Nonconsumptive effects of a predator weaken then rebound over time

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Abstract. Predators can influence prey traits and behavior (nonconsumptive effects [NCEs]), often with cascading effects for basal resources and ecosystem function. But critiques of NCE experiments suggest that their duration and design produce results that describe the potential importance of NCEs rather than their actual importance. In light of these critiques, we re-evaluated a toadfish (predator), crab (prey), and oyster (resource) NCE-mediated trophic cascade. In a 4-month field experiment, we varied toadfish cue (NCE) and crab density (approximating variation in predator consumptive effects, CE). Toadfish initially benefitted oyster survival by causing crabs to reduce consumption. But this NCE weakened over time (possibly due to prey hunger), so that after 2 months, crab density (CE) dictated oyster survivorship, regardless of cue. However, the NCE ultimately re-emerged on reefs with a toadfish cue, increasing oyster survivorship. At no point did the effect of toadfish cue on mud crab foraging behavior alter oyster population growth or sediment organic matter on the reef, which is a measure of benthic-pelagic coupling. Instead, both decreased with increasing crab density. Thus, within a system shown to exhibit strong NCEs in short-term experiments (days) our study supported predictions from theoretical models: (a) within the generation of individual prey, the relative influence of NCEs appears to cycle over longer time periods (months); and (b) predator CEs, not NCEs, drive longer-term resource dynamics and ecosystem function. Thus, our study implies that the impacts of removing top predators via activities such as hunting and overfishing will cascade to basal resources and ecosystem properties primarily through density-mediated interactions.

Key words: antipredator behavior; benthic-pelagic coupling; consumptive effect; ecosystem function; oyster reef; predator cue; prey state; risk; sediment organic matter; trophic cascade.

Introduction

A quarter century of research has clearly demonstrated that the mere presence of predators can alter prey traits such as behavior and morphology, imposing fitness costs on the prey from reduced foraging and costly defenses (Lima and Dill 1990, Abrams 1995, Brown 1999, Werner and Peacor 2003, Suraci et al. 2016). Furthermore, such nonconsumptive effects (NCEs) of predators on prey behavior, growth, and/or survivorship can cascade across multiple trophic levels in food webs to alter community composition (Peacor et al. 2012) and ecosystem function (Schmitz et al. 2008, Fig. 1). For example, fear of wolves and the resultant alteration of elk foraging explains the resurgence of hardwood trees in Yellowstone National Park (Ripple and Beschta 2007). Similarly, lynx induce the prolonged suppression of hare populations long after lynx population collapses (Elton and Nicholson 1942, Peckarsky et al. 2008). The indirect effects on lower trophic levels produced by NCEs are sometimes referred to as trait-mediated indirect effects (or interactions, TMIEs or TMIIs), which contrast with density-mediated indirect effects (or interactions, DMIEs or DMIIs) produced by CEs (Fig. 1). To limit jargon, we refer only to NCEs and CEs and their consequent indirect effects. Multiple experiments in a range of study systems collectively suggest that predator NCEs on prey behavior and traits may equal or sometimes exceed predator CEs (Preisser et al. 2005). Thus, a primary focus of community ecology over the last decade has been the use of controlled experiments to understand how the relative importance of CEs and NCEs depends on ecological context, including resource supply (Preisser et al. 2009), predator interactions and diversity (Sih et al. 1998, Byrnes et al. 2004), habitat complexity (Grabowski 2004), and more recently, climate change (Miller et al. 2014).

The growing number of NCE experiments is accompanied by several key critiques of their experimental design, suggesting the results may describe only the potential importance of NCEs, rather than their actual, realized importance in ecosystems. First, NCEs depend on the ability of prey to detect predator cues that exceed the ambient sensory background, and many NCE experiments occur in laboratory settings that do not replicate

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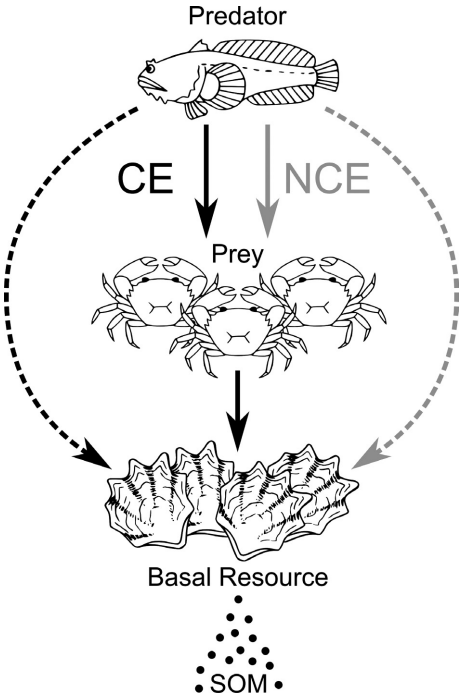

FIG. 1. Diagram of direct (solid lines) and indirect (dashed lines) interactions by which a toadfish predator can influence the community structure and ecosystem functioning of intertidal oyster reefs. Black solid line illustrates the direct consumptive effect (CE) of toadfish predation on the density of mud crabs, which can indirectly (black dashed line) influence the survivorship of oysters and consequently alter ecosystem properties, because suspension feeding by oysters leads to benthic-pelagic coupling and augmentation of sediment organic matter (SOM). Gray solid line illustrates the direct nonconsumptive effect (NCE) of toadfish cue on the foraging behavior of mud crabs, which can also indirectly (gray dashed line) influence the survivorship of oysters and SOM production. Drawing by T. Rogers.

ambient conditions found in the environment (Weissburg et al. 2014). Consequently, NCE experiments may artificially alter prey perception of risk and the likelihood of detecting strong NCEs. While this is a legitimate concern, it is important to acknowledge that numerous NCE experiments have been conducted in the field with ambient sensory background and still detected strong NCEs (Peckarsky and Dodson 1980, Beckerman et al. 1997, Preisser et al. 2005, Hill and Weissburg 2013, Suraci et al. 2016). The degree to which environmental heterogeneity influences the relative strength and generality of NCEs remains an important area for further empirical work.

The second critique is that the most common NCE experimental design involves comparing a fitness measure of the prey (e.g., foraging rate) in treatments with and without a predator cue (e.g., with or without a caged predator treatment; Abrams 2008). Although this design allows investigators to directly estimate the NCE on prey, it does not reveal how the NCE influences prey fitness in a natural setting with functional predators that also eat prey. For instance, while predators themselves may produce a range of cues that influence prey behavior, the dying prey consumed by functional predators may generate additional cues that alter the foraging rates of other nearby prey (Smee and Weissburg 2006, Scherer et al. 2016). Additionally, when predators are actively consuming prey, the immediate reduction in foraging (NCE) may be balanced by a gradual enhancement in foraging if the reduced prey density alleviates intraspecific competition among the remaining prey. Consequently, the presence of a predator could ultimately lead to greater resource consumption by prey, despite the reduced foraging rate (Abrams 2008). An alternative experimental design involves comparing some fitness measure of the prey in a treatment with functional predators and prey vs. a treatment with functional predators and dysfunctional prey—those with disabled antipredator behavior (Abrams 2008). Although this alternative design may be more realistic (cues are rarely present in nature without a predator, but prey may fail to detect a predator cue) and allow greater inference, it is highly difficult to implement (Abrams 2008).

Third, NCE experiments have usually involved time spans long enough to detect significant changes in both prey and resource population densities (Werner and Peacor 2003, Bolnick and Preisser 2005, Preisser et al. 2005), but not long enough for the system to reach dynamic equilibrium (Abrams 2008). While this critique is likely very important for multi-generational dynamics between predator and prey (Peacor et al. 2011), we focus here on the response of prey to predators within their lifetime (i.e., within-generation dynamics). At this time scale, experimental duration is important because (1) prey may habituate to the predator cue (Brown et al. 2015), so that shorter experiments may show stronger behavioral responses; (2) prey may change antipredator strategies over time, such as inducing morphological defenses rather than altering foraging behavior (Hoverman and Relyea 2012); (3) after a prolonged period of starvation, prey may eventually resume foraging regardless the risk of predation (Luttbeg et al. 2003); and (4) the prey behavioral response (e.g., reduced foraging) may increase resource density, but if prey densities remain high, they may eventually reduce the resource to its original density even with a much reduced foraging rate (Abrams 2008). Consequently, it is important for experiments to examine the strength of NCEs over a range of time scales. Until NCE experiments rigorously address these three critiques (particularly the latter two), it will remain unclear whether NCE theory is critical to developing predictive ecological models, or if NCEs could merely be subsumed within existing frameworks for describing predator-prey dynamics, as Abrams (2008) has suggested. Therefore, it is reasonable to question whether quantitatively isolating the relative influence of NCEs should remain a major focus of ecology.

One model system for investigating NCEs is a three-level food web (Fig. 1) in oyster reefs of the Southeastern Atlantic Bight (SAB, from North Carolina to northern Florida, USA). There, short-term (6 d) experiments

demonstrated that a benthic toadfish (predator) indirectly benefits the survival of juvenile oysters (basal resource) by causing crabs (prey) to spend more time and energy hiding rather than consuming oysters (Grabowski 2004, Grabowski and Kimbro 2005). Furthermore, a longer-term (90 d) experiment revealed that the toadfish-mediated NCE has the potential to indirectly affect oyster population dynamics (oyster reef biomass; Kimbro et al. 2014). The NCE may also indirectly affect ecosystem properties: suspension feeding by oysters leads to benthic-pelagic coupling and augmentation of sediment organic matter (SOM). Changes in fundamental sediment properties like SOM are valuable indicators to connect food web processes to ecosystem function (O'Connor et al. 2008, Lefcheck et al. 2016).

In order to evaluate whether NCEs persist over longer time-scales and better understand their role in structuring ecological communities and mediating ecosystem function, we conducted an experiment on simulated oyster reefs in the field (with realistic ambient sensory conditions, in response to the first critique above) that addressed three questions: (1) Does the strength of the NCE of a toadfish predator on the foraging behavior of crab prey depend on the density of crabs? By varying crab density in a +/− cue experiment, we approximated variation in the direct consumptive effect of predators on prey density (partially addressing the second critique that NCEs should be quantified in the presence of realistic CEs on prey density). (2) Does the strength of the NCE of a toadfish predator on the foraging behavior of crab prey depend on the duration of the experiment? We extended our experiment over an entire growing season to test for starvation and habituation effects on prey (addressing the third critique), though not multigenerational adaptation. (3) If the NCE of a toadfish predator on the foraging behavior of crabs indirectly affects basal resources (i.e., juvenile oyster survival), then does this trophic cascade scale up to influence oyster populations in terms of oyster reef growth (i.e., reef production), and oyster ecosystem function (benthic-pelagic coupling)?

Materials and Methods

Study system

This research was conducted within the Matanzas River estuary (MRE), north of Matanzas inlet, Florida, USA (29.91386° N, 81.28368° W). In this portion of the Guana Tolomato Matanzas National Estuarine Research Reserve (GTM NERR), shorelines are dominated by intertidal oyster (*Crassostrea virginica*) reefs that border *Spartina alterniflora* salt marsh. In this region, a primary consumer of oysters is the mud crab, *Panopeus herbstii* (Kimbro et al. 2014), which consumes juvenile oysters (<25 mm oyster shell height [SH]). In a previous study in the MRE, the average abundance of adult mud crabs ranged from 1 to 11 per m^2 of oyster reef (Garland and Kimbro 2015). The predator of these crabs most frequently studied in previous experiments has been the oyster toadfish, *Opsanus tau* (Grabowski 2004, Grabowski and Kimbro 2005, Kimbro et al. 2014); this sit-and-wait predator resides on oyster reefs throughout the southeastern U.S. and has been observed on oyster reefs within the MRE (D. L. Kimbro, *unpublished manuscript*). Toadfish create burrows in the oyster reefs. Because these burrows retain water, toadfish can remain on intertidal reefs even at low tide when the reefs are no longer submerged by water. On eight natural reefs at our study site, the average (±SD) density of burrows was $3.0 \pm 3.39/m^2$. However, these burrows may also have been created and used by another residential predator, the stone crab (*Menippe mercenaria*).

Food web manipulation experiment

Habitat.—In June 2012, we established 24 plots (1.21 × 1.21 m) that were separated from each other by 3 m of mudflat. The 24 plots were split into 2 rows (blocks) of 12 plots, which were also separated by 3 m. In each plot, we removed surface sediment to a depth of 0.5 m, inserted a fully enclosed (with roof and floor) Vexar plastic mesh cage (1.2 × 1.2 m × 0.61 m; 5 × 5 mm mesh openings), and deposited the excavated sediment inside the cage. Within each cage, we created a patch reef (1.0 m^2) out of 19 L of dead oyster shell (reef base) and 35 L of live oyster clusters (≥2 adult [>75 mm SH] oysters cemented together). This material was collected from nearby reefs and rinsed with fresh water to remove associated mobile invertebrates. Before constructing the reefs, we tested for effects of caging material on bulk water flow. This involved deploying chalk flow blocks of standard diameter and thickness inside four cages. Each cage with an internal flow block also received a flow block directly outside of the cage. The mass (g) of each flow block was weighed before deployment and then again after 5 d. By subtracting final mass from initial mass, we estimated bulk flow as a function of being inside vs. outside of the cage (Jokiel and Morrisey 1993). Estimates of bulk water flow did not differ as a function of being inside vs. outside of our experimental cages ($t = -0.35$, df = 6, $P = 0.74$).

Predator cue and prey density.—We randomly assigned each cage to one of twelve unique combinations of two fixed factors: predator cue (present or absent) and crab density (0, 2, 4, 6, 8, 10), resulting in a 2 × 6 factorial experiment ($n = 2$ replicates per level), with equal replication of treatments in each block. Assuming 10 crabs/m^2 is near the maximum natural ambient density (Garland and Kimbro 2015), we used these treatments to approximate a range of possible prey densities resulting from a range of direct predator consumptive effects (CE). Thus, cages with 0 crabs had an effective CE of $1 - 0/10 = 1$ and cages with 2 crabs had an effective CE of $1 - 2/10 = 0.8$, and so forth. For comparison, Kimbro et al. (2014) reported a CE of 0.3 over their 90-day experiment (roughly corresponding to our 6- and

8-crab treatments). We recognize that variation in crab density on natural reefs can reflect the influence of other biotic and abiotic factors. To maintain crab densities, we enclosed each reef with a vexar mesh cage. While it is likely that the cages altered mud crab movement, our video observations of individual crabs (3 h per crab) on natural oyster reefs revealed that crabs rarely moved among oyster clusters. This observation agrees with previous research (Grabowski 2004), which also demonstrated minimal crab movement in the presence of a residential predator (Grabowski 2004).

As a sit-and-wait predator, toadfish are highly sedentary and occupy relatively small burrows on oyster reefs. Therefore, in the center of each reef, we created a simulated toadfish burrow by removing 25 × 15 × 5 cm (length × width × depth) of surface sediment, inserted a fully enclosed (with roof and floor) Vexar plastic mesh cage (20 × 10 × 15 cm, 5 × 5 mm mesh openings), and deposited the excavated sediment back inside the burrow cage. For reefs assigned to the toadfish-cue treatment, we placed one toadfish inside the burrow cage (mean standard length = 208 mm). The volume of the simulated burrows was nearly twice as large as the average volume of natural burrows (mean = 1728.71 ± 682.09 cm^3, $n = 88$), but toadfish were observed every 3 d and released/replaced if they appeared stressed. Throughout the 4-month experiment, we observed and fed each toadfish two shrimp every 3 d. We used shrimp instead of crabs as food because the cues of dying conspecifics are known to enhance the antipredator response of prey and because our previous experiments showed that the refuge provided by oyster reefs limits the foraging success of toadfish (Grabowski 2004). Therefore, we decided against providing toadfish a consistent supply of mud crabs in order to prevent overestimating the strength of NCEs associated with toadfish. Before beginning the experiment, we also collected adult crabs (carapace width 20–30 mm) from nearby oyster reefs and used these crabs to create the assigned crab density of each reef. All animals were treated humanely in accordance with approved conditions set forth by the Institutional Animal Care and Use Committee at Florida State University. All surviving animals were released to their origin locations at the conclusion of the experiment.

Response variables.—We collected data at multiple time points over the 163-d experiment to evaluate how toadfish cue and crab density affected (1) juvenile oyster survivorship, (2) the biomass of the oyster reef (only measured at end of experiment), and (3) benthic-pelagic coupling, measured by changes in percent sediment organic matter (SOM). We evaluated juvenile oyster survivorship in each experimental unit in five sequential 19-day trials. To ensure consistency among trials, we purchased a stock of juvenile oysters (mean size = 8 mm) from a single hatchery (Research Aquaculture, Inc., Tequesta, Florida, USA) at the beginning and again at the midpoint of our study. Using marine epoxy, we attached 12 of the juvenile oysters to ceramic tiles (10 × 10 cm) and used aquarium-safe silicone to attach tiles onto concrete pavers (12 × 12 cm). On each reef, we deployed one tile 0.3 m from the toadfish burrow. In each trial, oyster survivorship was quantified after 19 d. These trials were repeated five times (starting on days 0, 19, 61, 80, and 99) during the 163-d experiment. The first stock of oysters was used in trials 1–2 and the second stock of oysters was used in trials 3–5.

In our analyses, we assumed that variation in oyster survivorship among treatments could be attributed solely to variation in mud crab foraging on oysters. But this interpretation is complicated for two reasons. First, oyster survivorship could have varied among cages as a result of environmental stress. However, high survivorship of oysters over 19 d in the complete absence of crabs suggests that this did not occur in our study. Second, the presence of mud crabs could have created a crab-mediated NCE that also contributed to variation in oyster survivorship. To evaluate this possibility, we installed an additional tile with juvenile oysters on each reef and enclosed it with a small vexar cage. At the end of the experiment (163 d), the survivorship of juvenile oysters was quantified. Because the number of remaining oysters in these protected cages was not correlated with increasing crab density, we concluded that crab-mediated NCEs did not contribute to variation in oyster survivorship over 163 d ($y = -0.10x + 5.0$, $R^2 = 0.04$, $P = 0.35$). Accordingly, over the course of our 19-d assays, we are confident that variation in oyster survival reflected variation in crab foraging.

To estimate how the treatments affected reef production, we measured the individual biomass of 96 oyster clusters (200–400 g; four per reef) and marked each cluster with a numeric plastic tag. Clusters were rinsed to remove sediments, and all fauna other than oysters were removed. Thus, oyster cluster biomass in this experiment equals all of the living and dead oyster tissue and shell attached to each other in the cluster. Four clusters were placed equidistantly around the perimeter of each reef, inside the cage. At the end of the experiment, we retrieved each cluster, rinsed and removed all attached organisms other than oysters, and quantified the change in oyster cluster biomass ([final weight − initial weight]/initial weight). This difference metric integrates changes in the density of adult and juvenile oysters as a function of survivorship, oyster growth, and oyster recruitment (Meyer and Townsend 2000, Grabowski et al. 2005, Kimbro et al. 2014).

The accumulation of SOM due to benthic-pelagic coupling is influenced by oyster density and biomass and therefore may be indirectly influenced by toadfish CEs and NCEs on crabs. To quantify how the treatments affected SOM over time, we collected a sediment sample from each reef on days 42, 97, and 163 of the experiment. Sediments were collected, homogenized, and then redistributed to each cage. We collected 1 cm deep sediment cores at the times above to quantify sediment organic

content in surface zones. Sediments were dried at 60°C for at least 48 h and combusted at 525°C to determine ash-free dry mass (AFDM). SOM is presented as the percentage of total sediment mass that is organic matter.

Statistical analyses

Oyster survivorship.—Oyster survival data were bounded between 0 and 1, ensuring that residuals would be asymmetrical and non-normally distributed. Therefore we used logistic regression (generalized linear model [glm] with binomial error distribution and logit link in R version 3.1.3; R Core Team 2014) to evaluate oyster survivorship as a function of toadfish cue (+/−; categorical fixed factor), crab density (continuous fixed factor), their interaction, and block (fixed factor) for each trial. In all five trials, we removed the blocking factor from the analysis because it was not statistically significant. In trials with a significant effect of predator cue (trials 1, 2, and 5), we used the coefficients of the fitted logistic regressions to compare the strengths of CEs and NCEs. Our estimate of NCE strength was generated from the unstandardized coefficients of the predator-cue regression, which we used to predict the survival of juvenile oysters on reefs without a CE (i.e., reefs with 10 crabs). Our estimate of CE strength was generated from the unstandardized coefficients of the no predator-cue regression, which we used to solve for the amount of crab reduction required to produce an effect on juvenile oyster survivorship that equaled the estimated NCE.

Reef production.—We used a linear mixed effects model to evaluate reef production (change in the biomass of each cluster) as a function of block (fixed factor), toadfish cue (fixed factor), crab density (fixed factor) and their interaction (fixed factor), with cage identity assigned as a random effect (there were four clusters per cage). The block factor was removed from the analysis because it was not statistically significant. The results of this analysis indicated that crab density (and therefore CE strength) was the only statistically significant effect. Because of the lack of a significant effect of toadfish cue on reef biomass, we pooled the toadfish cue present and absent treatments and plotted the change in oyster cluster biomass vs. crab density. In this plot, the slope of the relationship appeared to differ dramatically between lower and higher crab densities. Therefore, we used a Davies test (Davies 2002) to evaluate the null hypothesis that the slope was constant across the predictor variable. After finding that it was not, we conducted a piecewise linear regression to estimate the breakpoint (ignoring the random cluster effect momentarily), then performed two separate mixed-model regressions on either side of the breakpoint. The regressions had a fixed effect of crab density and a random effect of oyster cluster. The Davies test and piecewise regression were conducted using package "segmented" (Muggeo 2015), and mixed models were conducted using package "lme4" (Bates et al. 2016) in R 3.1.3.

Sediment organic matter.—We used a linear mixed effects model (package "lme4" [Bates et al. 2016] in R 3.1.3) to evaluate SOM as a function of block (fixed factor), crab density (fixed continuous factor), toadfish cue (fixed categorical factor), and time (days, fixed categorical factor). The block factor was dropped from the analysis because it was not significant. To account for repeated sampling of each cage, we designated cage (factor) as a random effect. Because the interaction term between crab density and time was significant, we partitioned the data into three subsets corresponding to each of the three sampling dates, and used linear regression to evaluate the relationship between SOM and crab density at each sampling date. In this analysis, the data were pooled for the toadfish cue treatments (present and absent) due to the lack of a significant effect of toadfish cue on SOM. For both the reef biomass and SOM results, we assumed normal error distribution and verified this assumption by a normal quantile–quantile plot.

Results

Oyster survivorship

In the absence of a toadfish predator cue, juvenile oyster survivorship (proportional) consistently declined with increasing mud crab density and thus decreasing CE of the toadfish predator. However, in the presence of a toadfish cue, the CE of the toadfish predator on mud crab density did not consistently cascade to affect oyster survivorship. During the first 19-d trial, survivorship of juvenile oysters decreased only slightly with increasing crab density (and weakening CE) when the predator cue was present (significant cue × crab density interaction; Table 1A, Fig. 2A). At maximum crab density and therefore no CE, NCE strength was 0.55 (out of 1.0). To interpret this result in terms of the relative strength of NCE vs. CE, predators would have to exert a CE of at least 0.59 by reducing crab density from 10 to ≤ 4 crabs per reef in order to match the observed strength of the NCE in this trial. From days 19–38, oyster survivorship decreased with increasing mud crab density. But oyster survivorship was still significantly higher in the presence of the predator cue (significant cue × crab density interaction; Table 1B, Fig. 2B). In order to match the strength of the NCE observed in this trial on reefs with 10 crabs (NCE = 0.46), predators would need to have maintained at least a CE of 0.57 by reducing crab density from 10 to ≤4 crabs per reef. From days 61–80 and then from days 80–99, there was no significant difference in survivorship between + and − cue treatments (Table 1C,D, Fig. 2C, D), indicating that toadfish cue no longer indirectly benefited oyster survival. From days 99–118, however, oyster survivorship was again significantly higher in the presence of predator cue (significant predator cue effect; Table 1, Fig. 2E). On reefs with 10 crabs, the toadfish NCE on oyster survival began to rebound in strength (NCE = 0.013). Averaged across crab density or CE

TABLE 1. Results from analysis of deviance on the number of live and dead juvenile oysters as a function of predator cue (present or absent) and crab density (0, 2, 4, 6, 8, 10) during a four-month field experiment.

Source	df	Deviance residuals	df	Residual deviance	*P*-value
(A) Trial 1					
Predator cue	1	76.76	22	420.19	<0.0001*
Crab density	1	233.01	21	187.18	<0.0001*
Predator cue × crab density	1	54.86	20	132.32	<0.0001*
(B) Trial 2					
Predator cue	1	11.79	22	137.53	0.0006*
Crab density	1	56.77	21	80.75	<0.0001*
Predator cue × crab density	1	18.79	20	61.96	0.0002*
(C) Trial 3					
Predator cue	1	0.53	22	250.23	0.47
Crab density	1	136.68	21	113.55	<0.0001*
Predator cue × crab density	1	1.49	20	112.06	0.22
(D) Trial 4					
Predator cue	1	0.36	22	257.10	0.55
Crab density	1	210.69	21	46.42	<0.0001*
Predator cue × crab density	1	0.15	20	46.27	0.70
(E) Trial 5					
Predator cue	1	6.45	22	239.67	0.01*
Crab density	1	203.14	21	36.51	<0.0001*
Predator cue × crab density	1	0.75	20	35.76	0.39

Notes: (A) Results for survivorship from days 0–19; (B) results for survivorship from days 19–38; (C) results for survivorship from days 61–80; (D) results for survivorship from days 80–99; and (E) results for survivorship from days 99–118. Results were fit with logistic regression analysis (binomial GLM with logit link).

* Statistically significant effect at an $\alpha = 0.05$.

strength, toadfish cue indirectly increased oyster survivorship by 15%. In order to match the strength of this NCE (0.013), toadfish would need to have maintained at least a CE of 0.28 by reducing crab density from 10 to ≤7 crabs per reef. Thus, a strong NCE was present in the first and last 1/3 of the experiment, but not the middle 1/3 of the experiment.

Reef production

Change in oyster cluster biomass (a proxy for reef production) differed on reefs as a function of mud crab density and thus CE of toadfish predator (linear mixed effects model: $F_{1,43} = 18.40$, $P < 1 \times 10^{-4}$), but not with toadfish cue ($F_{1,43} = 0.04$, $P = 0.84$) or the interaction of cue and crab density ($F_{1,43} = 2.21$, $P = 0.14$; Fig. 3, Appendix S1: Fig. S1 depicts the non-significant interaction). However, the effect of crab density was not strictly linear; a Davies test ($P = 0.030$) detected a breakpoint in the regression slope, and piecewise regression estimated the breakpoint to be at a mud crab density of 2.71 (±0.98 standard error). On reefs with ≤2.71 crabs, cluster biomass declined significantly with increasing crab density (weakening CE) over the four-month experiment (linear mixed effect model: $F_{1,14} = 9.31$, $P = 0.0086$; Fig. 3). In contrast, on reefs with ≥2.71 crabs, cluster biomass did not change as a function of crab density or strength in CE ($F_{1,14} = 0.17$, $P = 0.68$; Fig. 3). Given the limited range of data to the left side of the breakpoint (0–2.70 crabs), it remains unclear whether the initial decrease is linear or non-linear.

Sediment organic matter

The SOM on oyster reefs was significantly influenced by an interaction between mud crab density (CE of toadfish predator) and time, but there was no significant effect of predator cue (Table 2, Fig. 4), indicating the absence of a significant toadfish-mediated NCE. On days 42 and 97 of the experiment, the SOM on oyster reefs was not significantly affected by crab density (Fig. 4A, B). In contrast, by day 163, the SOM on oyster reefs decreased with increasing crab density ($F_{1,46} = 19.86$, $P < 0.001$; $R^2 = 0.30$, $y = -0.40x + 7.16$; Fig. 4C). As in the reef production analysis (Fig. 3), there appeared to be a breakpoint in this latter relationship, with the slope flattening out at higher crab densities (Fig. 4C). A Davies test on the SOM vs. crab density relationship from day 163 detected a breakpoint at a density of 4.44 crabs that was nearly significant at the $\alpha = 0.05$ level ($P = 0.052$).

DISCUSSION

At the beginning of this study, the presence of a predatory fish indirectly increased the survivorship of juvenile oysters by causing crabs to reduce their consumption of oysters. But this NCE-mediated trophic cascade weakened over time, so that after 2 months, crab density

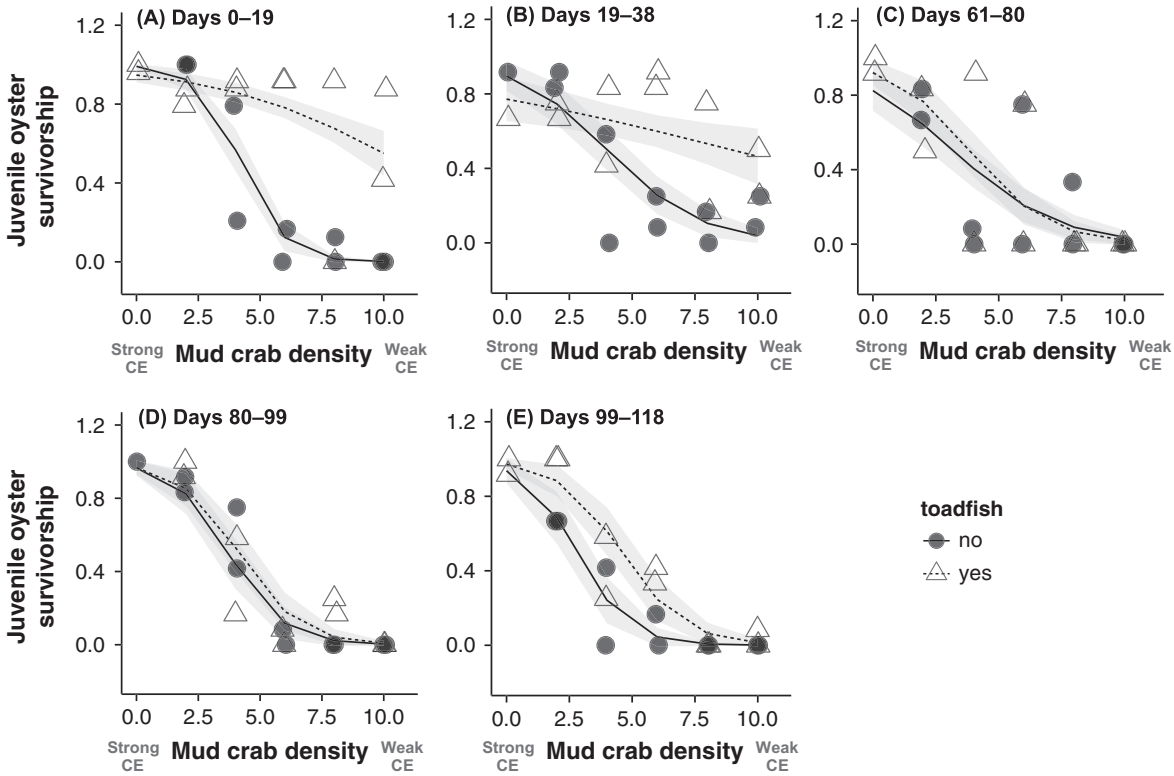

FIG. 2. Proportional survivorship of juvenile oysters (vertical axis) as a function of mud crab density (axis) over a series of 19-d trials spanning the 163-d experiment. Dates of each trial are given in the panel. Mud crabs consume juvenile oysters, and were either exposed (open triangles, dotted curve) or not (closed circles, solid curve) to cues from an enclosed toadfish (a mud crab predator). The gradient in mud crab density approximates the consumptive effect of a predator on mud crab density (high density = weak CE, and vice versa). Lines indicate the fit of a generalized linear model (binomial error; logit link); shading indicates 95% confidence interval on the regression line.

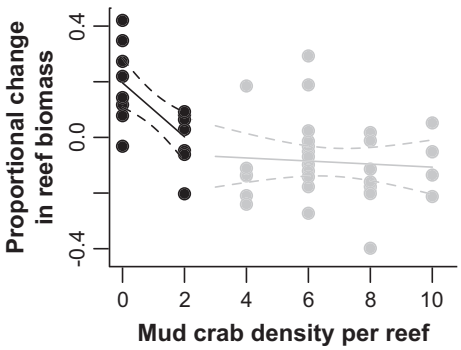

FIG. 3. The proportional change in reef biomass (vertical axis) as a function of mud crab density (horizontal axis) over a 4-month experiment. The gradient in mud crab density approximates the consumptive effect of a predator (high density = low consumption, and vice versa); there was not a significant nonconsumptive predator effect on reef biomass, so these data include treatments with and without the predator cue. Curves display the fit of a linear mixed-effect model (±95% confidence interval) estimated separately for 0–2 crabs (black symbols and line) and 4–10 crabs (gray symbols and line).

(representative of differences in CEs) dictated the survivorship of individual oysters, with high survivorship on reefs containing fewer than four crabs (CE ≥ 0.8) and low survivorship on reefs containing more than four crabs (CE ≤ 0.6). However, towards the end of this 4-month experiment, a NCE re-emerged on reefs with predatory fish, which indirectly increased oyster survivorship by 15% when averaged across crab density or CE strength. Thus, our findings support theoretical predictions of temporal dynamics in the relative strength of NCEs (Abrams 2008).

While the strength of toadfish NCEs on crab foraging behavior and oyster survival oscillated throughout the experiment, at no point did these NCEs indirectly alter reef production or SOM, an important end product of oyster filter feeding. Instead, reef production (Fig. 3) and SOM on reefs decreased with increasing crab density (decreasing CE strength; Fig. 4C), although both relationships appeared to flatten out at higher crab densities. Therefore, although NCE-mediated trophic cascades on oyster survivorship are strong over shorter durations (Grabowski 2004, Kimbro et al. 2014), it appears that the relative influence of a NCE-mediated trophic cascade on oyster survivorship varies substantially over longer time periods. By contrast, understanding factors that exert significant control on prey density (such as strong predator CEs), even without an explicit quantification of behavioral responses to predators, may be sufficient for predicting

TABLE 2. Results from analysis of variance on percent organic matter of sediment on oyster reefs as a function of predator cue (present or absent), crab density (0, 2, 4, 6, 8, 10), and time (days 42, 97, 163) during a 4-month field experiment.

Source	df	Sums square	MSE	*F*-ratio	*P*-value
Predator cue	1, 20	0.24	0.24	0.06	0.81
Crab density	1, 20	3.66	3.66	0.92	0.35
Time	2, 112	2.40	1.20	0.299	0.74
Predator cue × crab density	1, 20	0.21	0.21	0.05	0.82
Predator cue × time	2, 112	16.01	8.01	2.00	0.14
Crab density × time	2, 112	98.59	49.29	12.31	<0.001*
Predator cue × crab density × time	2, 112	0.15	0.07	0.02	0.98

* Statistically significant effect at an $\alpha = 0.05$.

ecosystem functioning of this foundation species over longer periods within the generation time of prey.

Although toadfish presence did not indirectly influence the population dynamics and ecosystem functioning of oyster reefs, it did influence crab foraging and in turn the survivorship of individual oysters for the majority of the experiment (Fig. 2A, B, E). This result supports predictions about the importance of NCEs and resulting trophic cascades in habitats with residential predators in general (Schmitz et al. 2004) and with toadfish in particular (Grabowski 2004). However, the strength of the NCE waned and then rebounded over the course of our study, demonstrating that this interaction is extremely time-dependent. There are three potential explanations for this time-dependence. First, seasonal variation in environmental variables during summer and fall may have influenced the strength of NCEs during our experiment. However, previous empirical sampling on oyster reefs in northeastern Florida estuaries determined that temperature and salinity did not vary during this time period (Byers et al. 2015). Second, if prey were constantly exposed to predation risk, then the NCE may have weakened because the prey habituated to the risk (Trussell et al. 2011). And third, if resources became scarce or if prey began to starve after prolonged exposure to risk, then metabolic demand may have caused prey to increase their foraging behavior at the expense of their anti-predator strategy (Luttbeg et al. 2003). This third explanation based on the physiological state of the prey seems more likely, because the initially strong NCE (Fig. 2A, B) weakened at the midpoint of the experiment (Fig. 2C, D) and then regained strength towards the end of the experiment (Fig. 2E). Thus, the results of our season-long experiment add further support to conclusions about the importance of prey state drawn from model predictions (Luttbeg et al. 2003) and controlled laboratory experiments (Matassa et al. 2016).

By extending the duration of the experiment to encompass an entire growing season, we were able to evaluate if the time-varying NCE was strong enough to indirectly impact the population growth of oysters (net outcome of recruitment, growth, and survivorship). At the end of the 4-month experiment, toadfish presence (NCE) did not indirectly affect the change in reef biomass. In contrast, an increase from 0 to 2.7 crabs (decrease of CE on crabs from 1.0 to 0.8) resulted in a significant loss of reef biomass (Fig. 3). Interestingly, weakening the CE and increasing crab density further did not cause additional biomass loss. This result has two implications. First, theory suggests that if there is temporal variability in the strength of the predator cue and if prey forage more during low-risk periods, then the periodic enhancement of prey foraging may compensate for foraging reductions due to NCEs in high-risk periods (Luttbeg et al. 2003). Consequently, strong NCEs may be detectable by short-term experiments but not when measured across an entire season (Luttbeg et al. 2003). In contrast, CEs rarely decrease prey populations over the short term, but their cumulative effect on prey populations increases over the long term (Peacor and Werner 2001, Werner and Peacor 2003). Our results agree with this theoretical prediction. In particular, because our experiment was a press experiment with constant risk exposure, the seasonal absence of an NCE on reef biomass was most likely due to variation in prey state (starvation vs. satiation), not variation in predation risk; though there may have been short-term variability in cue strength or detectability due to small-scale hydrodynamics (Weissburg et al. 2014) and feeding events of the predator (Scherer et al. 2016).

A second implication stems from the lack of a further decrease in reef biomass as crab density increased from 2.7 to 10 crabs (CE weakened from 0.8 to 0.0), which suggests that crabs do more than just eat juvenile oysters. Previous research demonstrated that the foraging activity of crabs removes sediment from the reef surface, and that sediment removal can create a net positive effect of crabs on oyster populations in high sedimentation conditions (Kimbro et al. 2014). In addition, at high densities, mud crabs may have interfered with each other, so that their collective effect on oysters was less than predicted based on the effects of individual mud crabs (Sih et al. 1998). These non-trophic activities of crabs might produce unexpected feedbacks in the system and warrant further research (Hastings et al. 2007).

The extended duration of our experiment also allowed us to determine if the time-varying NCE on crab foraging indirectly altered the impacts of oysters on ecosystem function. Throughout the 163-d experiment, the presence of toadfish (NCE) did not indirectly influence SOM

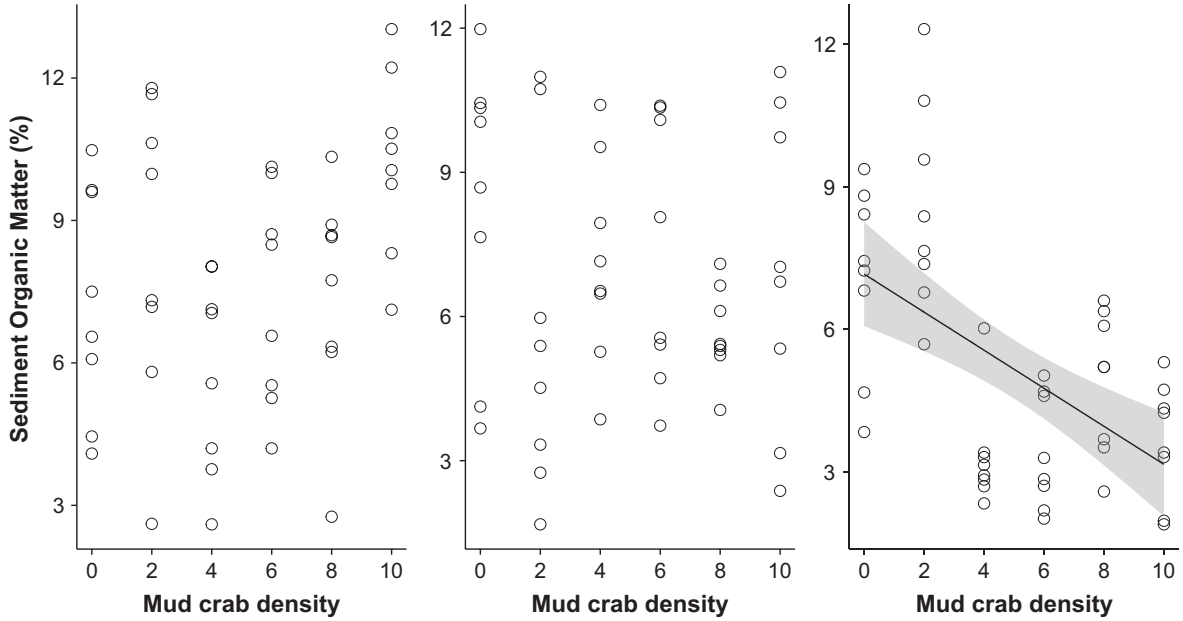

FIG. 4. The percent sediment organic matter (vertical axis) within experimental oyster reef as a function of mud crab density (horiztonal axis) over a 4-month experiment. The gradient in mud crab density approximates the consumptive effect of a predator (high density = low consumption, and vice versa); there was not a significant nonconsumptive predator effect on reef biomass, so these data include treatments with and without the predator cue. Curves indicate the fit of a linear regression (±95% confidence interval) for data collected at the beginning (A), middle (B), and end (C) of the experiment.

(Fig. 4A, B). Not until the end of the experiment did the density of crabs (CE strength) decrease SOM (Fig. 4C). The negative effect of crab density on SOM appeared to flatten out at higher crab densities, suggesting that the same predator interference or non-trophic effects that modify the relationship between crab density and reef biomass are also operational at the level of SOM production.

The delayed manifestation of an effect of crabs on SOM suggests two non-mutually exclusive explanations. First, crab excretion may have contributed to SOM on reefs during the first 100 d of the experiment, such that any reduction in oyster-mediated SOM due to the effects of crabs on oysters (Robinson et al. 2014) was balanced by crab-production of pseudofeces that enhances SOM. Second, similar to the population level effects of CEs, ecosystem level effects due to oyster filter-feeding may manifest gradually through time because the effect of toadfish on crabs, oyster reefs, and SOM production (Fig. 1) involves trophic and non-trophic components operating on different time scales. Specifically, interactions between toadfish and crabs can cause rapid changes in individual oyster survivorship, while the effect of oyster filter feeding on SOM within a relatively large oyster reef may take considerably longer because it requires continuous incremental changes in the properties of a large pool of sediment. In addition, crab cues may still influence oyster filtration behavior and SOM production (i.e., crab-mediated NCE) even when crabs are avoiding toadfish and not consuming oysters. Examining the relative influence of oysters and crabs on SOM production and the spatial-temporal dynamics of these engineering interactions offer a promising direction for future research on oyster reefs (Jones et al. 1994, Hastings et al. 2007).

Theory suggests that an important aspect of time-dependent NCEs is the natural variation in risk (Luttbeg et al. 2003, Trussell et al. 2011). Meanwhile, the "pressed" nature of our experiment (Bender et al. 1984) resulted in constant predation risk. If burrow occupancy by toadfish varies naturally in frequency and duration, then our experimental design (i.e., toadfish confined to a single burrow) could have desensitized mud crabs to toadfish cues, thereby artificially weakening the NCE and underestimating its true natural effect (Trussell et al. 2011, Weissburg et al. 2014). In this scenario, the cue essentially became part of the ambient background and the crabs habituated to it. However, we likely reduced this artifact by conducting our experiment in a natural setting with regular ebb and flood tides that introduced some natural variation in the concentration of waterborne chemical cues (Kimbro 2012). In addition, the strength of predatory NCEs has been demonstrated to increase when predators feed and decrease when they fast (Scherer et al. 2016). Because caged toadfish in our experiment were fed every 3 d throughout the whole experiment, the cues in our experiment were more likely to be pulsed, not pressed. Finally, because estimates of bulk water flow did not differ as a function of being inside vs. outside of our experimental cages, it is unlikely that our experimental cages created an artifact by altering the ambient sensory background for prey when the reefs were submerged at high tide.

To interpret the results of our study, it is important to consider that our experimental design lacked a functional

predator treatment, which would have allowed predators to naturally consume prey and alter prey traits/behavior (Abrams 2008). This could help reconcile differences between the results of our current experiment and that of Kimbro et al. (2014), which used a functional predator treatment as well as additional trophic level treatments to calculate the direction and magnitude of predatory NCEs. This previous experiment demonstrated that NCEs indirectly influenced individual oyster survivorship on a weekly time scale and oyster reef biomass over a seasonal time scale, but not at all sites. Specifically, they found that the strength of a toadfish and blue crab (predators) NCE-mediated trophic cascade on juvenile oysters was strongest at sites with low levels of oyster supply (North Carolina and Florida) and weakest at sites with high levels of oyster supply (South Carolina and Georgia). Furthermore, they found that mud crabs ameliorated sediment burial of oysters when their foraging behavior was not suppressed by predators in Florida estuaries, where sedimentation rates are naturally high. Due to asynchronous spatial gradients in oyster supply and sedimentation rates, the positive indirect effect of predators on reef biomass in North Carolina became increasingly negative with decreasing latitude. Clearly, their inclusion of a functional predator treatment demonstrated that this behaviorally-mediated trophic cascade is highly context dependent. Therefore, whether toadfish NCEs on reef production dampen in strength over time needs to be experimentally evaluated further over varying spatial contexts and with a functional predator treatment.

One additional concern about predator cue experiments expressed by Abrams (2008) was that short-term experiments do not account for the numerical response of the prey to the NCE-induced increase in resource density. This complication is unlikely to arise in our study system because recruitment of oysters to individual reefs (i.e., the supply of the juvenile oyster resource) is spatially decoupled from reproduction on those reefs by dispersal during the larval stage (Narváez et al. 2012); in other words, spatial variability in the presence of predator cue is likely to occur at a finer spatial scale than that at which resource reproduction and recruitment are coupled. However, this consideration may be important when comparing NCE strength among large-scale regions with variation in resource supply (Kimbro et al. 2014).

The evidence for the importance of predator NCEs for population and community dynamics is copious and persuasive (Werner and Peacor 2003, Preisser et al. 2005, Peckarsky et al. 2008, Peacor et al. 2011). Nonetheless, there is a vigorous debate about the proper scale at which to estimate the relative strength of NCEs, and the degree to which common experimental approaches successfully isolate and reveal NCEs vs. introducing artifacts that inflate their perceived influence (Luttbeg et al. 2003, Abrams 2008). Our results support two key theoretical predictions: that NCEs weaken when measured over longer time scales within the generation of individual prey, but may reemerge and oscillate; and that CEs rather than NCEs are the primary driver of longer-term, ecosystem-level consequences of predation. However, even our study was too short to test theoretical predictions over multi-generational time scales (Luttbeg et al. 2003, Abrams 2008, Peacor et al. 2011). Additional empirical work will contribute to our understanding of the influence of NCEs on ecosystems over varying temporal and spatial scales.

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