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Subtle changes in prey foraging behavior have cascading effects in a shallow estuary

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ABSTRACT: Direct consumption of prey and the effect of predator intimidation on prey behavior are recognized determinants of food web structure, but our understanding of the mechanisms that cause behavioral cascades (trait-mediated indirect effects, TMIE) are lacking, especially for larger, mobile species. Mechanisms of TMIE were measured by both continuous *in situ* monitoring (via telemetry) of predator (red drum *Sciaenops ocellatus*) and prey (blue crab *Callinectes sapidus*) behavior and resource (hard clam *Mercenaria mercenaria*) mortality with and without structure (artificial seagrass). The presence of a predator significantly reduced the mortality of the resource (TMIE), but the TMIE was not affected by the presence of seagrass. The behavioral results indicated that the red drum did not significantly reduce the blue crab's overall movement or habitat domain but did reduce the prey's ability to optimally forage on clam patches. The mechanisms of TMIE were disruptions of short time periods of high prey activity. Our findings highlight subtle mechanisms of TMIE that could be overlooked if qualitative and not quantitative behavioral measurements are conducted. These qualitative results have implications for interpretations of previous TMIE studies as well as risk taking models.

KEY WORDS: Indirect effects · Non-consumptive effects · Structure · Predator–prey interactions · Prey behavior · Red drum · Blue crab · Movement · Telemetry

INTRODUCTION

Predator–prey interactions are important determinants of community dynamics (Menge 1995). Predators influence prey not only through direct predation (consumptive effects, CE) but also by causing the prey to alter their behavior (non-consumptive effects, NCE). The impact of the predator on the prey can also cascade to lower trophic levels and affect the prey's prey (resource). Consumption of prey by predators can alter resources through density-mediated indirect effects (DMIE) and fear induced changes in prey behavior can affect resources resulting in trait-mediated indirect effects (TMIE; see Abrams 2008 for definitions). Behavioral changes (TMIE) are of equal or greater importance than direct predation (DMIE) when measuring the effect of the predator on the resource (Werner & Peacor 2003, Schmitz et al. 2004, Preisser et al. 2005). In an effort to predict the relative importance between DMIE and TMIE or NCE and CE, a framework has recently been hypothesized using predator and prey functional roles (Schmitz et al. 2004, Preisser et al. 2007, Schmitz 2008). Understanding whether these functional roles are context dependent is necessary to determine the applicability of the framework (Schmitz et al. 2004), such as whether anti-predator behavior is altered by habitat complexity and/or predator type. Further, given that structured habitats are common in natural environments and affect predator–prey interactions through altering encounter rates, competition, and hunting mode (Grabowski & Powers 2004, Michel & Adams 2009), investigations of TMIE should include assessment of how structured habitat alters TMIE.

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NCE result from a change in prey behavior, but actual measurement of behavioral modification is rare due to the inherent difficulties in monitoring the movement of terrestrial and aquatic mobile fauna as well as the potential introduction of artifacts by observers. Past research on the mechanisms that cause TMIE have inferred the change in behavior of the prey from observations on whether individuals are active or not (Lima 1998, Bolker et al. 2003). These observations are often used to infer a reduction in movement, even though authors have noted these limited observations are not a valid proxy for behavior (Huang & Sih 1991, Bolker et al. 2003). The accuracy of measuring behavioral changes is important because community dynamic models assume that prey vary activity levels continuously and alter their behavior either instantaneously or gradually (Bolker et al. 2003). Because of the complex behavior of mobile prey, coarse descriptors of predator and prey behavior (e.g. present/absent, moving/stationary) fail to adequately quantify potential behavioral mechanisms.

For mobile predators and prey, particularly those that have some level of learned behavior, tracking prey movements at a high resolution is necessary, with the frequency of samples a function of animal mobility. High-resolution tracking of animal behavior, to our knowledge, has never been used to study TMIE in an aquatic environment. Advances in acoustic telemetry have overcome the difficulties of tracking animals at high resolutions, for long periods of time, and over large spatial distances (>2 m) in turbid marine environments. With the advent of multiple hydrophone arrays, we can track animals with a high degree of temporal (determined by the transmission interval of an acoustic tag) and spatial accuracy (±1 m) (Niezgoda et al. 2002).

The present study directly measured individual responses of predators, prey, and resources to manipulations of predator presence and structure within a tri-trophic level experiment. Specifically, the effect of artificial seagrass on the predator–prey interactions between red drum *Sciaenops ocellatus*, blue crab *Callinectes sapidus*, and hard clams *Mercenaria mercenaria* was assessed by measuring the behavior of red drum (predator) and blue crab (prey) and the mortality of 3 densities of hard clams (resource). We tested the following hypotheses: (1) the presence of the predator will cause a reduction in the distance moved and area used by the prey, which in turn will reduce the foraging of the prey and increase the survival of the resource, (2) prey will forage more in the high density resource patches when not under the threat of predation, and (3) the presence of structure will attenuate the TMIE by providing the prey with a refuge from predation that is in close proximity to the resource patches. The results of the study provide insight into how TMIE are transmitted down trophic levels through changes in prey behavior, which we contend are necessary for predicting and modeling NCE and TMIE.

MATERIALS AND METHODS

Telemetry system and transmitter attachment. We used an acoustic tracking system, the Lotek Wireless MAP 600 multi-port system (MAP), to examine animal behavior. The MAP uses 8 fixed hydrophones to receive coded sounds emitted by ultrasonic transmitters attached to animals (tags). The position of the tag is triangulated when 3 or more hydrophones receive the acoustic transmission. Stationary transmitters were placed randomly throughout the study area to quantify the error in position calculation and to check for drift. Positions from the stationary tags were used to filter the processed data to achieve an accuracy of <1 m. The MAP has been tested in a similar shallow estuarine environment and was found to have an accuracy of <1 m in tracking the movements of blue crabs (Niezgoda et al. 2002).

Crabs were tagged with Lotek Wireless MAP 8-5 acoustic transmitters (8 mm diameter × 34 mm long, mass in air 4.2 g). The Map 8-5 tags had a burst interval of 5 or 15 s, depending on the tag. The transmitters were attached by methods similar to those of Niezgoda et al. (2002) in which a tag was mounted vertically to the top of the crab's carapace. No apparent effect of the tag on the crab's behavior was observed after tagging. Previous studies have used tags twice the weight of these on crabs of similar size and found that crab behavior was not affected (Micheli 1997, Clark et al. 1999). Blue crabs were captured using crab traps in the waters surrounding Dauphin Island. Crabs used for the study (n = 48) had carapace widths that ranged from 140 to 195 mm (mean ± SE, 165.26 ± 2.44 mm). The weight of the crabs used was 193 to 402 g (279.79 ± 8.43 g) to ensure that the tags were less than 3% of the body weight. This size also meant that crabs were too large (>85 cm carapace width) to be consumed by the red drum (Scharf & Schlicht 2000) and allowed only sublethal interactions between the predator and prey.

Red drum were caught using hook and line in waters surrounding Dauphin Island and held in flow-through saltwater tanks. The red drum used had a mean total length of 662 ± 63.95 mm and a weight of 3572 ± 1193 g. This size was chosen to ensure that the transmitters were less than 2% of fish body weight (Eristhee & Oxenford 2001, Bridger & Booth 2003). Red drum were tagged with internal Lotek Wireless MAP 11 acoustic transmitters (11 mm diameter × 56 mm long, mass in air 9.2 g) that had burst intervals of 2 or 5 s.

Experimental design. The study was conducted in an enclosed natural embayment at the Dauphin Island

Sea Lab on Dauphin Island, Alabama from May to July 2005. The embayment was chosen to maximize animal retention while reducing potential enclosure artifacts when confining nekton within cages (Peterson & Black 1994). In an effort to guarantee animal retention within the embayment, Vexar® (MasterNet) fences were set up to block any potential exit points and to divide the larger embayment into 2 smaller enclosures, also referred to as ponds, each approximately 400 m^2 (Fig. 1). The pond had a sand-mud bottom with an average depth of 0.75 m and a 0.5 m tidal range.

The experiment had a two-by-two-factorial design with the 2 factors being structure (artificial seagrass presence/absence) and predator (red drum presence/absence). Blue crabs and clams were placed in all treatments. Treatments were replicated 3 times. Trials were run for 2 to 3 d, which allowed ample time to determine changes in crab behavior as a result of the treatment and have a measurable depletion of prey. Predator treatments were always run concomitantly on both sides of the pond to ensure that the presence of the predator on one side of the pond was not affecting the behavior of the crabs in the adjacent enclosure via transmission of odors (Powers & Kittinger 2002). Trials with predators were alternated with trials without predators to reduce any temporal artifacts. Structure was assigned randomly to the enclosures throughout the experiment.

All trials contained six 1 m^2 resource patches with 2 patches of each of 3 clam densities: 50, 150, and 300 clams. The clams were obtained from the Research AquaCulture commercial hatchery in Stuart, Florida. The clams used in the experiments had an average shell height of 23.4 ± 0.19 mm (range = 11 to 35 mm), which is within the size range consumed by blue crabs (Micheli 1997, N. R. Geraldi pers. obs.). Size ranges of clams were determined from a random sample of 50 clams per trial. Resource patches were placed in 2 rows of 3 with approximately 2 m between rows and 1.5 m between patches in each row (Fig. 1). Resource patch placement was not uniform because we attempted to place them equidistant from each other at consistent depths. The resource patches were made by sinking fixed wooden frames into the ground. Clams for each patch were haphazardly placed in 2 wood trays (1 × 0.5 × 0.05 m) and covered with sand. The 2 trays containing clams were temporarily covered with a 5 mm mesh screen and carefully lowered into the fixed frame by a free diver before the mesh was removed. Clam densities within resource patches were grouped so that each row had one of each of the densities and the densities within each row were randomly assigned to each prey patch.

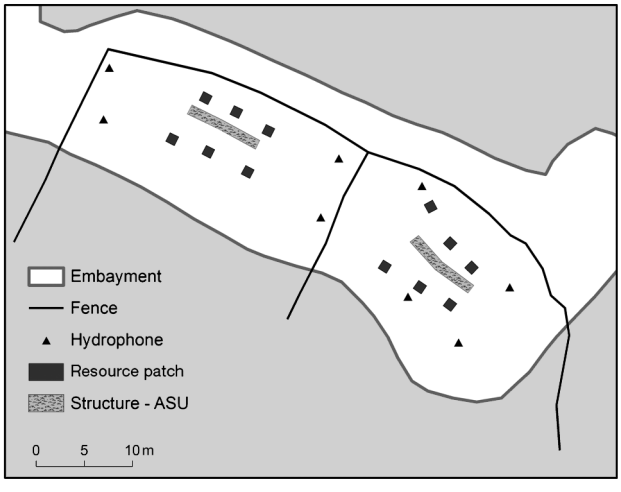

Fig. 1. Experimental set-up of the embayment. Separate trials were run in each pond created by the fence. Structures (artifical seagrass units, ASU) were present only during the appropriate trials

Artificial seagrass units (ASUs) were added to the trials with structure and covered approximately 2% of the individual enclosure (8 m^2). The ASU was constructed of 0.75 × 15 cm green ribbon tied to a sheet of 5 mm mesh Vexar® plastic netting and was designed to mimic turtlegrass *Thalassia testudinum* with a density of 1500 ribbons m^{-2}. The 8 × 1 m ASU was placed in the center of the enclosure and anchored to the substrate using rebar stakes (Fig. 1). Past studies have found that the abundances of fish and crustaceans in ASUs are similar to those in natural seagrass (Kenyon et al. 1999, Upston & Booth 2003). For the trials with a top predator, one tagged red drum was added to the individual enclosure at least 1 h before the beginning of the trial to allow for acclimation. One red drum was used for 2 trials because only 5 were caught.

Prior to the start of each trial, crab traps and gill nets were set in the embayment for a minimum of 24 h to remove crabs and other animals that were potential predators on clams or crabs. Despite attempting to remove all crabs from the enclosure before the beginning of the experiment, untagged crabs were caught between trials. The ponds were fished for an average of 3.3 d with an average catch of 5 untagged blue crabs (mean carapace width 110 mm). Thus, results of clam mortality and intra-species interactions could not be attributed solely to the 4 tagged crabs in each trial. However, the untagged crabs would have reacted to the presence of structure or predator in a similar way as the tagged crabs and thus only prevented the calculation of clam predation by each crab. All trials began in the afternoon between 14:00 and 17:00 h. Four tagged crabs were introduced into each trial and tracking was initiated immediately. Although results could be influenced by acclimation behavior, data showed no evidence of higher or lower rates of movement at the

beginning of the trials. Crabs were only used in a single trial, although in 2 trials, a tagged crab from a previous trial that was assumed to have escaped was detected within the embayment.

All dead clams recovered had been chipped or crushed, and most were crushed beyond recognition so that we were unable to measure total recovery rate. Past studies have found that juvenile clams did not move or change behavior in the presence of predators (Micheli 1997, Powers & Kittinger 2002). As a result, dead or missing clams were assumed to have been eaten by blue crabs because they were the only clam predators present in the experiment.

Statistical analysis. The effect of structure and predator on clam survival (TMIE) was initially tested using a 2-way ANOVA with percent mortality of clams per day as the dependent variable and 2 independent factors each with 2 levels, presence/absence of both structure and predator (Table 1). Because structure had no effect on clam mortality (F value = 0), crab movement or behavior (N. R. Geraldi pers. obs.), structure was excluded from further analyses. In addition to more parsimonious findings, the removal of structure increased our replication from 3 to 6. The effect of predator on TMIE was tested with a 1-way ANOVA with percent mortality of clams per day as the dependent variable and predator (presence/absence) as the independent variable. Clam mortality was expressed as mortality per day to standardize results because 2 trials were 1 d longer than all others. Cochran's test was used to ensure that response variables conformed to the ANOVA's assumption of homogeneous variance for all statistical tests.

To determine if the presence of the predator altered the ability of the crabs to forage on different densities of resource patches, the percent mortality per day without predators was subtracted from the percent mortality per day with predators for each of the 3 different density patches and analyzed with a 1-way ANOVA with initial clam density as the independent variable. Because trials with predators and without predators were run in succession and not simultaneously, identical sides of the pond were paired with the next trial on that side and the difference was calculated. The effect of predator on mortality per day was also determined by pairing trials without and with predators and subtracting them. Using the difference between trials with and without predators as the dependent variable allowed us to determine the effect of predators on initial clam density without artificially inflating replication (n = 18 instead of n = 6), which would have happened if predator was included as a factor. The difference between trials without a predator and with a predator was analyzed with a 1-way ANOVA with mortality per day as the dependent variable.

Table 1. Two-way ANOVA testing the effects of predator and structure on clam mortality

Independent variable	df	F	p
Predator	1	4.18	0.075
Structure	1	0	0.984
Predator × Structure	1	0.47	0.514

Hawths analysis tool (Beyer 2004), an independent Arc View extension, was used to determine the straight-line distances moved by crabs between each consecutive position. The effect of a predator on the hourly movement of the crabs was determined by calculating the mean movement (m h^{-1}) per crab per trial and analyzed as the dependent variable in a 1-way ANOVA with predator as the independent variable. Movement was also broken up into 12 h increments to determine if a predator altered crab behavior as the experiment progressed. An average movement per hour was found for each trial with and without predators for each of 3 time periods (0–12, 13–24, and 25–36 h). The difference between with-predator and without-predator trials was then calculated as explained previously. The effect of predator presence was then analyzed using a repeated measures ANOVA with the 3 time periods as the dependent variables and the difference between trials with and without a predator as the independent variable. The 50 and 90% kernel home ranges of each crab for each trial were determined using Hawths tools (Beyer 2004). The home range of each trial was calculated by averaging each individual crab's home range per trial. Separate 1-way ANOVAs were used to determine the effect of the independent variable, predator, on the dependent variables, 50 and 90% home range.

The effect of a predator on the time spent on resource patches was analyzed by the proportion of crab positions within a 0.5 m buffer around the patches for each trial. The buffer was used because of the error associated with measuring the exact position and orientation of the 1 m^2 resource patches and the error in positioning. To standardize the number of positions between trials due to burst intervals or filtering, the proportion of positions was used instead of total positions. An ANOVA with predator as the independent variable was used to determine the significance of the predator's presence on time spent by crabs on resource patches. To determine if the presence of a predator altered the time spent by crabs in the different density resource patches in 12 h increments through the experiment (0–12, 13–24, and 25–36 h), a repeated measures ANOVA with the 3 resource patch densities and the 3 time periods (repeated measure) as independent variables was run. The dependent variable was difference between the proportion of positions with

and without predators. To test for a relationship between time spent on resource patches and clam mortality, a regression was run with percent clam mortality as the dependent variable and number of crab positions within a 0.5 m buffer around the resource patch as the independent variable.

RESULTS

The TMIE or the effect of the red drum on clam mortality through altering crab behavior was significant (n = 6, $F_{1,10}$ = 4.94, p = 0.05); clam mortality was on average 21% d^{-1} in the presence of red drum but was 30% d^{-1} in the absence of red drum (Fig. 2). The presence of the predator, determined by subtracting trials without a predator from those with a predator, did not affect the percent mortality per day between the 3 different resource density patches (n = 6, $F_{2,15}$ = 0.06, p = 0.945; Fig. 3A). There was a marginally significant difference between the resource patches when the difference between trials without and with predators was calculated for mortality per day (n = 6, $F_{2,15}$ = 2.71, p = 0.099); Fig. 3B).

The MAP system successfully tracked the animals with sub-meter accuracy and approximately 20% of the total acoustic transitions were used after filtering to ensure accuracy, thus giving us approximately 2.5 positions min^{-1} $ind.^{-1}$. The mean distance moved each hour of the day for both the red drum and blue crabs showed a crepuscular pattern (Fig. 4). The standard error shown was calculated between trials after the hourly movement of crabs within a trial was averaged. Movements of crabs with and without a predator were similar except for the twilight hours (Fig. 4B). The mean hourly movement of crabs was not significantly affected by the presence of a predator (n = 6, $F_{1,10}$ = 3.14, p = 0.108; Fig. 5). When movement was examined in 4 h intervals, the presence of the red drum significantly reduced the hourly movement of crabs between 17:00 and 21:00 h (n = 6, $F_{1,10}$ = 5.13, p = 0.047; Figs. 4 & 5B), which was the same time period that the red drum increased their movement (Fig. 4A). Crab movement was broken up into 12 h increments to determine if movement was altered as a result of predator presence through exposure time (Fig. 5C). The difference between crab movement without and with a predator did not significantly change throughout the experiment (n = 6, $F_{2,15}$ = 0.3, p = 0.747). Kernel home range was calculated to determine if the area used by crabs was affected by a predator. Both the 50% kernel home range, which averaged 10 ± 2 m^2 (n = 6, $F_{1,10}$ = 0.10, p = 0.755), and the 90% kernel home range, which averaged 74 ± 10 m^2 (n = 6, $F_{1,10}$ = 0.0, p = 0.97), were not significantly affected by the presence of a predator.

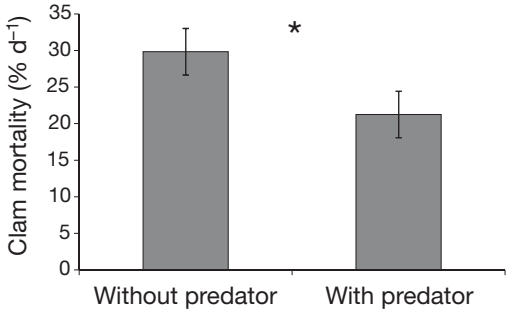

Fig. 2. *Mercenaria mercenaria.* Mean (± SE) percent mortality of clams per day without and with a red drum predator. Percent mortality per day was significantly higher in trials without a predator. *p = 0.05

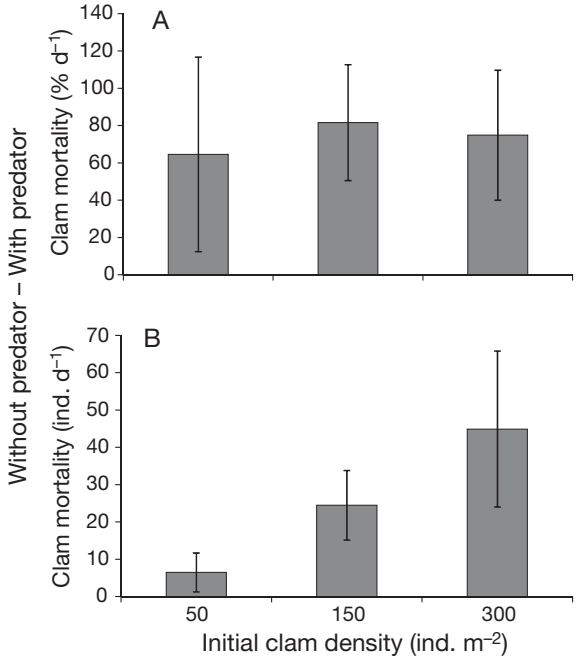

Fig. 3. *Mercenaria mercenaria.* Effects of initial clam density on the mean (±SE) difference in (A) percent mortality of clams per day and (B) mortality of clams per day between trials without and with red drum predators. No significant difference was found between percent mortality per day, but mortality per day was marginally significant (p = 0.099)

The amount of time crabs spent on the resource patches was highly variable between trials, even after the positions of crabs within trials were pooled (Fig. 6). Differences between trials with and without a predator were evident between 10:00 and 16:00 h, when error bars generally did not overlap. The predator did not significantly affect the time crabs spent in the resource patches (n = 6, $F_{1,10}$ = 2.18, p = 0.170; Fig. 7A), but on average, crabs without a predator present spent 40% more time in resource patches than crabs with a predator present (0.23 ± 0.05 and 0.14 ± 0.05, respectively).

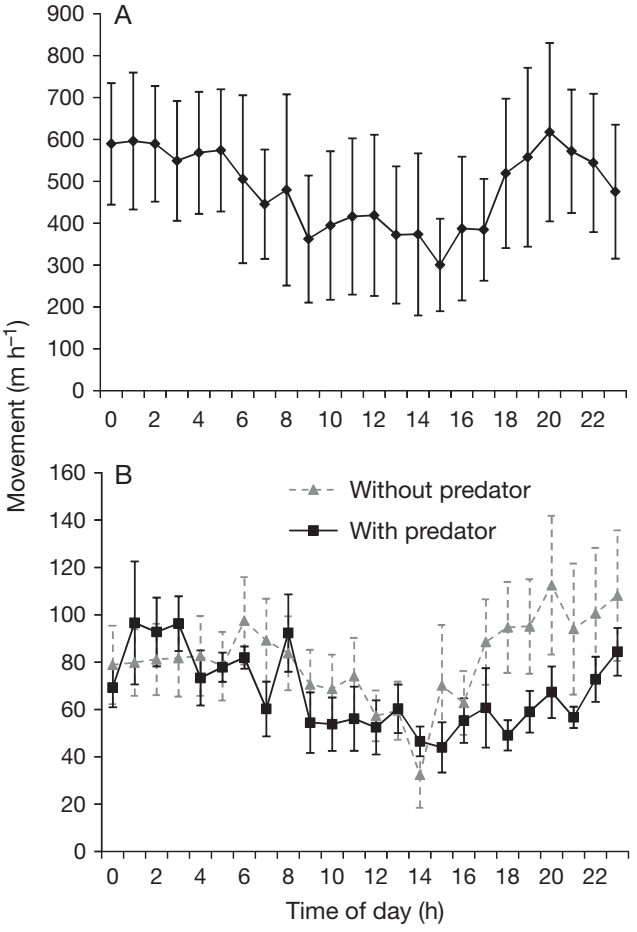

Fig. 4. *Sciaenops ocellatus* and *Callinectes sapidus*. Mean (± SE) daily movement (m h^{-1}) within each trial of (A) tagged red drum and (B) blue crabs without and with a red drum predator

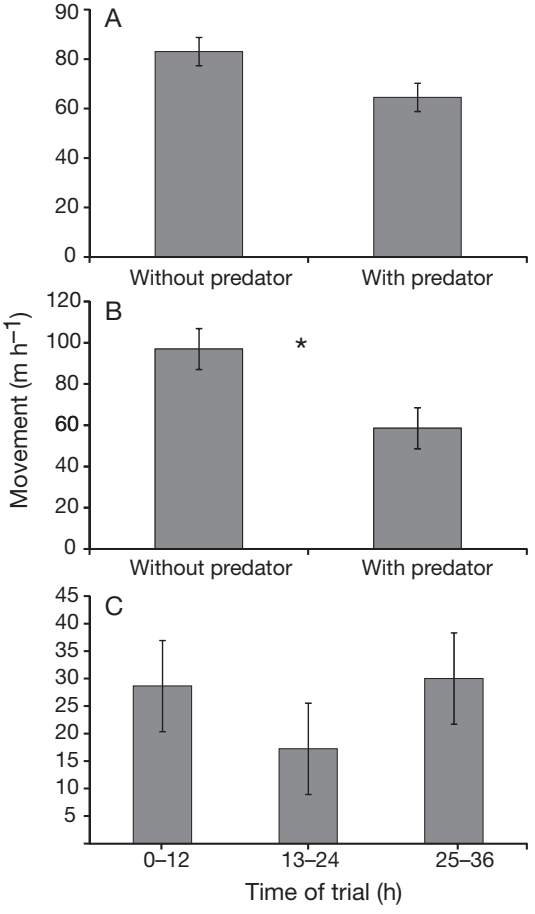

Fig. 5. *Callinectes sapidus*. Mean (± SE) movement of crabs (m h^{-1}) (A) for the entire trial, (B) between 17:00 and 21:00 h each day without and with a predator, and (C) difference in the hourly movement of blue crabs between trials without and with a predator for 3 consecutive time periods within trials. Significance was tested with 3 separate 1-way ANOVAs with the independent variables being (A,B) predator and (C) time of trial. *$p < 0.05$

The difference between trials without and with a predator did not significantly change the time spent in resource patches as the time within trials progressed (Table 2). A marginally significant effect of initial density on time spent in resource patches occurred ($p = 0.07$) with the difference between trials with predator and without predator being greater in high density patches than in low density resource patches. Clam mortality was significantly related to the amount of time spent on the resource patch by crabs ($p < 0.01$), but time spent by crabs in the prey patch explained only 12% of the variance in clam mortality (adjusted $r^2 = 0.12$).

DISCUSSION

Intimidation by predators can trigger behavioral cascades with disproportionate consequences on non-adjacent trophic levels (Preisser et al. 2005). We found that the presence of red drum had a significant indirect effect on the clams through the change in behavior of

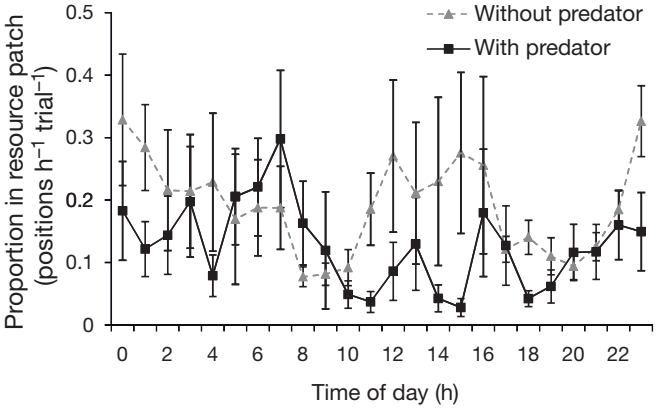

Fig 6. *Callinectes sapidus*. Mean (±SE) proportion of crab positions per hour per trial within resource patches throughout the day

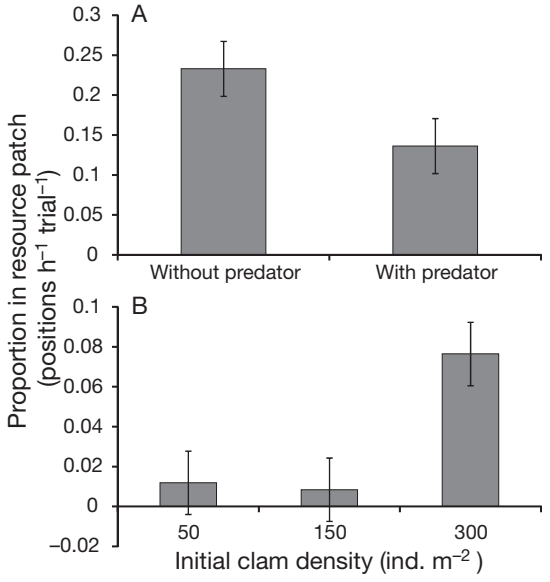

Fig. 7. *Callinectes sapidus.* (A) Mean (± SE) proportion of blue crab positions within clam resource patches for trials without and with a red drum predator. (B) Mean (± SE) difference in the proportion of crab positions within individual resource patches between trials without and with predators when compared to initial clam densities. A 2-way ANOVA was run with initial density and trial period as independent variables and initial density was marginally significant (p = 0.07)

the blue crab. The novelty of this experiment comes from our ability to directly and continuously measure the predator–prey behavioral interaction in a natural environment. Telemetry allowed us to begin to elucidate the mechanism of the TMIE, which was not a presumed overall reduction in prey movement or home range, but changes in movement over small time periods that decreased the prey's time spent feeding on high density resource patches.

Our findings agree with past traditional studies that prey are efficient foragers, finding resource patches and spending more time in the highest density patches (our Fig. 3B; Stephens & Krebs 1986). The threat of predation reduced both the time spent by prey in the high density resource patches and the number of clams eaten in the high density resource patches, both of which likely resulted from the predator impeding the prey's ability to locate high concentrations of resources. This result seems counterintuitive to our findings that overall movement and home range were not altered by anti-predator behavior. The missing link between NCE and TMIE may be explained by changes in daily behavior. The daily activity of the prey was reduced by predator presence during dusk, which was the peak activity period of prey in the absence of a predator. Many species have periods of high activity, which are thought to relate to periods of low predation (Lima 1998), but dusk seems to correspond to periods of high predator activity (Fig. 3). Dusk may be a disproportionally important foraging period, during which anti-predator behavior decreases movement and inhibits the prey's ability to gain knowledge of the location and density of resources (Fig. 3). The intra-day behavior of the prey provides insight into the mechanisms of NCE and why they may not be detected in qualitative experiments.

Table 2. Two-way ANOVA testing the effects of initial resource patch density and trial period on time spent by crabs in resource patches. The independent variable was the difference between trials with and without a predator

Independent variable	df	*F*	p
Initial density	2	4.3	0.07
Trial time	3	2.11	0.20
Initial density × Trial	6	1.23	0.30

The results that structure did not affect the behavior of the transient prey or TMIE was unexpected given that blue crabs have been found to have higher predation on clams in habitats connected by seagrass (Micheli & Peterson 1999). The difference in predation was attributed to blue crab anti-predator behavior. The range in crab size was smaller (105–129 mm) than the size of crabs used in this experiment (140–195 mm), which could explain the difference, although both size ranges are considered to be adult crabs and potential crab predators most likely overlap between these size ranges. Adult crabs, which are transient species, may be associated with structure because of foraging, not refuge seeking, behavior, and NCE may not be affected by structure.

To our knowledge this was the first study to continuously measure animal position to elucidate the mechanisms of TMIE. Because TMIE are behaviorally induced, quantitative and not qualitative measures of natural behavior are integral in understanding the mechanisms that cause such interactions. Many predator–prey models depend on assumptions taken from observations of animal position (Bolker et al. 2003). Full dynamic optimization models are used to predict the anti-predator behavior of prey and assume an immediate and continuous change in prey behavior. We found that activity may be altered by predator presence during discrete time periods during the day. Incorporating these results will alter the findings of such models (Bolker et al. 2003).

Schmitz et al. (2004) developed a framework which predicts the relative strengths of either TMIE or DMII depending on the prey's and predator's habitat domain as well as the predator's hunting mode. Habitat domain encompasses both microhabitat choice and extent of spatial movement. Our results indicated that

blue crabs did not prefer seagrass or change their behavior when it was present. Mobile, transient species like blue crabs that utilize many habitats may not have microhabitat preferences and thus their habitat domain is determined by the extent of spatial movements. The habitat domain framework is dependent on understanding what variables may alter the functional roles of interacting species (Schmitz 2007). Our results that show a transient prey did not alter its home range in the presence of a predator or structure strengthen the applicability of this framework.

Reviews on TMIE highlight the importance of fear induced by predators in aquatic and terrestrial systems (Preisser et al. 2005). Past studies on behavioral cascades have been conducted on large mobile species (see Dill et al. 2003), but these studies were not controlled, replicated experiments. Understanding of the mechanisms behind these indirect behavioral interactions is limited and most replicated experiments on TMIE are conducted on small scales (Stallings 2008). Generalizations and models of TMIE are based on these small-scale experiments, but large transient prey may react differently to predation pressure. The large scale of this study (>100 m^2) allowed us to directly quantify highly mobile predator and prey behavior in a natural environment and detect subtle mechanisms of TMIE. Direct measurements of animal behavior in a natural setting are integral to further our ability to determine, model, and predict TMIE.

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