new environments, the relative importance of CEs and NCEs will depend on the ability of prey to recognize novel predators, the speed at which they adapt anti-predator defenses, and the effectiveness of those defenses. Observing CEs and NCEs across species' native and newly expanded ranges, as well as areas where expansion is predicted to occur, could reveal important insights on how range expansions might affect predator–prey interactions, and ultimately community structure. Understanding species-specific responses to distribution shifts, as well as broader ecosystem impacts, will be crucial to effective management and conservation efforts in the future.

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## LITERATURE CITED

- Appelberg, M., B. Söderbäck, and T. Odelström. 1993. Predator detection and perception of predation risk in the crayfish *Astacus astacus*. *Nordic Journal of Freshwater Research* 68:55–62.
- ASMFC [Atlantic States Marine Fisheries Commission]. 2015. American lobster benchmark stock assessment and peer review report. ASMFC American Lobster Stock Assessment Review Panel, Woods Hole, Massachusetts, USA.
- Banks, P. B., and C. R. Dickman. 2007. Alien predation and the effects of multiple levels of prey naiveté. *Trends in Ecology and Evolution* 22:229–230.
- Bell, R. J., D. E. Richardson, J. A. Hare, P. D. Lynch, and P. S. Fratantoni. 2015. Disentangling the effects of climate, abundance, and size on the distribution of marine fish: an example based on four stocks from the Northeast US shelf. *ICES Journal of Marine Science* 72:1311–1322.
- Bretz, F., T. Hothorn, and P. Westfall. 2010. Multiple comparisons using R. CRC Press, Boca Raton, Florida, USA.
- Brodie, E. D. III, and E. D. Brodie Jr. 1999. Predator–prey arms races. *BioScience* 49:557–568.
- Brown, G. E. 2003. Learning about danger: chemical alarm cues and local risk assessment in prey fishes. *Fish and Fisheries* 4:227–234.
- Brown, G. E., D. P. Chivers, C. K. Elvidge, C. D. Jackson, and M. C. O. Ferrari. 2014. Background level of risk determines the intensity of predator neophobia in juvenile convict cichlids. *Behavioral Ecology and Sociobiology* 68:127–133.
- Brown, G. E., M. C. O. Ferrari, C. K. Elvidge, I. Ramnarine, and D. P. Chivers. 2013. Phenotypically plastic neophobia: a response to variable predation risk. *Proceeding of the Royal Society B: Biological Sciences* 280:20122712.
- Chivers, D. P., M. I. McCormick, M. D. Mitchell, R. A. Ramasamy, and M. C. Ferrari. 2014. Background

- level of risk determines how prey categorize predators and non-predators. *Proceeding of the Royal Society B: Biological Sciences* 281:20140355.
- Chivers, D. P., D. B. Wisenden, and R. J. F. Smith. 1996. Damselfly larvae learn to recognize predators from chemical cues in the predator's diet. *Animal Behaviour* 52:315–320.
- Cox, J. G., and S. L. Lima. 2006. Naiveté and an aquatic–terrestrial dichotomy in the effects of introduced predators. *Trends in Ecology & Evolution* 21:674–680.
- Dawkins, R., and J. R. Krebs. 1979. Arms races between and within species. *Proceeding of the Royal Society B: Biological Sciences* 205:489–511.
- Diamond, J., and T. J. Case. 1986. Overview: introductions, extinctions, exterminations, and invasions. Pages 65–79 *in* J. Diamond and T. J. Case, editors. *Community ecology*. Harper and Row, New York, New York, USA.
- Doney, S. C., et al. 2012. Climate change impacts on marine ecosystems. *Marine Science* 4:11–37.
- Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282:473–476.
- Ferrari, M. C., M. I. McCormick, M. G. Meekan, and D. P. Chivers. 2015. Background level of risk and the survival of predator-naïve prey: Can neophobia compensate for predator naivety in juvenile coral reef fishes? *Proceeding of the Royal Society B: Biological Sciences* 282:20142197.
- Freeman, A. S., and J. E. Byers. 2006. Divergent induced responses to an invasive predator in marine mussel populations. *Science* 313:831–833.
- García Molinos, J., B. S. Halpern, D. S. Schoeman, C. J. Brown, W. Kiessling, P. J. Moore, J. M. Pandolfi, E. S. Poloczanska, A. J. Richardson, and M. T. Burrows. 2015. Climate velocity and the future global redistribution of marine biodiversity. *Nature Climate Change* 6:83–88.
- Garrison, L. P., and J. S. Link. 2000. Dietary guild structure of the fish community in the Northeast United States continental shelf ecosystem. *Marine Ecology Progress Series* 202:231–240.
- Grabowski, J. H. 2004. Habitat complexity disrupts predator–prey interactions but not the trophic cascade on oyster reefs. *Ecology* 85:995–1004.
- Greenberg, R. 1990. Ecological plasticity, neophobia, and resource use in birds. *Studies in Avian Biology* 13:431–437.
- Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* 94:421–425.
- Hare, J. A., et al. 2016. A vulnerability assessment of fish and invertebrates to climate change on the Northeast US Continental Shelf. *PLOS ONE* 11: e0146756.
- Harley, C. D., A. R. Hughes, K. M. Hultgren, B. G. Miner, C. J. Sorte, C. S. Thornber, L. F. Rodriguez, L. Tomanek, and S. L. Williams. 2006. The impacts of climate change in coastal marine systems. *Ecology Letters* 9:228–241.
- Hobbs, R. J., et al. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography* 15:1–7.
- Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models. *Biometrical Journal* 50:346–363.
- IPCC. 2014. *Climate Change 2014: synthesis Report*. Page 151 *in* Core Writing Team, R. K. Pachauri, and L. A. Meyer, editors. *Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. IPCC, Geneva, Switzerland.
- Kimbrow, D. L., J. E. Byers, J. H. Grabowski, A. R. Hughes, and M. F. Piehler. 2014. The biogeography of trophic cascades on US oyster reefs. *Ecology Letters* 17:845–854.
- Kordas, R. L., C. D. Harley, and M. I. O'Connor. 2011. Community ecology in a warming world: the influence of temperature on interspecific interactions in marine systems. *Journal of Experimental Marine Biology and Ecology* 400:218–226.
- Lima, S. L. 1998a. Nonlethal effects in the ecology of predator-prey interactions. *BioScience* 48:25–34.
- Lima, S. L. 1998b. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior* 27:215–290.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- Matassa, C. M., and G. C. Trussell. 2015. Effects of predation risk across a latitudinal temperature gradient. *Oecologia* 177:775–784.
- McMahan, M. D. 2017. *Ecological and socioeconomic implications of a northern range expansion of black sea bass, *Centropristis striata**. Dissertation. Northeastern University, Boston, Massachusetts, USA.
- McMahan, M. D., D. C. Brady, D. F. Cowan, J. H. Grabowski, and G. D. Sherwood. 2013. Using acoustic telemetry to observe the effects of a groundfish predator (Atlantic cod, *Gadus morhua*) on movement of the American lobster (*Homarus americanus*). *Canadian Journal of Fisheries and Aquatic Science* 70:1625–1634.

- McMahan, M. D., D. F. Cowan, Y. Chen, G. D. Sherwood, and J. H. Grabowski. 2016. Growth of juvenile American lobster *Homarus americanus* in a changing environment. *Marine Ecology Progress Series* 557:177–187.
- MDMF [Massachusetts Division of Marine Fisheries]. 2015. United States Department of Interior Fish and Wildlife Service Region 5 Wildlife and Sport Fish Restoration Program: 2015 Annual Performance Report. MDMF, Boston, Massachusetts, USA. <http://www.mass.gov/eea/docs/dfg/dmf/programsandprojects/2015-resource-annual-report.pdf>
- MDMR [Maine Department of Marine Resources]. 2015. Annual report on the Maine-New Hampshire Inshore Trawl Survey 2015. MDMR, West Boothbay Harbor, Maine, USA. <https://www.maine.gov/dmr/science-research/projects/traulsurvey/reports/documents/2015.pdf>
- Mercer, L. P. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Atlantic), black sea bass. *Biological Report* 82. U.S. Fish and Wildlife Service, Washington, D.C., USA.
- Nelson, D. A., D. Perry, and E. Baker. 2003. Natural spawning of black sea bass, *Centropristis striata*, at the NMFS Milford Laboratory and the UMASS Dartmouth Laboratory with observations on spawning behavior. *Journal of Shellfish Research* 22:297–298.
- Nye, J. A., J. S. Link, J. A. Hare, and W. J. Overholtz. 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. *Marine Ecology Progress Series* 393:111–129.
- Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* 49:666–685.
- Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.
- Peacor, S. D., and E. E. Werner. 2001. The contribution of trait-mediated indirect effects to the net effects of a predator. *Proceedings of the National Academy of Sciences USA* 98:3904–3908.
- Peckarsky, B. L., et al. 2008. Revisiting the classics: considering nonconsumptive effects in textbook examples of predator–prey interactions. *Ecology* 89:2416–2425.
- Perry, A. L., P. J. Low, J. R. Ellis, and J. D. Reynolds. 2005. Climate change and distribution shifts in marine fishes. *Science* 308:1912–1915.
- Pershing, A. J., et al. 2015. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Science* 350:809–812.
- Peters, G. P., R. M. Andrew, T. Boden, J. G. Canadell, P. Ciais, C. Le Quéré, G. Marland, M. R. Raupach, and C. Wilson. 2013. The challenge to keep global warming below 2°C. *Nature Climate Change* 3:4–6.
- Pinsky, M. L., B. Worm, M. J. Fogarty, J. L. Sarmiento, and S. A. Levin. 2013. Marine taxa track local climate velocities. *Science* 341:1239–1242.
- Poloczanska, E. S., et al. 2013. Global imprint of climate change on marine life. *Nature Climate Change* 3:919–925.
- Preisser, E. L., and D. I. Bolnick. 2008. The many faces of fear: comparing the pathways and impacts of nonconsumptive predator effects on prey populations. *PLOS ONE* 3:e2465.
- Preisser, E. L., D. I. Bolnick, and M. F. Benard. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology* 86:501–509.
- R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Scales, J. A., A. A. King, and M. A. Butler. 2009. Running for your life or running for your dinner: What drives fiber-type evolution in lizard locomotor muscles? *American Naturalist* 173:543–553.
- Schmitz, O. J., A. P. Beckerman, and K. M. O'Brien. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* 78:1388–1399.
- Schmitz, O. J., J. H. Grabowski, B. L. Peckarsky, E. L. Preisser, G. C. Trussell, and J. R. Vonesh. 2008. From individuals to ecosystem function: toward an integration of evolutionary and ecosystem ecology. *Ecology* 89:2436–2445.
- Schmitz, O. J., V. Krivan, and O. Ovadia. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters* 7:153–163.
- Selden, R. L., R. D. Batt, J. W. Morley, and M. L. Pinsky. 2016. The Influence of Predator–prey Interactions on Climate-induced Range Shifts in Marine Communities. In: American Geophysical Union, Ocean Sciences Meeting 2016, abstract# ME41A-04.
- Sih, A., D. I. Bolnick, B. Luttbeg, J. L. Orrock, S. D. Peacor, L. M. Pintor, E. Preisser, J. S. Rehage, and J. R. Vonesh. 2010. Predator–prey naïveté, antipredator behavior, and the ecology of predator invasions. *Oikos* 119:610–621.
- Sih, A., P. Crowley, M. McPeck, J. Petranka, and K. Strohmeier. 1985. Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics* 16:269–311.
- Smee, D. L., and M. J. Weissburg. 2006. Hard clams (*Mercenaria mercenaria*) evaluate predation risk using chemical signals from predators and injured

- conspecifics. *Journal of Chemical Ecology* 32:605–619.
- Spanier, E., T. P. McKenzie, J. S. Cobb, and M. Clancy. 1998. Behavior of juvenile American lobsters, *Homarus americanus*, under predation risk. *Marine Biology* 130:397–406.
- Steneck, R. S. 1997. Fisheries-induced biological changes to the structure and function of the Gulf of Maine ecosystem. Pages 151–165 in G. T. Wallace and E. F. Braasch, editors. *Proceedings of the Gulf of Maine Ecosystem Dynamics Scientific Symposium and Workshop*. RARGOM Report. Regional Association for Research on the Gulf of Maine, Hanover, New Hampshire, USA.
- Tang, F., T. Minch, K. Dinning, C. J. Martyniuk, R. Kilada, and R. Rochette. 2015. Size-at-age and body condition of juvenile American lobsters (*Homarus americanus*) living on cobble and mud in a mixed-bottom embayment in the Bay of Fundy. *Marine Biology* 162:69–79.
- Trussell, G. C. 2000. Phenotypic plasticity in latitudinally separated populations of *Littorina obtusata*. *Evolutionary Ecology Research* 2:803–822.
- Trussell, G. C., P. J. Ewanchuk, and M. D. Bertness. 2002. Field evidence of trait-mediated indirect interactions in a rocky intertidal food web. *Ecology Letters* 5:241–245.
- Trussell, G. C., P. J. Ewanchuk, and C. M. Matassa. 2006. The fear of being eaten reduces energy transfer in a simple food chain. *Ecology* 87:2979–2984.
- Trussell, G. C., and M. O. Nicklin. 2002. Cue sensitivity, inducible defense, and trade-offs in a marine snail. *Ecology* 83:1635–1647.
- Wahle, R. A. 1992. Body-size dependent anti-predator mechanisms of the American lobster. *Oikos* 65:52–60.
- Wahle, R. A., C. Brown, and K. Hovel. 2013. The geography and body-size dependence of top-down forcing in New England's lobster-groundfish interaction. *Bulletin of Marine Science* 89:189–212.
- Walther, G. R. 2010. Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2019–2024.
- Watson, J., and J. A. Estes. 2011. Stability, resilience, and phase shifts in rocky subtidal communities along the west coast of Vancouver Island, Canada. *Ecological Monographs* 81:215–239.
- Werner, E. E., and B. R. Anholt. 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *American Naturalist* 142:242–272.
- Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84:1083–1100.
- Wilkinson, E. B., J. H. Grabowski, G. D. Sherwood, and P. O. Yund. 2015. Influence of predator identity on the strength of predator avoidance responses in lobsters. *Journal of Experimental Marine Biology and Ecology* 465:107–112.
- Williams, J. W., and S. T. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* 5:475–482.
- Wisenden, B. D. 2000. Olfactory assessment of predation risk in the aquatic environment. *Philosophical Transactions of the Royal Society B: Biological Sciences* 355:1205–1208.
- Witman, J. D., R. J. Etter, and F. Smith. 2004. The relationship between regional and local species diversity in marine benthic communities: a global perspective. *Proceedings of the National Academy of Sciences USA* 101:15664–15669.

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