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# Using acoustic telemetry to observe the effects of a groundfish predator (Atlantic cod, *Gadus morhua*) on movement of the American lobster (*Homarus americanus*)<sup>1</sup>

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**Abstract:** American lobster (*Homarus americanus*) landings have more than quadrupled in the last two decades (1990–2010), coinciding with the collapse of Gulf of Maine groundfish fisheries such as Atlantic cod (*Gadus morhua*). Recently there has been speculation that the release of lobster from predatory control may have resulted in both lower predation rates and increased foraging areas. We used fine-scale acoustic telemetry within a 200 m × 250 m field enclosure to test the hypothesis that cod induce lobsters to decrease movement and seek refuge. We found a large amount of variation in the behavioral response of individual lobsters to predators; however, the addition of cod into the enclosure reduced maximum daily home range area and significantly reduced the distance traveled from shelter habitat area for all individuals. When predators were removed from the enclosure, lobsters responded by increasing home range area and significantly increasing the distance traveled from shelter habitat area. These results represent the first experimental evidence for American lobster range contraction and subsequent expansion in the presence and absence of cod, respectively.

**Résumé :** Les débarquements de homards (*Homarus americanus*) ont plus que quadruplé au cours des deux dernières décennies (1990–2010), coïncidant avec l'effondrement des pêches aux poissons de fond, comme la morue (*Gadus morhua*), dans le golfe du Maine. Il a récemment été proposé que la disparition du contrôle des homards par la prédation puisse s'être traduite par des taux de prédation réduits et de plus grandes zones d'alimentation. Nous avons utilisé la télémétrie acoustique de haute résolution dans un enclos en mer de 200 m sur 250 m pour vérifier l'hypothèse voulant que la morue incite les homards à restreindre leurs déplacements et à trouver refuge. Nous avons noté d'importantes variations en ce qui concerne la réaction comportementale individuelle des homards à la présence de prédateurs; cela dit, l'ajout de morues dans l'enclos a entraîné une diminution de la superficie maximum du domaine vital quotidien et une diminution significative de la distance des excursions en dehors de la zone d'habitat refuge pour tous les individus. Quand les prédateurs étaient retirés de l'enclos, la superficie du domaine vital des homards augmentait et la distance des excursions en dehors de la zone d'habitat refuge augmentait significativement. Ces résultats constituent les premières preuves expérimentales de la contraction du domaine vital du homard en présence de morues et de son expansion en leur absence. [Traduit par la Rédaction]

## Introduction

It is well-established that predators strongly influence the structure and function of ecological communities (Hairston et al. 1960; Paine 1969, 1980; Crooks and Soulé 1999). Communities are structured by predation both directly when predators consume prey, thereby influencing their densities (e.g., Sih et al. 1985; Estes et al. 1998; Williams and Martinez 2000), and indirectly through the cascading effects of predator–prey interactions within food webs (e.g., Schmitz et al. 1997; Peacor and Werner 2001; Berger et al. 2008). In addition to density-mediated indirect effects, indirect effects emerge from shifts in prey behavior, such as changes in activity levels (Werner 1991; Anholt and Werner 1998), foraging behavior (Werner and Mittelbach 1981; Grabowski 2004; Pedersen et al. 2011), and habitat selection (Werner et al. 1983; Schmitz et al. 1997; Grabowski and Kimbro 2005). Prey behavior can influence both individual fitness and trophic interactions and can be more important than consumptive effects for understanding commu-

nity structure (Peacor and Werner 2001; Grabowski 2004; Preisser et al. 2005).

Atlantic cod (*Gadus morhua*) is an iconic species in the North Atlantic noted for its historically high abundance and critical role as a top predator that has been fished extensively over the past several centuries (Goode 1884; Rich 1929; Rose 2007). As a result of heavy exploitation (primarily, but also interactively with climate forcing in some instances; e.g., Rose et al. 2000; Rose 2004), cod stocks throughout much of the North Atlantic have undergone major declines in abundance over recent decades. For instance, in Newfoundland and Labrador, the northern cod stock (North Atlantic Fisheries Organization (NAFO) divisions 2J3KL) was diminished to 1% of its historical biomass (COSEWIC 2003), resulting in a two decade-long moratorium on fishing. In the Gulf of Maine (GOM, USA), cod stocks did not decline as drastically as those observed in Newfoundland and Labrador or other parts of Canada. In particular, the GOM cod stock (NAFO division 5Y) declined from about 45 000 t in the early 1980s to about half that in the

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mid-1990s (Mayo et al. 2009). However, the most recent assessment indicates that the stock is not rebuilding and continues to be overfished (NEFSC 2012). Furthermore, while cod stock biomass declined by only about 50%, cod are now largely absent from nearshore areas of midcoast and eastern Maine (Ames 2004; Wroblewski et al. 2005). Moreover, cod declines along the Maine coast may be very similar (in terms of percent loss) to the collapse in the Canadian cod stocks.

During the 1980s, as GOM Atlantic cod stocks were in steady decline, nearshore landings of the American lobster (*Homarus americanus*) began to increase in Maine (Acheson and Steneck 1997; Steneck and Wilson 2001; Maine Department of Marine Resources 2011). By 2011, nearshore lobster stocks in the GOM had reached record levels of stock abundance and recruitment (ASMFC 2009), and the National Marine Fisheries Service listed the American lobster as the second most valuable commercially fished species in the United States (National Marine Fisheries Service 2011). Fishery-independent data from surveys of juvenile lobsters throughout coastal Maine also have demonstrated that lobster populations increased over the past two decades (Steneck and Wilson 2001). Meanwhile, Atlantic cod and other large groundfish species remain functionally absent in this nearshore ecosystem, and this once dominant, large-bodied predator has been largely replaced by smaller-bodied fish, such as cunner (*Tautoglabrus adspersus*) and sculpin (*Myoxocephalus scorpius*) (Witman and Sebens 1992; Steneck 1997).

Removing apex predators from an ecosystem can release intermediate predators from predatory control, resulting in subsequent cascading effects on lower trophic levels (Estes et al. 1998; Crooks and Soulé 1999; Myers et al. 2007). Cod were once a dominant predator in the GOM and have been shown to consume lobsters, especially in shallow rocky environments common to coastal Maine (Bigelow and Schroeder 1953; Sherwood and Grabowski 2010). The sharp decline of cod and other large groundfish in the nearshore waters of the GOM during the latter half of the twentieth century likely reduced the risk of lobsters being consumed by predators (Steneck 1997; Jackson et al. 2001) and may have released lobsters to forage unimpeded in areas with less shelter availability such as mud and sand bottom (Patterson et al. 2009; Pedersen et al. 2011). Laboratory studies have demonstrated that juvenile lobsters (<40 mm carapace length) alter their behavior in the presence of predators by increasing time spent in shelter and decreasing the distance and frequency of foraging (Wahle 1992; Spanier et al. 1998). Yet it is unclear if predatory fish inhibit the foraging and mating behavior of adult lobsters.

This study examined the nonconsumptive effects of predators on the American lobster using acoustic telemetry to track fine-scale lobster movement before and after the addition of Atlantic cod predators into a large enclosed embayment. Specifically, we examined whether the presence of cod affected lobster shelter use and movement behavior (i.e., home range and distance from shelter). We hypothesized that the presence of cod would induce lobsters to move less and increase shelter usage.

## Methods

### Study site

We conducted the experiment in a large, enclosed natural embayment previously used to hold commercially caught lobsters for several months at a time (but not since 1997). The oblong circular enclosure, located in Friendship, Maine (43°57'36.40"N, 69°20'42.08"W; Fig. 1), measured roughly 200 m × 250 m and was approximately 4 m deep at its deepest point (at low tide). Water entered the enclosure through a narrow channel on the northeast opening. This channel was partially blocked by a dam, which caused a reduced tidal flux of roughly 2 m. Substrate within the enclosure consisted of rocky habitat, eel grass, and mud bottom (Fig. 1). Within the channel, rocky habitat consisted of low relief

(<0.5 m high) cobble and boulder piles that create crevices offering ample refuge for juvenile and adult lobsters. There were also 20 hand-molded concrete shelters and 20 cinderblocks located southwest of the channel providing additional shelter. Directly adjacent to the rocky habitat there were occasional small (<10 m<sup>2</sup>) patches of seagrass (*Zostera marina*) habitat; however, the vast majority of remaining habitat in the enclosure was mud bottom. The top of the channel was open to the ocean, allowing natural immigration and emigration of organisms. Because of this opening, there was a large resident population of lobsters within the enclosure as well as many other micro- and macro-organisms commonly found in coastal Maine waters. We placed mesh wire across the opening prior to the start of the experiment to prevent escape of experimental organisms. It is important to note that the enclosure contained natural habitats where lobsters are typically found and lobster densities (~1·m<sup>-2</sup> in the cobble bottom; M.D. McMahon, unpublished data) common to midcoast Maine.

### Acoustic system

A Vemco (Halifax, Canada) Positioning System (VPS) was used to observe lobster and cod movement behavior. The system consisted of an array of five VR2W acoustic receivers and five synchronization tags moored with each receiver to correct for clock drift. Each VR2W receiver was equipped with a hydrophone that detected Vemco coded transmitters within the receiver's range. Transmitters emitted a signal at 69 kHz that included an ID number and allowed for identification of specific tags. The signal was repeated after a random delay between 60 and 180 s, which minimized the probability of signal collision among tags. Tags were 29 mm in length, 9 mm in diameter, and weighed 4.7 g (in air).

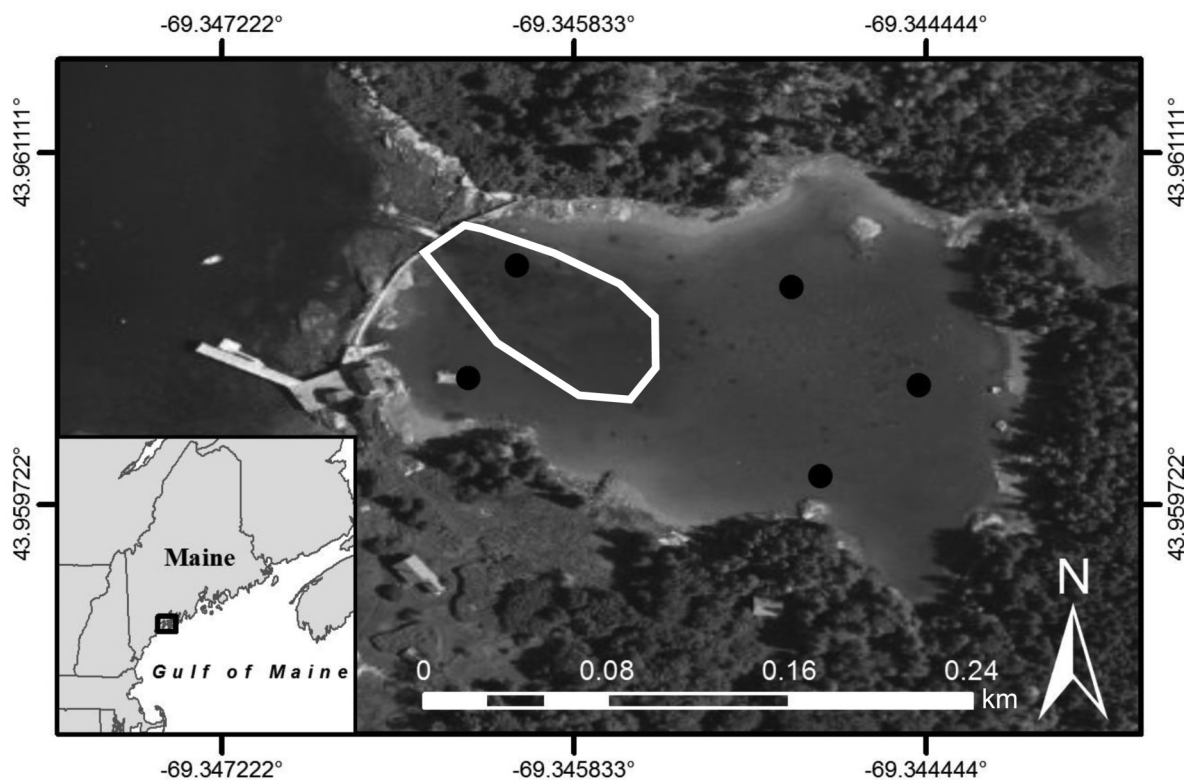
A range test was conducted prior to beginning the experiment to determine the array design that maximized detection efficiency. Receivers were positioned so that detection ranges overlapped, increasing the likelihood that each tag would be detected by multiple receivers. Espinoza et al. (2011) tested the efficiency of the VPS system and found that an array design similar to ours resulted in fine-scale positional accuracy (2.13 ± 1.31 m) within the array.

### Tagging and experimental design

Lobsters were caught from within the Friendship enclosure, and each lobster was measured, sexed, and fitted with a V9-2L tag on 3 September 2009. Lobsters ranged in size from 61.2 to 83.0 mm carapace length (CL; mean = 70.6 mm CL) and were large enough to avoid being consumed by the cod used in this study. Of the five lobsters, four were female and one was male. They were all in the intermolt stage and had no visible signs of injury (i.e., missing appendages). Lobsters were identified by tag number as Lobsters 1–5. Tags weighed approximately 1% of the animal's body mass and were similar in size and shape to transmitters that have previously been shown to have no influence on the movement of rock lobster (*Jasus lalandii*; Atkinson et al. 2005). Tags were attached around the base of the right claw with a plastic cable tie. The lobsters were then released back into the enclosure and left for a period of 21 days prior to the addition of cod (termed "pre-cod").

On 24 September 2009, Atlantic cod were caught by hook and line in Muscongus Bay, Maine (immediately adjacent to the Friendship enclosure). Cod ranged in size from 44.0 to 53.5 cm total length (mean 47.2 cm total length). The fish were brought back to the enclosure in a live well, measured, and tagged with a V9-2L tag. Tags were secured via loop tags (Floy tag) inserted between the first and second rays of the second dorsal fin. The fish were released into the enclosure immediately following tagging and remained in it for 4–10 days (termed "during-cod"). Lobster movement behavior was observed for an additional 17 days after cod were removed (termed "post-cod") to examine how lobsters respond to release from predation risk. Data were downloaded

**Fig. 1.** Experimental enclosure located in Friendship, Maine (43°57'36.40"N, 69°20'42.08"W). Black circles indicate location of acoustic receivers. White outline indicates the majority of the rocky shelter habitat.



from the receivers twice during the experiment, which concluded on 19 October 2009.

#### Analytical methods

Data were filtered prior to analysis to remove positions with high error estimates (i.e., >9 m, sensu Espinoza et al. 2011). Movement was analyzed during the 8 consecutive days before cod were added to the enclosure to establish lobster movement behavior in the absence of a predator. Since lobsters were obtained from within the enclosure, tagged, and released immediately, acclimation likely occurred rapidly. Furthermore, using the last 8 days of the pre-cod period minimized the possibility that the observed lobster movement patterns were a result of acclimation to the environment or stress from capture and handling. For the during-cod period, we analyzed the 8 consecutive days after cod were added to the enclosure. The portion of the post-cod period that was analyzed began 2 days after the last cod was removed and also spanned 8 consecutive days. The 2-day delay between treatment periods allowed for flushing and deterioration of possible olfactory cues that may have remained after the predators were removed. Flushing time for an enclosure of this size is approximately 1 day (Sanford et al. 1992); however, tidal flushing was partially restricted by the gates in the channel. Waiting an additional day after the last cod escaped was a conservative estimate of the time it took for olfactory cues to be flushed from the system.

Home range was calculated using a bivariate kernel density estimator with a diagonal bandwidth matrix (Botev et al. 2010). This method allowed us to determine the density distribution of detected positions. Kernel estimation describes the probability of finding an animal in a given area based on density of detections and is less sensitive to outliers than other methods of home range estimation (Seaman and Powell 1996). We used the detection density at any location as an estimate of the time spent at that particular position and as an indication of habitat use and preference.

The areas containing 95% and 50% of the kernel density distribution were used to describe home range area and core area of activity, respectively. The overall home range and core area of activity were calculated for each individual lobster for the entire 8-day treatment period, as well as for each individual cod. Daily (24 h) home range and core areas were also calculated for each individual lobster during each time period and treated as individual replicates. Kolmogorov–Smirnov (K–S) test was used to compare the distribution of daily home range and core area between time periods.

The core area of activity was then further refined to represent the area containing 10% of the kernel density distribution (i.e., areas with high density of detections but little or no movement). Lobsters typically reside predominantly in shelter habitat (Steneck 2006), and direct observation confirmed that the areas of high kernel density consisted of rocky bottom and eel grass, whereas the outskirts of the home range area generally consisted of unstructured mud bottom. Contours were used to delineate the areas containing 10% of the kernel density distribution for each individual during each time period. The distance of any given detection from the area defined by the contour was used as a measure of the distance traveled from core shelter habitat area. These data were not independent of each other; therefore, prior to statistical analysis, the data were subsampled to remove autocorrelation (Turchin 1998). Detections for each individual were systematically subsampled using a resolution determined from an autocorrelation function. The number of resulting detections for each individual within each time period varied; however, the loss of data due to subsampling did not substantially influence the movement results. We then used the Wilcoxon rank sum test to test if the distance from shelter habitat areas of individual detections differed between time periods for each lobster. All of the above analyses were performed in Matlab R2010b (Mathworks, Natick, Massachusetts).

Fig. 2. (a) Home range area of an individual *Gadus morhua* in the during-cod time period. (b) Movement track of an individual *Homarus americanus* (Lobster 3, female, 73 mm carapace length) in the pre-cod time period. Solid gray line indicates the boundary of the enclosure.

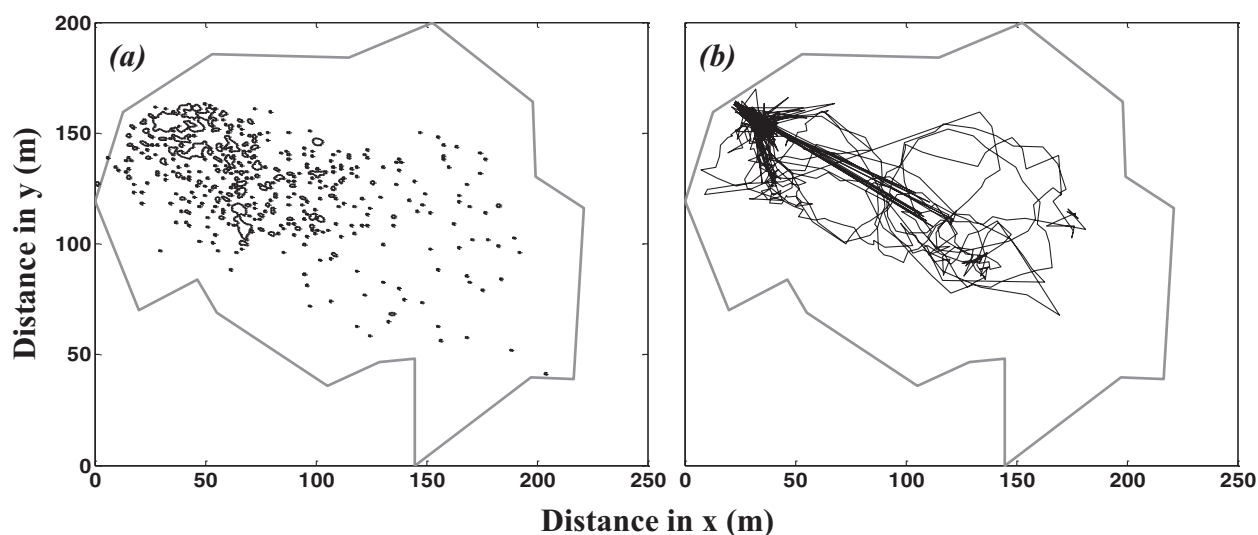


Table 1. Percent change in core area of activity and home range area of *Homarus americanus* between time periods.

	Core area			Home range area		
	Pre-During	During-Post	Pre-Post	Pre-During	During-Post	Pre-Post
Lobster 1	-25%	+54%	+38%	-17%	+62%	+54%
Lobster 2	+98%	+20%	+98%	+84%	+47%	+91%
Lobster 3	-54%	+37%	-27%	-59%	+63%	+11%
Lobster 4	-6%	+4%	-2%	-4%	+7%	+3%

Note: Pre-cod to during-cod = Pre-During, during-cod to post-cod = During-Post, and pre-cod to post-cod = Pre-Post. Increased and decreased area indicated by (+) and (-), respectively.

## Results

A total of five lobsters and three cod were tagged and tracked in this experiment. One lobster (female) escaped from the enclosure 10 days after release; therefore, four lobsters were used in the analyses. There were differences in cod density in the during-cod period because of cod escapement. In particular, 4 days after cod were added to the enclosure, the mesh wire running across the channel opening collapsed because of a buildup of macroalgae that created excess pressure during outgoing tides. The channel remained open for the remainder of the experiment. Immediately after this incident, one cod escaped. The second cod escaped after 6 days in the enclosure and the third after 10 days. It is possible that other predators may have entered the enclosure after the mesh wire was removed; however, large predators are rare in coastal Maine (Witman and Sebens 1992; Hovel and Wahle 2010) and were never observed within the enclosure during the experiment.

Prior to analysis, the movement pathway of each lobster was plotted. Movement patterns of all four lobsters did not appear to be constrained by the edges of the enclosure (i.e., lobsters spent <1% of time along the edge of the enclosure; Fig. 2b). In addition, we found that many of the largest movements occurred during the daytime despite the nocturnal nature of lobsters. Therefore, we chose to analyze data from the entire 24 h day cycle to encompass all of the observed movement behavior.

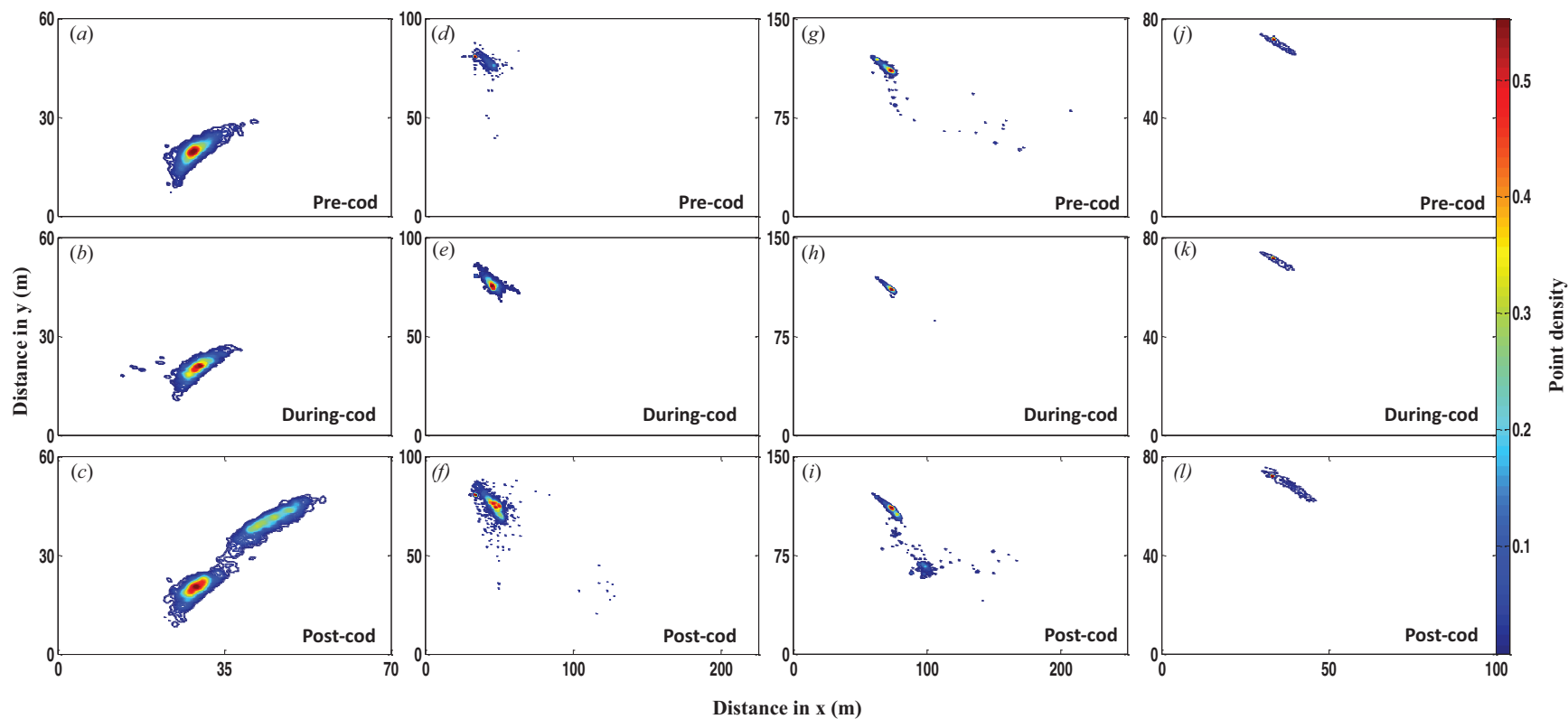
The overall home range size for all cod was  $915.1 \pm 129.4 \text{ m}^2$ . The overall home range size for all lobsters was  $315.3 \pm 157.6 \text{ m}^2$  in the pre-cod period,  $338.8 \pm 141.5 \text{ m}^2$  in the during-cod period, and  $786.1 \pm 321.8 \text{ m}^2$  in the post-cod period; however, the overall core area and home range area among the three treatment periods varied among individuals. For Lobsters 1 and 3, both the core area and home range area decreased between the pre-cod and during-

cod periods and increased between during-cod and post-cod periods (Table 1; Figs. 3a, 3b, 3c, 3g, 3h, and 3i). In addition, the home range area for both of these individuals was larger (11% and 54%) in the post-cod period than in the pre-cod period. Lobster 2 showed a substantial increase in both the core area (98%) and home range area (84%) between the pre-cod and during-cod periods, and both continued to increase in the post-cod period (Table 1; Figs. 3d, 3e, and 3f). Lobster 4 showed a slight decrease between the pre-cod and during-cod periods, followed by a slight increase between the during-cod and post-cod periods for both the core and home range area (Table 1; Figs. 3j, 3k, and 3l).

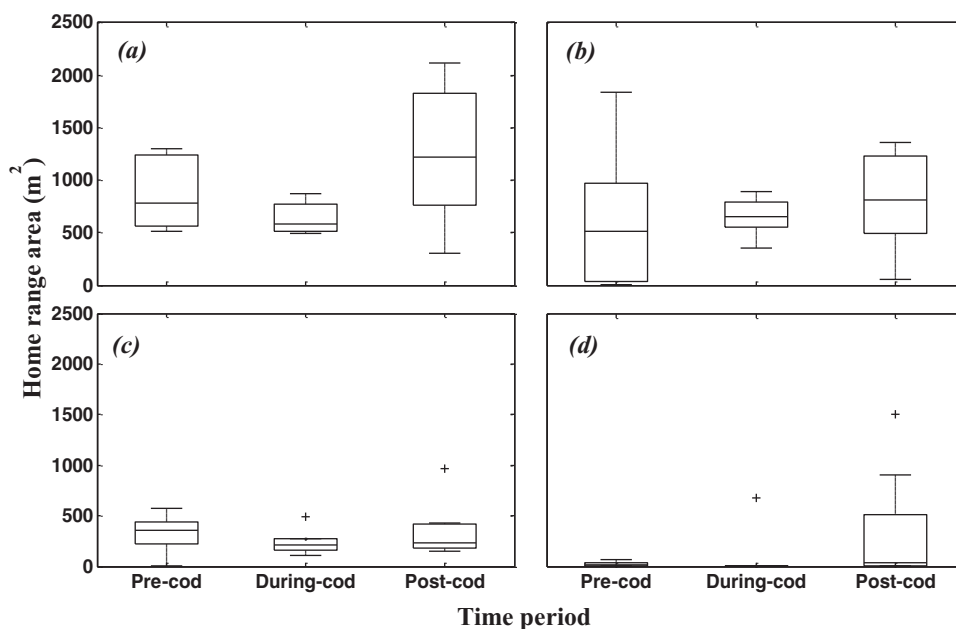
Counter to the above two lobster metrics, the maximum daily (24 h) home range area decreased for all four lobsters between pre-cod and during-cod periods and increased between the during-cod and post-cod periods (Fig. 4). However, the mean daily home range area for each time period varied among individuals. Lobster 3 showed a significant decrease in mean daily home range area between the pre-cod and during-cod periods at a 95% confidence level ( $p < 0.05$ , K-S test) and Lobster 2 at a 90% confidence level ( $p = 0.09$ , K-S test). Lobster 1 and Lobster 4 did not show a significant difference in mean daily home range area between pre-cod and during-cod periods. Only Lobster 4 showed a significant increase in mean daily home range area between the during-cod and post-cod periods ( $p < 0.05$ , K-S test). Lobster 1 and Lobster 2 showed a decrease in the maximum daily core area between the pre-cod and during-cod periods and an increase between the during-cod and post-cod periods; however, there was no significant difference in the distribution of daily core area among periods for Lobsters 1-4.

The average distance traveled from core shelter habitat area for all individuals was  $8.8 \pm 3.2 \text{ m}$  in the pre-cod period,  $4.8 \pm 1.7 \text{ m}$  in

**Fig. 3.** Kernel density area of *Homarus americanus*. (a, b, c) Lobster 1, male, 83 mm carapace length (CL), (d, e, f) Lobster 2, female, 71 mm CL, (g, h, i) Lobster 3, female, 73 mm CL, and (j, k, l) Lobster 4, female, 65 mm CL) for pre-cod, during-cod, and post-cod time periods. Color bars indicate point density within kernel density contours; warm (i.e., red) colors indicate higher point density, whereas cool (i.e., blue) colors indicate lower point density.



**Fig. 4.** Boxplot of daily home range area of *Homarus americanus* ((a) Lobster 1, male, 83 mm carapace length (CL), (b) Lobster 2, female, 71 mm CL, (c) Lobster 3, female, 73 mm CL, (d) Lobster 4, female, 65 mm CL) within each time period (pre-cod, during-cod, post-cod). For each box, the central mark represents the median, the edges of the box are 25th and 75th percentiles, whiskers extend to extreme data points, and outliers are plotted individually (+).



the during-cod period, and  $10.1 \pm 5.0$  m in the post-cod period. The distance each lobster traveled from core shelter habitat area significantly decreased for all four lobsters between pre-cod and during-cod periods (Lobster 1:  $p < 0.05$ ; Fig. 5a; Lobsters 2–4:  $p < 0.01$ ; Table 2; Figs. 5b, 5c, and 5d) and significantly increased between during-cod and post-cod periods for three of the four lobsters (Lobsters 2–4:  $p < 0.01$ ; Table 2; Figs. 5b, 5c, and 5d). In addition, the distance traveled from core shelter habitat area for Lobsters 2, 3, and 4 significantly increased between the pre-cod and post-cod periods ( $p < 0.05$ ; Table 2; Figs. 5b, 5c, and 5d).

## Discussion

The results of this field experiment suggest that indirect effects of a predator (Atlantic cod) can influence lobster movement. Although results varied among individuals, when cod were present inside the enclosure, all individuals exhibited predator-avoidance behaviors by decreasing their maximum daily home range area and decreasing the distance they traveled from shelter habitat area. McMahan (2011) also found that lobster movement was reduced in the presence of cod when conducting a similar experiment in another large natural enclosure. Additionally, our results agree with laboratory studies that have found that lobsters exhibit shelter-seeking behavior and reduced foraging in the presence of predators (Wahle 1992; Spanier et al. 1998; Wilkinson 2012).

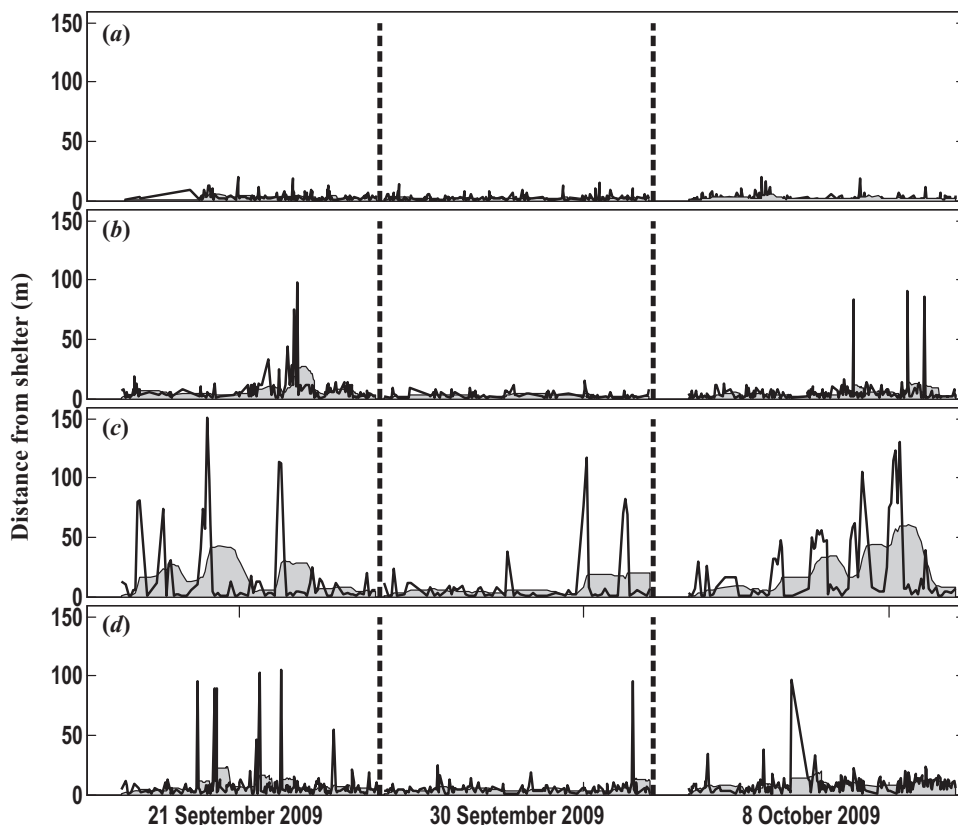
Although we did not intend for predators to escape, this phenomenon was fortuitous in that it allowed us to examine how lobsters respond to being released from the threat of predation. When predators escaped from the enclosure, lobsters increased both their home range area and the distance that they traveled from shelter habitat area. These movement patterns suggest that when released from the threat of predation, lobsters may increase both the distance that they travel and frequency that they forage, which consequently may impact lobster growth rates. Orrock et al. (2013) found that prey tend to decrease movement and growth rates in response to predators when shelter is available.

During the pre-cod and during-cod periods, the home range of all lobsters combined was lower than the home range estimates

found in a similar experiment by Scopel et al. (2009); however, during the post-cod period, the home range increased substantially and was consistent with their findings. There were several differences in the experimental design of these studies that may have caused discrepancies in home range values, including the size of the enclosures, the nature of the habitat within the enclosures, and the location where study animals were collected. In addition, both home range area and distance traveled from shelter habitat area varied widely among individuals in this experiment. For some individuals, movement consistently decreased when predators were present and increased when they were absent. For one individual, home range area increased when predators were present, but the distance traveled from shelter habitat area decreased, suggesting that the lobster utilized more area within shelter habitat but decreased the frequency of longer distance movements outside of shelter habitat. Similar studies have also found large variations in movement behavior among individuals (Golet et al. 2006; Scopel et al. 2009), which emphasizes the complexity of behavior and the importance of incorporating individual variation in models of animal behavior. Given the low replication ( $n = 4$ ) in our study, additional work is needed to determine the degree of variation in how lobsters respond to the threat of predation from cod and other predators.

The post-cod movement patterns revealed that lobsters typically increase their activity level after being released from the threat of predation, which may indicate that compensatory feeding is occurring to account for lost foraging time. In particular, distance traveled from shelter habitat area for three of the four lobsters was significantly greater, and home range area for all of the lobsters increased between 3% and 91% after cod escaped versus before cod were added to the experimental enclosure. These observed changes in behavior suggest that lobsters may respond rapidly by reestablishing their range when predators are no longer present and that they may increase their foraging efforts after high risk periods to compensate for the energy lost from reduced foraging while avoiding predators. While ecological studies investigating the effects of predation risk on prey behavior and growth by exposing prey to constant risk versus no risk have contributed

**Fig. 5.** Distance traveled by *Homarus americanus* ((a) Lobster 1, male, 83 mm carapace length (CL), (b) Lobster 2, female, 71 mm CL, (c) Lobster 3, female, 73 mm CL, (d) Lobster 4, female, 65 mm CL) from individual shelter areas for pre-cod, during-cod, and post-cod time periods. Vertical dashed lines delineate changes in time periods (dates on x axis represent midway point for each time period). Gray shaded areas represent the 12 h running average.



**Table 2.** Percent change in distance traveled from shelter habitat area of *Homarus americanus* between time periods.

	Distance from shelter habitat		
	Pre-During	During-Post	Pre-Post
Lobster 1	-29%*	+12%	-19%
Lobster 2	-61%*	+43%*	+31%*
Lobster 3	-45%*	+60%*	+27%*
Lobster 4	-37%*	+45%*	+25%*

**Note:** Pre-cod to during-cod = Pre-During, during-cod to post-cod = During-Post, and pre-cod to post-cod = Pre-Post. Increased and decreased area indicated by (+) and (-), respectively. Statistical significance is indicated (\*,  $p < 0.05$ ).

greatly to our understanding of how prey respond to predators, these studies have also been criticized because they do not incorporate the temporal variability in predation risk that is common in nature (Sih et al. 2000; Ferrari et al. 2008, 2009; Trussell et al. 2011). The studies that have incorporated predation risk in pulses provide some insight into whether prey exhibit compensatory feeding and growth during periods of low predation risk. Prey that exhibit reduced foraging under risk typically respond to the absence of risk by increasing their activity levels (Sih and McCarthy 2002; Laurila et al. 2004). However, increased foraging behavior during low risk periods does not necessarily result in growth increases after the threat has been removed (Capellán and Nícieza 2007). Furthermore, Trussell et al. (2011) found that prey subjected to pulses of risk experienced strong negative effects on their growth, suggesting that compensatory feeding and growth may not occur even if activity levels increase. While lobsters increased

activity levels after they were released from predators, we did not quantify lobster foraging activity or growth. Further investigation is merited into the consequences of the release of lobster from the risk of predation on their foraging rates, growth rates and efficiency, and reproductive effort, all of which collectively influence lobster fitness.

When exposed to predation risk, foraging animals often face a trade-off between food acquisition and predator avoidance (Sih 1980; Werner et al. 1983; Lima and Dill 1990). We observed that predators induced a decrease in the distance and frequency of movement for lobsters during an 8-day period, suggesting that shelter use increased. Increased shelter use in response to predation has been shown to decrease growth in many species (reviewed in Orrock et al. 2013). However, had we continued to observe lobster movement under predation risk beyond 8 days, it is possible that we would have eventually detected an increase in movement as the risk of lobster starvation increased (e.g., Anholt and Werner 1998). Spanier et al. (1998) observed that lobsters deprived of food developed a temporary “risk-reckless” response in which they spent more time moving and consumed more food than recently fed lobsters in the presence of a predator cue. Yet these lobsters were less selective when choosing prey items and ultimately consumed fewer calories than lobsters foraging in the absence of predators. This finding suggests that hungry lobsters under the threat of predation may adopt different foraging strategies that could lead to insufficient or suboptimal food intake, which may reduce molt increment and lengthen intermolt interval (Waddy et al. 1995). Therefore, if lobsters choose to risk being consumed to gain nourishment, growth rates of survivors may still be negatively affected. The distribution of prey within the enclosure may also have influenced lobster movement behavior;



however, it is unlikely that prey distribution changed among the observed time periods, and thus we expect that any potential influence of prey fields would have been consistent throughout the experiment.

Given the observed differences in lobster behavior after both the addition and removal of cod from the enclosure, we infer that predator cues induced lobsters to alter their behavior. Previous studies have shown that crustaceans sense and respond to olfactory cues released by predators (e.g., Wahle 1992; Appelberg et al. 1993; Spanier et al. 1998). For instance, Appelberg et al. (1993) observed that crayfish increased shelter usage in response to the odor of predator fish species, but not in response to visual stimuli without an accompanying odor. The home range area of the cod in our study was nearly three times larger than lobster home range area. Cod movement patterns indicated that they utilized almost the entire area within the enclosure throughout the duration of the experimental treatment, so lobsters may have been exposed to a combination of both visual and olfactory cues. We did not manipulate and control the type of cues lobsters were exposed to and consequently cannot definitively say if olfactory or visual cues were more prominent in the enclosure. However, our behavioral data suggests that direct encounters between lobsters and cod were probably rare (i.e., lobsters and cod were within 5 m of each other <7% of the time when both were present in the enclosure). Therefore, it is unlikely that lobsters were exposed to many visual cues, whereas olfactory cues from the predators were likely dispersed throughout the enclosure given their large home range. The enclosure experienced a daily tidal flux, but steel plates prevented water from draining out entirely. Therefore, olfactory cues may not have entirely flushed out of the system with each tidal cycle. The low flow nature of the enclosure may in fact have amplified olfactory cues, in turn amplifying the behavioral response of the lobsters. However, the rapid increase in lobster movement after cod escaped suggests that olfactory cues were flushed out of the system soon after the fish had vacated the enclosure and that these cues were routinely flushed with the tide or degraded quickly.

Two previous diet studies of cod have shown that they rarely consume lobsters (Hanson and Lanteigne 2000; Link and Garrison 2002), suggesting that cod are not an important lobster predator. Both studies involved very large sample sizes (15 000–20 000+ cod stomachs per study) using cod caught in trawl surveys. Given that the trawl surveys predominantly target soft sediment habitat and are incapable of sampling primary lobster habitat (i.e., cobble-boulder habitat), these studies may have underrepresented the importance of lobster to the diet of cod. Furthermore, Hanson and Lanteigne (2000) explicitly stated that there is poor overlap between their study areas and where lobsters are normally distributed. Sherwood and Grabowski (2010) found that only red Atlantic cod consumed lobsters, and these cod are typically found in hard substrates common to inshore coastal Maine; however, even in this study, lobsters were not extremely important to the diet of red cod. Even if cod are not important consumers of lobsters, our results suggest that they influence lobster behavior. Thus, these diet studies, collectively with our results, suggest that the recovery of cod populations in coastal waters of the GOM might have larger implications via behavioral cascading interactions rather than direct consumption of lobsters.

While cod and lobster populations in the GOM have been on opposite trajectories over the past two decades, Moland et al. (2013) found that densities of both European lobster (*Homarus gammarus*) and cod increased within marine protected areas during a 4-year period. While it is a somewhat counterintuitive pattern to see both predator and prey species increase simultaneously, these results suggest that harvesting pressure on lobsters was greater than cod consumption of lobsters in these regions. This trend may reverse if predators such as cod remain in the reserves, grow to appreciable size, and consume more lobsters. In general, the re-

lease from fishing pressure can have a strong influence on ecosystems, in some cases weakening predator–prey interactions (Mumby et al. 2007), or transforming communities into states that are not present outside of protected areas (Edgar et al. 2009). If the European lobster also responds to cod by reducing its home range and the distance it is willing to travel from shelter, our results suggest that the European lobsters within marine protected areas may be increasing in abundance but more spatially confined owing to the high cod abundances within them.

Overfishing of cod and other demersal fish populations in coastal portions of the GOM may possibly have resulted in an expansion of lobster home ranges and willingness to travel further from shelter habitat. Home range expansion may in turn increase prey consumption, growth rates, and fecundity (Ahrens et al. 2011). Although efforts to rebuild Atlantic cod stocks have been unsuccessful, there is still potential for cod to rebound in the GOM. Recent efforts to rebuild anadromous fish populations (i.e., alewife, *Alosa pseudoharengus*) along the coast of Maine may influence cod recovery, since these species are a nutritious and predictable food source (Ames 2004; Hall et al. 2011). If cod should recover, especially in nearshore areas, resource managers should be prepared for the potential impacts to the lobster fishery. Continued research on the direct and indirect effects of predator presence on lobster density, growth, and behavior will be crucial to our understanding of the ecological consequences of increased predator abundance and the potential implications for the lobster fishery.

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