

Environmental forcing and predator consumption outweigh the nonconsumptive effects of multiple predators on oyster reefs

DAVID L. KIMBRO ^{1,5} HANNA G. TILLOTSON,^{2,3} AND J. WILSON WHITE ⁴

¹Department of Marine and Environmental Sciences, Marine Science Center, Northeastern University, Nahant, Massachusetts 01908 USA

²Department of Biology, Florida State University, Tallahassee, Florida 32306 USA

³Florida Department of Environmental Protection, Tallahassee, Florida 32399 USA

⁴Department of Fisheries and Wildlife, Coastal Oregon Marine Experiment Station, Oregon State University, Newport, Oregon 97365 USA

Citation: Kimbro, D. L., H. G. Tillotson, and J. W. White. 2020. Environmental forcing and predator consumption outweigh the nonconsumptive effects of multiple predators on oyster reefs. *Ecology* 101(7): e03041. 10.1002/ecy.3041

Abstract. The ability to predict how predators structure ecosystems has been shown to depend on identifying both consumptive effects (CEs) and nonconsumptive effects (NCEs) of predators on prey fitness. Prey populations may also be affected by interactions between multiple predators across life stages of the prey and by environmental factors such as disturbance. However, the intersection of these multiple drivers of prey dynamics has yet to be empirically evaluated. We addressed this knowledge gap using eastern oysters (*Crassostrea virginica*), a species known to suffer NCEs, as the focal prey. Over 4 months, we manipulated orthogonally the life stage (none, juvenile, adult, or both) at which oysters experienced simulated predation (CE) and exposure to olfactory cues of a juvenile oyster predator (crab), adult predator (conch), sequentially the crab and then the conch, or none. We replicated this experiment at three sites along an environmental gradient in a Florida (USA) estuary. For both juvenile and adult oysters, survival was reduced solely by CEs, and variation in growth was best explained by among-site variation in water flow, with a much smaller and negative effect of predator cue. Adults exposed to conch cue exhibited reduced growth (an NCE), but this effect was outweighed by a positive CE on growth: Surviving oysters grew faster at lower densities. Finally, conch cue reduced larval settlement (another NCE), but this was swamped by among-site variation in larval supply. This research highlights how strong environmental gradients and predator CEs may outweigh the influence of NCEs, even in prey known to respond to predator cues. These findings serve as a cautionary tale for the importance of evaluating NCE processes over temporal scales and across environmental gradients relevant to prey demography.

Key words: environmental gradient; predation; trait-mediated effect; density-mediated effect; antipredator response; larval recruitment; predator cue; risk; ontogeny.

INTRODUCTION

Predation can strongly influence biodiversity and ecosystem functioning, but accurately predicting these influences may depend on accounting for both the consumptive effects (CE) and nonconsumptive effects (NCE) of predators (Paine 1966, Schmitz 2008, Trussell et al. 2017). For example, lynx (*Lynx canadensis*) consumption of snowshoe hare (*Lepus americanus*) produces a 10-yr hare population cycle that greatly affects the vegetation and nutrient cycling of North American boreal forests (Krebs et al. 1995). However, when lynx abundance declines, the hare population has a delayed numerical response that cannot be accurately predicted without considering how the NCEs of lynx continue to impair maternal hare

physiology and reproduction well after the peak in lynx abundance (Sheriff et al. 2011). As ecologists continue to develop theoretical frameworks to predict how predatory CEs and NCEs interact to influence prey demography, a common question is whether the influence of NCEs exceeds that of CEs (Abrams 2008, Schmitz 2008, Peers et al. 2018). But the answer to this question is not simple because of several complicating factors.

The first complication is that the relative effects of CEs and NCEs may shift over time and prey ontogeny (Peacor and Werner 2001). For instance, in northern U.S. freshwater streams, fear of sculpin (*Cottus cognatus*) predation initially impairs the foraging success, and thus individual growth (a NCE) of juvenile Atlantic salmon (*Salmo salar*). However, the sculpin CE also reduces intraspecific competition among juvenile salmon and promotes faster salmon growth at the subsequent life stage by maintaining low salmon density (Ward et al. 2011). Therefore, predicting predator effects requires understanding how CEs and NCEs may reinforce or

Manuscript received 18 November 2019; accepted 23 January 2020; final version received 27 February 2020. Corresponding Editor: Sergio Navarrete.

⁵ E-mail: d.kimbrow@northeastern.edu

counterbalance one another over time with respect to prey ontogeny and resource availability (Abrams 2008, Kimbro et al. 2017a). In this predator–prey dynamic, the relative strengths of CE and NCE likely depend on resource availability: if there is greater density-dependent competition for salmon and/or lower resources, then salmon would likely benefit more from the CE of reduced densities.

A second complication in contrasting CE and NCE strength is that most prey interact with multiple predator species, and the effects of multiple predators often cannot be predicted from the independent effects of each predator (Sih et al. 1998). Those multiple predators may also target different life stages of the prey. For example, the CE of arboreal predators on African treefrog (*Hyperolius spinigularis*) eggs causes the surviving eggs to hatch and release earlier as larvae into pools (Vonesh and Osenberg 2003). Although this antipredator trait response could reduce larval growth (a NCE), the early-hatched larvae actually grow out of vulnerable size classes faster because of reduced competition for resources, and are thus less vulnerable to their main aquatic predator, dragonfly larvae. Thus, the egg-stage trait response interacts with resource availability not only to offset a NCE in growth but also to dampen the subsequent larval-stage CE (Vonesh and Osenberg 2003). Here, evaluating the relative effects of CEs and NCEs requires the consideration of multiple predators and prey ontogeny, as well as environmental factors such as the resource base affecting posthatch growth rates.

A third consideration in evaluating the relative importance of NCEs is the potential for experimental artifacts that could erroneously amplify NCEs (Abrams 2008, Weissburg et al. 2014, Peers et al. 2018). One aspect of this problem involves introducing predator cues without allowing (or simulating) actual consumption of prey, so that the effect of the cue is measured in a context that would never occur naturally (NCE without CE; Abrams 2008, Peers et al. 2018). Additionally, prey can only develop the trait responses that lead to NCEs if they are able to detect predator cues against the ambient sensory background (Weissburg et al. 2014, Peers et al. 2018). Because many systems are organized by spatial and temporal gradients in environmental variability, it may be possible to predict when NCEs should and should not emerge. For example, in aquatic systems, prey at a site with slow-flowing water and minimal turbulence may detect waterborne olfactory cues of predators, creating strong NCEs and weak CEs, whereas prey at a nearby site with higher velocity and more turbulent flow may not detect predator cues, creating strong CEs and weak NCEs (Smee and Weissburg 2006). In a slightly different example on marine rocky shores, Ellrich et al. (2015) found that predatory snail cues inhibited recruitment of larval barnacles (prey) at sites with a moderate supply of barnacle propagules. But at a site with a higher supply of barnacle propagules (due to higher phytoplanktonic food supply), snail cues did not inhibit barnacle

recruitment because conspecific barnacle cues overwhelmed the predator cue Ellrich et al. (2015). Thus, conducting experiments across environmental gradients (and simulating CE as necessary) can reveal the range of possible CE and NCE interactions in natural systems, allowing us to make better predictions about their true relative importance.

In this study, we addressed the foregoing complications of NCE evaluation by conducting an experiment with simulated CEs that spanned the ontogeny of the prey. In addition, we designed the experiment so that predator cues were subjected to ambient environmental conditions across field sites that varied in abiotic factors likely to affect cue persistence and prey resource availability. The prey species was the eastern oyster, *Crassostrea virginica*: a habitat-forming species in estuaries of the U.S. Atlantic and Gulf coasts. On reefs created by eastern oysters, multiple studies have shown that fish predators indirectly increase oyster survival through a density-mediated indirect effect by consuming (a CE) small xanthid crabs (*Panopeus herbstii*), which feed on juvenile oysters (Grabowski 2004). Additionally, in both controlled and natural field settings as well as over weekly and seasonal timescales, the xanthid crabs exhibit a trait response to the risk of fish predation, spending more time hiding and less time feeding. This often—but not always—leads to higher oyster survival through a trait-mediated indirect effect (Grabowski 2004, Kimbro et al. 2014, 2017a). The xanthid crabs, in turn, exert both CEs and NCEs on their oyster prey, at least in the juvenile oyster stage. In controlled settings, crab cues cause juvenile oysters to produce thicker shells that help reduce predation, at the cost (NCE) of reduced soft-tissue somatic growth (Scherer et al. 2016). Adult oysters, while large enough to be invulnerable to xanthid crabs, are consumed by—and possibly have an antipredator response to—larger predators such as the crown conch, *Melongena corona* (Gosnell et al. 2017). However, it is unknown whether or how the CEs and NCEs of these two predators interact across life stages of the oyster to generate emergent multiple predator effects, and whether NCEs consistently arise across environmental gradients. These questions are particularly pressing as increasingly frequent regional droughts alter estuarine salinities in the southeastern United States, facilitating greater abundance and activity of oyster predators including the crown conch and potentially threatening the sustainability of oyster populations (Garland and Kimbro 2015, Kimbro et al. 2017b).

Our test of relative NCE importance across prey ontogeny and environmental variability consisted of a manipulative experiment at three sites that span 5 km of abiotic conditions within an estuary on the Atlantic coast of Florida, USA (Appendix S1; Garland and Kimbro 2015). At each site, we orthogonally manipulated the exposure of oysters to predator cues (none, crab, conch, or multiple [first crab and then conch]) that may lead to NCEs as well as the life stage (none, juvenile,

adult, or both) at which oysters are exposed to simulated consumption (CE). We evaluated the effects of these treatments on the survival and growth of both juvenile and adult oysters as well as on the recruitment of oyster larvae. This approach allowed us to evaluate the relative importance of NCEs on oyster demography given natural variation in the sensory environment, the presence of CEs, and the potential for emergent NCEs caused by interactions between predator cues across prey life stages.

METHODS

Study system

This research was conducted at three sites in the southern portion of the Matanzas River estuary, because of their relative location between a tidal inlet (Matanzas inlet) and freshwater input (Pellicer creek) that represent spatial gradients in environmental conditions (Appendix S1: Fig. S1). At these sites, shorelines are dominated by oyster reefs that border salt marsh (*Spartina alterniflora*) and mangrove (primarily *Avicennia germinans*) habitats, and the primary predators of oysters are the mud crab (*Panopeus herbstii*) and the crown conch (*Melongena corona*). Mud crabs primarily consume juvenile oysters (oyster length <25 mm; Kimbro et al. 2014, Kimbro et al. 2017a) and conchs primarily consume adult oysters (oyster length >25 mm; Garland and Kimbro 2015, Booth et al. 2018). Hereafter, we will refer to the sites as being “close,” (29 39.503 N, 81 13.316 W), “mid,” (29 40.253 N, 12.944 W), and “far” (29 41.704 N, 81 14.046 W) from the freshwater input, Pellicer Creek.

Overview of experiment

The basic unit of replication was what we term an “experimental unit” (Appendix S2: Figs. S1–S3). This experimental unit held focal oysters in a cage that excluded predation and also held predators in nearby cages to release olfactory cues that the focal oysters could detect (to create NCEs). Because we were interested in effects over ontogeny, we started each experiment with juvenile oysters and allowed some to mature into adulthood. During the experiment, half of the oysters were sacrificed after 1 month for data collection. Exposure to predator cues (mud crab or conch) during the juvenile oyster stage occurred in the first month of the experiment (oysters were <20–25 mm). Exposure to predator cues occurred during the adult oyster stage over the subsequent 4 months. The four predator cue treatments were: none, juvenile predator cue (mud crab) throughout the experiment, adult predator cue (conch) throughout the experiment, and stage-appropriate cue in both juvenile and adult stages (hereafter, “multiple predator” treatment). Within each cue treatment, we orthogonally varied simulated consumptive effects (CEs): none,

juvenile-stage only, adult-stage only, or both stages. We simulated CEs by manually removing oysters, so that it was possible to have consumption in the absence of cue, as might happen if environmental conditions precluded cue detection (Abrams 2008).

We destructively sampled half of the oysters (randomly selected) at the end of the first month to quantify effects at the juvenile stage. As a result, culled oysters in certain treatments were reclassified in analysis, as they did not have the opportunity to experience adult-stage cues and CEs. Therefore, culled oysters originally assigned to the adult-stage CE treatment were classified as controls during analysis, and those assigned to experience culling during both stages were classified as being culled during the juvenile-stage only. Similarly, oysters in the multiple predator (MP) cue treatment were reclassified as being exposed to only mud crab cues.

With this multiple-life stage, multiple-cue, and multiple-CE experimental design, we can envision several possible sets of likely results (Fig. 1). First, if predator cues did not produce NCEs, then only CEs would be detected. In terms of growth, the CEs should alleviate competition by reducing oyster density, leading to faster oyster growth in the treatments with longer durations of the CE (and thus lower survival; the “adult-only” and “both” treatments; Fig. 1, top). Alternatively, if NCEs were very strong, they may suppress oyster growth regardless of the reduction in density due to CE given the energetic and starvation costs of reduced feeding activity (Fig. 1, bottom). An intermediate outcome is that NCEs are present but very weak, either because of environmental turbulence weakening the cue or because the prey’s energetic resources (phytoplankton, in the case of oysters) are sufficiently abundant that the reduced density from the CE allows compensatory growth that offsets the NCE (Fig. 1, middle). For easy comparison to these hypothetical outcomes, we present our results in a format similar to Fig. 1

Details of experiment

Each experimental unit consisted of a focal oyster cage (18 × 13 × 18 cm) centered between two opposing smaller cages for predators (13 × 13 × 13 cm; Appendix S2: Figs. S1–S2). One predator was placed in each of the two smaller cages, which were held flush to the exterior of the central focal cage with cable ties, so that oysters in the central cage were exposed to predator cues from two directions, but were protected from being eaten. All cages were constructed with PVC-coated wire mesh (6-mm mesh openings) and were sewn shut as well as together with Maxi Edge trimmer line (0.17-cm diameter). To mimic the turbulent dispersion of waterborne cues on natural oyster reefs (Smee and Weissburg 2006), we placed four sun-bleached oyster shells in each predator cage to disperse water flow. At each site, we established four transects (6-m length) parallel to the shoreline and separated by 3 m on a mudflat. Along

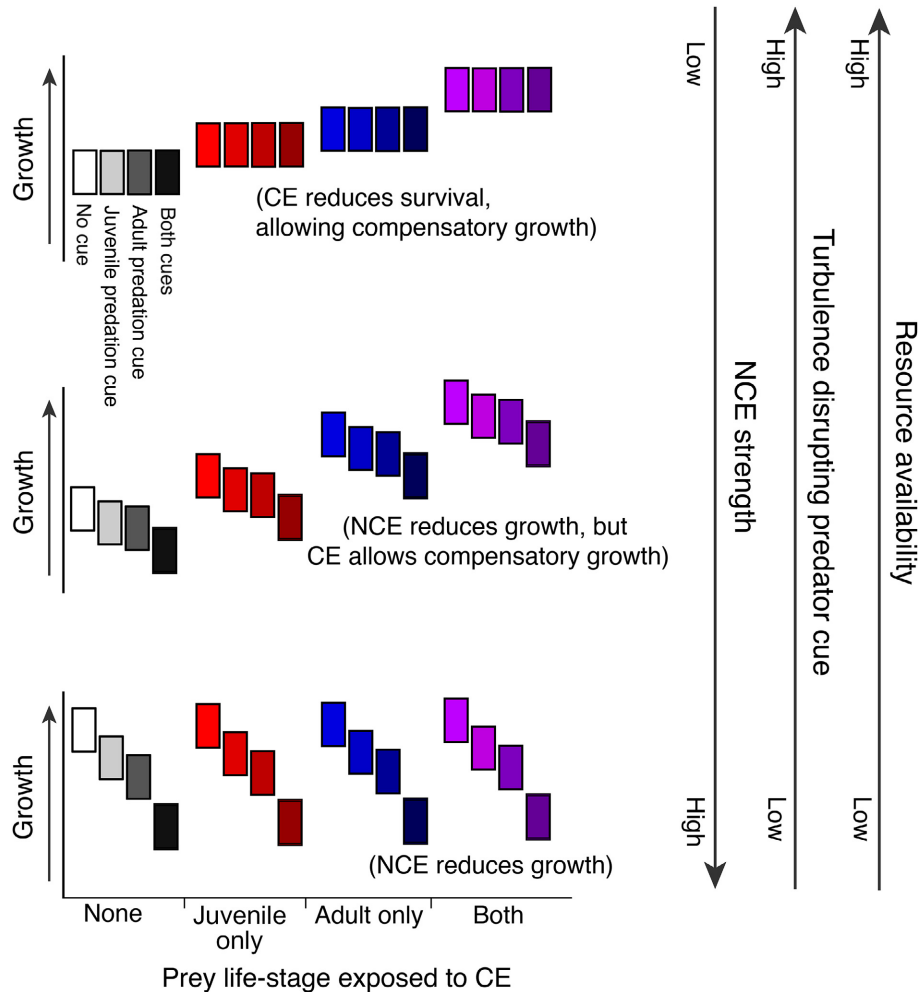


FIG. 1. Illustration of possible experimental results under different scenarios. Along the horizontal axis, each row shows prey growth for oysters grouped by the life stage to which simulated predation (CE) was applied: no CE (gray scale), CE on juvenile prey (red scale), CE on adult prey (blue scale), as well as CE on juvenile and then adult prey (purple scale). In each CE treatment, color shading indicates cue treatments (noted in upper left panel). Each bar represents the interquartile range of data, as in the boxplots shown in later figures. The first row shows expected results if CEs but not NCEs are present because of environmental turbulence disrupting prey perception of risk and/or resource availability allowing for compensatory growth. The second row illustrates weak NCEs due to environmental turbulence that does not fully disrupt prey perception of risk, and/or sufficient resources combined with reduced density from the CE to allow compensatory growth that offsets the NCE. The third row shows very strong NCEs that suppress oyster growth regardless of the reduction in density due to CE given the energetic and starvation costs of reduced feeding activity.

each transect, six experimental units were deployed at 1-m intervals. In this estuary, settlement of larval oysters to the benthos primarily occurs in two large pulses in the spring and fall of each year. The experiment began in June 2012, after the spring recruitment pulse, and ended in November 2012, after the fall recruitment pulse.

Within each site, experimental units were randomly assigned among four levels of the cue factor: no cue, mud crab cue, crown conch cue, and multiple predator cue (mud crab cue as juveniles, then crown conch cue as adults). There were 24 total experimental units per site ($n = 6$ for each cue treatment). The mud crabs had a mean carapace width of 38 mm, and the crown conchs

had a mean shell length of 83 mm. Predators were replaced weekly with new animals collected from nearby oyster reefs. Each replicate of a cue treatment contained two mud crabs or two conchs. This density of experimental predators per unit area is within the range of natural predator density on oyster reefs throughout the MRE (Booth et al. 2018).

Within each central oyster-holding cage, we installed 12 ceramic tiles (8×8 cm) by drilling a hole into the top of the tiles and fastening the tiles to the inner wall with cable ties. Prior to the installation of tiles, juvenile oysters of equal age and size (6–8 mm shell length) were produced in a local hatchery (Research Aquaculture

Inc., Jupiter, Florida, USA). Ten of these juvenile oysters were adhered to each tile with superglue (Loctite gel).

Within each predator cue treatment, we randomly assigned the 12 tiles among four levels of simulated consumptive effect: none, juvenile stage only, adult stage only, or both stages. This produced $6 \times 3 = 18$ replicates for each combination of predator cue and simulated CE at each site. Simulated predation rates were based on oyster survival curves from previous field experiments in this estuary (Garland and Kimbro 2015). On a weekly basis, we manually culled juvenile oyster density according to a log-transformed survival curve for juvenile oysters ($\log\text{-survival} = -0.0072 \text{ days} + 0.074$, $\sim 5\%$ removal per week). This prescribed culling was applied until the oysters grew to 20–25 mm, which is when they become less vulnerable to mud crabs and approach sexual maturity. Once oysters reached 25 mm in length, we manually culled oysters on a weekly basis in accordance with a log-transformed survival curve for adult oysters ($\log\text{-survival} = -0.029 \text{ days} + 0.049$, $\sim 19\%$ removal per week).

Quantifying juvenile oyster responses (after 1 month)

Our experiment produced three types of data for juvenile oysters. First, we quantified the remaining abundance of juvenile oysters to estimate postsettlement survival after 1 month. Second, we measured the length (mm) of each oyster and subtracted the average of these lengths from the average length of oysters at the beginning of the experiment to estimate growth over one month. Shell length was measured as the farthest distance from the umbo to the opposing tip of the shell. Third, for the half of the juvenile oysters destructively sampled after 1 month, when oyster lengths reached 20–25 mm, we assessed their phenotypic response to predator cues. Specifically, we calculated a condition index, which illustrates the degree to which an oyster allocates energy to the production of shell versus tissue mass, with the former typically receiving more energy in the presence of predators (see Johnson and Smee 2012 and Appendix S3 for detailed protocol).

Quantifying adult oyster responses (after 4 months)

After 4 months (124 d), we harvested all experimental units to quantify adult oyster survival, growth, and condition index in accordance with the methods outlined above for juvenile oysters. In addition, we quantified the abundance of larval recruits on each tile to estimate how site, predator cue, and CE influenced the natural colonization of oysters. Note that in both juvenile and adult oysters, we did not necessarily expect to detect an effect of predator cue on survival (though it would be possible, if stress has a physiological cost), but did quantify survival to confirm that our CE treatments had the intended effect.

Quantifying environmental factors

During the experiment, we monitored several physical variables at each site. These variables included the proportion of time oysters were exposed at low tide, water salinity, water temperature, water flow, and chlorophyll *a* (chl *a*; see Appendix S3 for methods).

Statistical analyses

All analyses were conducted using R 3.6.1 (R Core Team 2019). Specific R packages used are noted below.

Juvenile oyster responses (after 1 month).—We used a generalized linear mixed-effects model (GLMM) with binomial error and logit link (i.e., logistic regression) to test whether the survival of juvenile oysters depended on site, predator cue, and/or simulated predation (CE). For this analysis, the experimental unit was treated as a random effect. Because the full model with fixed effects of site, predator cue, and CE would not converge due to the large number of parameters relative to degrees of freedom, we conducted a separate GLMM for each site. For the juvenile growth and condition index results, we used a linear mixed effects model to test whether oyster growth depended on site, predator cue, and/or CE. Mixed models were fit with the lme4 package (Bates et al. 2015). When we detected effects of site, predator cue, or simulated CE ($P < 0.05$), we conducted a Tukey's post hoc test to compare means among the levels of site, predator cue, and/or CE. Post hoc tests were conducted with the package multcomp (Hothorn et al. 2008). When we detected a significant interaction between main effects, we restricted our mean comparisons to test for relative differences in CEs and NCEs within each site, not among sites.

Furthermore, in models with significant main effects of site, predator cue, and/or CE, we calculated marginal R^2 values for each effect in order to evaluate the relative influence of each factor on the response variable (MuMIn package; Barton 2019). In addition, when cue and/or CE were significant, we calculated NCE and CE strengths or effect sizes (denoted as Ψ) according to Kimbro (2012):

$$\psi_{\text{NCE}} = 1 - (\text{Response}_{\text{cue}} / \text{Response}_{\text{nocue}}).$$

$$\psi_{\text{CE}} = 1 - \left(\text{Response}_{\text{CE,juvenile,adult,orboth}} / \text{Response}_{\text{noCE}} \right).$$

To evaluate the effects of environmental factors on spatial variation in juvenile oyster growth and survival, we took a model selection approach. For this analysis, we only used results from the no-CE and no-cue control treatments. Candidate single-factor, linear mixed effects models included a null model (intercept only) and models with either temperature, salinity, proportional aerial

exposure, chl *a*, or flow as the explanatory variable with the experimental unit as a random effect. That is, the average survival or growth on each tile was the unit of replication, but lack of independence between tiles within each experimental unit was accounted for by the random effect. The environmental (explanatory) variables were estimated at the site level, rather than within site, so replicates within each site shared the same value of each explanatory variable. Because we had only three sites, we only considered univariate models rather than models with higher-dimension interactions between fixed effects. To identify the model offering the most parsimonious explanation of variability in growth and survival, we used Akaike's information criterion corrected for small sample size (AIC_c). Linear mixed-effects models were fit using package lme4 (Bates et al. 2015), and we estimated the marginal coefficient of variation (the proportion of variance explained by the fixed effects; Nakagawa et al. 2017) for each of the "best" models using package MuMIn (Barton 2019). Average survival rates were arcsine square root transformed for this analysis to meet the distributional assumptions of linear regression.

Adult oyster responses (after 4 months).—The analysis of the adult oyster responses mirrored the analysis of the juvenile oysters described above. We used a generalized linear mixed effects model (GLMM) with binomial error, logit link, and caging unit as a random effect to test whether the survival of adult oysters depended on site, predator cue, and/or CE. Because the full model with site, predator cue, and CE would not converge, we conducted a separate GLMM for each site. For the growth and condition index of adult oysters, we used separate linear mixed effects models to test whether each response depended on site, predator cue, and/or CE. When we detected effects of site, predator cue, CE, or an interaction between these main effects ($P < 0.05$), we conducted a Tukey's post hoc test to compare means among treatments. When appropriate, we also calculated marginal R^2 and effect sizes (Ψ_{CE} and Ψ_{NCE}) of fixed effects as describe above.

Spatial variability in growth necessitated adjustments to the collection and analysis of the adult data. Specifically, oysters at sites closest to and farthest from the freshwater input reached adult sizes and experienced adult CE and predator cue treatments at different times (day 33 and 72, respectively). As a result, at the site closest to freshwater input, we harvested three of the four tiles in each cage unit on day 77, which is when further CE was not possible without depleting all oysters. The unharvested tiles remained in the field without exposure to predator cues and CE until the end of the experiment (day 124). Although the early harvest allowed us to quantify oyster responses immediately upon finishing the application of the predator cue and CE treatments at the site closest to freshwater, the one unharvested

replicate allowed us to have equivalent experimental duration across all three sites.

In the GLMM of oyster survival (proportional) at the site closest to freshwater input, the results were the same regardless of duration (77 or 124 days). Therefore, our analysis of the proportional survival results at this site included all available data. Because the response variables of growth increment and recruitment were not proportional, we standardized them by duration (response/77 d or response/124 d) to facilitate comparing results across sites.

Oyster larval recruitment (after 4 months).—The analysis of the larval recruitment results mirrored the analysis of results on juvenile oyster growth. We used a linear mixed effects model to test whether oyster larval recruitment depended on site, predator cue, and/or CE. When we detected effects of site, predator cue, simulated CE, or an interaction between these main effects ($P < 0.05$), we conducted a Tukey's post hoc test to compare means among treatments only within each site. Furthermore, we calculated marginal R^2 and effect sizes to evaluate relative importance of site, NCE and CE on oyster larval recruitment.

RESULTS

Juvenile oyster responses (after 1 month)

Survival.—After 1 month, the survival of juvenile oysters at all sites was reduced by the (simulated) CE of predators ($P < 0.001$ at all sites; Fig. 2A–C). At the close, mid, and far sites, CE strengths (Ψ_{CE}) were 0.38, 0.52, and 0.37 (respectively), with marginal R^2 values of 0.52, 0.30, and 0.06 (respectively). In contrast, survival was not affected by predator cue or the interaction between CE and predator cue (Appendix S4: Table S1). According to model selection, the proportion of time exposed during low tide was the most parsimonious explanation for spatial variation in survival in the absence of CE and predator cues (AIC_c weight = 0.97): survival decreased with increasing aerial exposure (linear mixed-effect regression; marginal $R^2 = 0.58$; Appendix S5: Fig. S1 and Appendix S6: Tables S1–S3).

Growth.—The growth of juvenile oysters depended significantly on site ($P < 0.001$) and predator cue ($P = 0.02$; Fig. 2D–F), but not on the CE of predators ($P = 0.40$) or any interactions among these main effects (Appendix S4: Table S2). Specifically, growth differed among all sites (Tukey's honestly significant difference [HSD], $P < 0.001$), and the order of sites from least to greatest growth was mid < far < close distance to freshwater input. Averaged across all sites, juvenile oysters in the no-cue treatment grew faster than did oysters in the mud crab and conch cue treatments (Tukey's HSD, $P = 0.05$ and 0.01, respectively), with NCE strengths

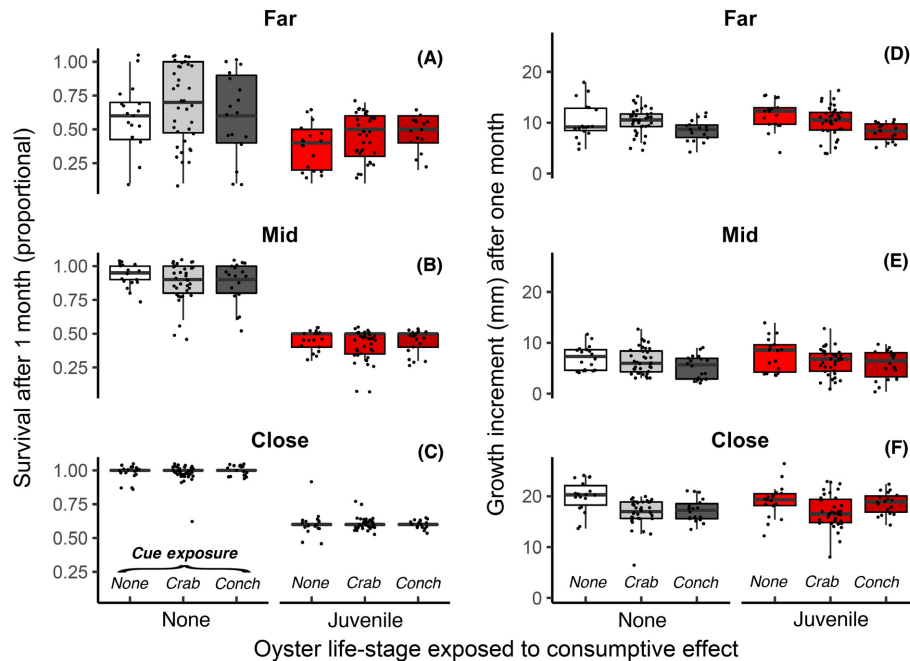


FIG. 2. Survival (left panels) and growth (right panels) of juvenile oysters at sites located relatively far (A, D), mid (B, E), and close (C, F) distances from the nearest freshwater input. Within each site, data are grouped on the horizontal axis by the life stage to which simulated predation (CE) was applied: no CE (gray scale) and CE on juvenile oysters (red scale). In each CE treatment, color shading and text above horizontal axis indicate predator cue treatment. On each box, the thick black line indicates the median, the box indicates the interquartile range, and the whiskers indicate the middle 95% of the data. Individual data are plotted as points.

(Ψ_{NCE}) of 0.12 and 0.15, respectively. However, the proportion of variance explained by site (marginal $R^2 = 0.73$) was much larger than the proportion of variance explained by predator cue (marginal $R^2 = 0.02$). According to model selection, water flow was the most parsimonious explanation for spatial variation of oyster growth in the absence of CE and predator cues (AIC_c weight = 0.97): growth increased with increasing water flow (linear mixed-effect regression; marginal $R^2 = 0.75$; Appendix S5: Fig. S2 and Appendix S6: Tables S1–S3).

Condition index.—The condition index of juvenile oysters did not depend significantly on site ($P = 0.42$), predator cue ($P = 0.79$), CE ($P = 0.69$), or any two- and three-way interactions among the main effects (Appendix S4: Table S3).

Adult oyster responses (after 4 months)

Survival.—After 4 months, the survival of adult oysters farthest from freshwater input was reduced by simulated predation (CE; $P < 0.001$, marginal $R^2 = 0.26$), but not by predator cue ($P = 0.89$) or the interaction between CE and predator cue ($P = 0.99$; Fig. 3A; Appendix S4: Table S4). At the end of 4 months, significantly more oysters survived in the no-CE treatments than in any of the CE treatments (Tukey's HSD $P < 0.001$), with CE strengths (Ψ_{CE}) of 0.5, 0.82, and 0.82 for the juvenile-,

adult-, and both-CE treatments (respectively). Meanwhile, significantly more oysters survived for 4 months in the juvenile-CE treatment than in the adult- and both-CE treatments (Tukey's HSD, $P < 0.001$), which did not differ from each other.

At the middistance site, survival depended on an interaction between CE and predator cue ($P < 0.001$; Fig. 3B; Appendix S4: Table S4). However, this interaction is difficult to interpret, because within each of the four levels of the CE factor, there were no statistically significant differences among the four levels of predator cue (Tukey's HSD, $P > 0.05$). Overall, at the mid-distance site, oyster survival in the no-CE treatment was significantly higher than the other three levels of the CE factor (Tukey's HSD, $P < 0.05$), with a marginal R^2 of 0.26 for the fixed effect of CE and CE strengths (Ψ_{CE}) of 0.5, 0.15, and 0.55 for the juvenile-, adult-, and both-CE treatments (respectively). Survival was somewhat higher in the no-cue and crab-cue treatments of the adult-only CE treatments, perhaps explaining the CE \times cue interaction, but again those differences were not statistically significant. No oysters grew into the “adult” size class at this site (note small sizes in Fig. 3E), so culling of adult oysters was never applied. Consequently, oyster survival in the adult-CE was significantly higher than survival in the juvenile- and both-stage CE treatments (Tukey's HSD, $P < 0.05$), which did not differ from each other (Tukey's HSD, $P > 0.05$).

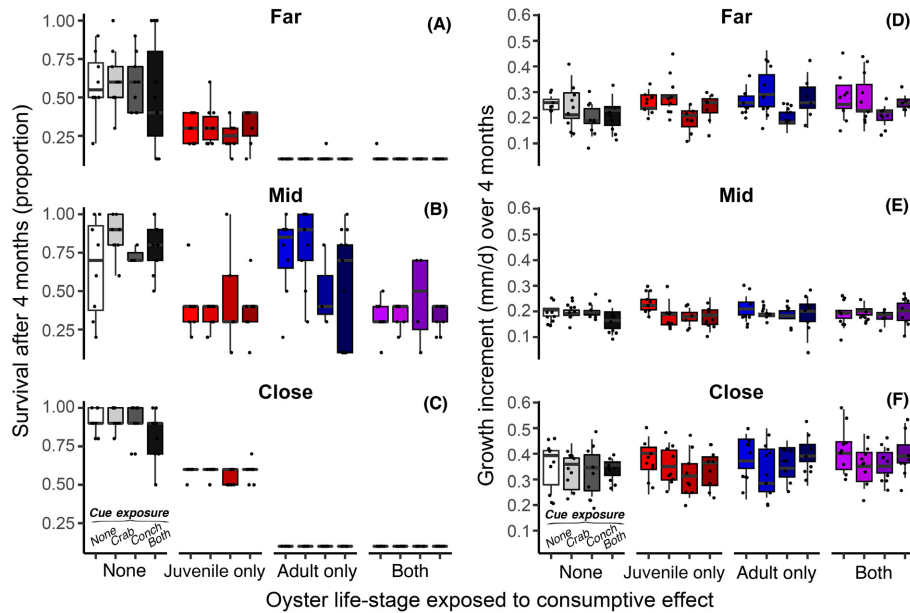


FIG. 3. Survival (left panels) and growth (right panels) of adult oysters at sites located relatively far (A, D), mid (B, E), and close (C, F) distances from the nearest freshwater input. Within each site, data are grouped on the horizontal axis by the life stage to which simulated predation (CE) was applied: no CE (gray scale), CE on juvenile oysters (red scale), CE on adult oysters (blue scale), as well as CE on juvenile and then adult oysters (purple scale). In each CE treatment, color shading and text above horizontal axis indicate predator cue treatment. On each box, the thick black line indicates the median, the box indicates the interquartile range, and the whiskers indicate the middle 95% of the data. Individual data are plotted as points.

At the site closest to freshwater input, adult survival depended on the CE of predators ($P < 0.001$, marginal $R^2 = 0.51$), but not on predator cue ($P = 0.78$) or the interaction between CE and predator cue ($P = 0.73$; Fig. 3C; Appendix S4: Table S4). This result was consistent in the analysis of the partial (day 77) and final harvest data (day 122) combined and with the analysis of only the final harvest data (day 122; Fig. 3C illustrates all data). Significantly more oysters survived in the no-CE treatment than in any of the CE treatments (Tukey's HSD; $P < 0.001$), with CE strengths (Ψ_{CE}) of 0.35, 0.89, and 0.89 for the juvenile-, adult-, and both-CE treatments (respectively). Meanwhile, more oysters survived in the juvenile-CE treatment than in the adult- and both-CE treatments (Tukey's HSD, $P < 0.001$), which did not differ from each other (Tukey's HSD, $P < 0.001$).

According to model selection, the most parsimonious explanatory models for variation among sites in adult oyster survival in the absence of the CEs and predator cues were the null model and proportion of time exposed during low tide (AIC_c weights = 0.67 and 0.24, respectively), with survival decreasing with increasing time exposed (linear mixed-effect regression, marginal $R^2 = 0.31$; Appendix S7: Fig. S1 and Appendix S6: Tables S1–S3).

Growth.—Adult oyster growth depended on site ($P < 0.001$), predator cue ($P < 0.001$), and CE

($P < 0.01$), but not on any two- or three-way interactions among the main factors (Appendix S4: Table S5; Fig. 3D–F). Adult oyster growth differed significantly among all sites (Tukey's HSD, $P < 0.001$); the order of sites from slowest to fastest growth was mid < far < close distance to freshwater input. Across all sites, oysters in the no-cue and the multiple-predator-cue treatments grew equally and significantly more than did oysters exposed to conch cue for the whole experiment (Tukey's HSD, $P < 0.01$, conch $\Psi_{NCE} = 0.07$). The growth of oysters exposed to mud crab cue did not differ significantly from any other cue treatment (Tukey's HSD, $P > 0.05$; crab $\Psi_{NCE} = 0.04$).

Also, across all sites, oysters in the no-CE treatment grew significantly less than did oysters exposed to juvenile-, adult-, and both-CEs (Tukey's HSD, $P < 0.05$), with CE strengths (Ψ_{CE}) of -0.04 , -0.06 , and -0.06 , respectively. Note that this positive influence of CEs is difficult to discern in Fig. 3 and is most evident at the far (Fig. 3D) and close sites (Fig. 3F). The growth of oysters exposed to juvenile-CE did not differ from the adult- and both-CE treatments (Tukey's HSD, $P > 0.05$). Although all three fixed effects were statistically significant, the influence of site (marginal $R^2 = 0.20$) was far stronger than predator cue (marginal $R^2 = 0.03$) and culling (marginal $R^2 = 0.02$).

According to model selection, the most parsimonious explanatory models for variation among sites in adult oyster growth in the absence of the CEs and predator

cues were the null model and proportion of time exposed during low tide (AIC_c weights = 0.62 and 0.20, respectively), with growth decreasing with increasing time exposed (linear mixed-effect regression, marginal $R^2 = 0.08$; Appendix S7: Fig. S2 and Appendix S6: Tables S1–S3).

Condition index.—The condition index of adult oysters did not depend significantly on site, predator cue, CE, or any interaction among the factors of site, predator cue, and simulated predation (Appendix S4: Table S6).

Oyster larval recruitment (after 4 months)

The recruitment of oyster larvae depended on the interaction between site and CE ($P < 0.0001$) as well as the main effect of predator cue ($P < 0.0001$; Appendix S4: Table S7; Fig. 4). Within the mid (Fig. 4B) and close (Fig. 4C) sites, larval recruitment in the CE treatments did not differ significantly from each other (Tukey's HSD, $P > 0.05$). But within the far site (Fig. 4A), larval recruitment to the adult-CE treatment was significantly less than larval recruitment to the no-CE ($P = 0.06$), juvenile-CE ($P < 0.01$), and both-CE treatments ($P < 0.01$). Across all sites, larval recruitment was significantly greater in the no-cue treatment than in the conch-cue treatment (Tukey's HSD, $P = 0.02$; conch $\Psi_{NCE} = 0.07$). Larval recruitment to all other predator cue treatments did not differ from each other significantly. Although predator cue (marginal $R^2 = 0.03$) and the interaction between site and CE (marginal $R^2 = 0.02$) were statistically significant, they explained

much less of the proportional variance than did the main effect of site (marginal $R^2 = 0.20$).

DISCUSSION

Although the nonconsumptive effects of multiple predators can potentially drive the population dynamics of prey, we found that the demographic rates of oysters on reefs in Florida are primarily governed by the consumptive effects of predators and environmental differences among sites within an estuary. Across all sites, juvenile oyster growth was primarily influenced by environmental differences among sites (likely differences in water flow, which would affect delivery of oysters' phytoplankton prey) and only secondarily by predator cues. Meanwhile, juvenile oyster survival was driven primarily by simulated consumption (as expected) and to a lesser degree by spatial variation in low-tide exposure (with greater exposure presumably leading to higher physiological stress and thus lower survival). This suggests that predator CEs and environmental forcing overwhelm the importance of NCEs during the juvenile life stage. Both predator CEs and environmental factors continued to be important in the adult oyster life stage. Adult survival varied among sites, but within each site was determined by predator CEs only. Similarly, adult oyster growth displayed a spatial pattern that largely matched that established in the juvenile life stage; growth was also somewhat faster if oyster densities had been reduced by CEs, alleviating intraspecific competition. The magnitude of this compensatory growth effect overshadowed the only NCE we detected in adults, a slight reduction in

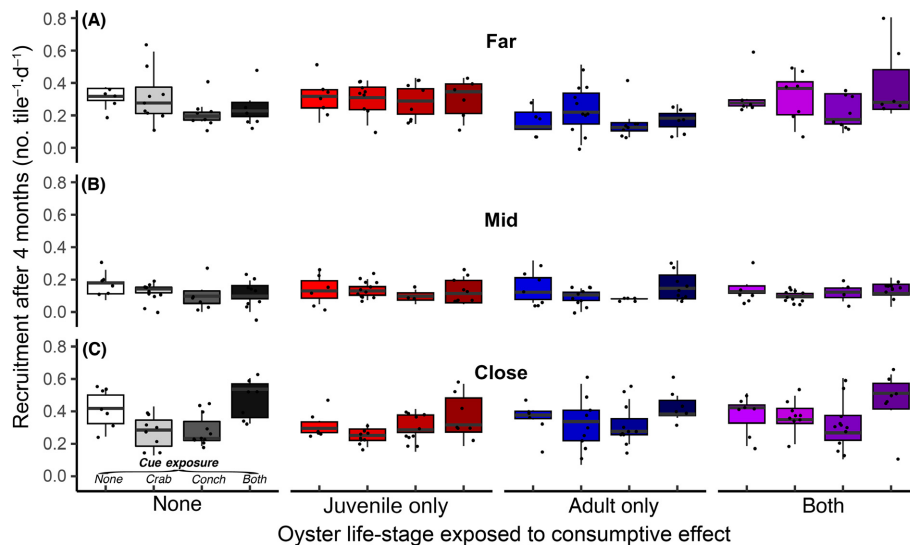


Fig. 4. Oyster larval recruitment at sites located relatively far (A), mid (B), and close (C) distances from the nearest freshwater input. Within each site, data are grouped on the horizontal axis by the life stage to which simulated predation (CE) was applied: no CE (gray scale), CE on juvenile oysters (red scale), CE on adult oysters (blue scale), as well as CE on juvenile and then adult oysters (purple scale). In each CE treatment, color shading and text above horizontal axis indicate predator cue treatment. On each box, the thick black line indicates the median, the box indicates the interquartile range, and the whiskers indicate the middle 95% of the data. Individual data are plotted as points.

adult growth due to conch cue. Adult survival also varied among sites, but within each site was determined by predator CEs only. Finally, larval recruitment of oysters at all sites was higher in the absence of a cue from a predator that focuses on adult oysters. Collectively, these results suggest that the base of a food web long believed to be structured by NCEs (Grabowski 2004, Johnson and Smee 2012, Kimbro et al. 2014) does in fact exhibit a NCE on growth and recruitment, but the relative importance of these NCEs for oyster population dynamics is quickly negated by predation, compensatory growth, and environmental forcing.

Although variation in oyster vital rates mostly occurred at the scale of sites, we detected three *statistically* significant NCEs on juvenile growth, adult growth, and larval recruitment. Cues from both juvenile (crab) and adult (conch) predators induced a negative NCE on juvenile oyster growth, and the conch cue also induced a negative NCE on adult oyster growth at all sites. However, the reduction in adult oyster density by simulated predation decreased intraspecific competition for space, creating a positive CE that opposed the negative NCE on growth. In addition, conch cue also reduced oyster larval recruitment at all sites, similar to the NCEs observed on dispersive propagules of organisms in other ecosystems (e.g., fish recruitment to coral reefs; Benkitt 2017). At one of our sites, there was a further reduction in recruitment in the adult-CE treatment. Simulated predation apparently increased the space available for larval recruitment, suggesting that the benefit of low adult density—and potentially less intraspecific competition—did not compensate for the risk of the conch cue. Consequently, the suppression of larval recruitment can independently occur from the cues of conspecific competitors and a predator. On the one hand, our results, along with similar empirical results from a rocky shore system (Ellrich et al. 2016) indicate that NCEs can influence multiple vital rates of prey populations in natural settings. On the other hand, our results suggest that the actual magnitude of NCEs in the field may be relatively weak (and their strength modulated by environmental factors, as in Ellrich et al. 2015 and Ellrich and Scrosati 2016) or counterbalanced by the consumptive effects of predators in a compensatory manner over time. Therefore, experiments focused on a single vital rate in isolation of consumptive effects and competition will have limited applicability to the dynamics of natural systems, as predicted by Abrams (2008).

Because higher-order predators are believed to cause strong NCEs on midtrophic consumers (crabs) in oyster reef communities (Grabowski and Kimbro 2005) and many other systems (e.g., Schmitz 2008), it is important to consider why biologically significant NCEs were not found in the current study. We offer two explanations. First, in previous studies of oyster reef communities, Kimbro et al. (2014, 2017a) focused on how a nonlethal predator interaction influenced the foraging behavior of a midtrophic consumer (crab) and referred to this

interaction as a “nonconsumptive effect.” Such antipredator behaviors (foraging reductions and habitat shifts) appear to be the most common response analyzed in studies under the “ecology of fear” umbrella (Preisser et al. 2005). Although these trait responses could cause an NCE, they do not directly translate into fitness metrics such as prey growth, survival, and reproduction and therefore do not represent a “nonconsumptive effect” of a predator on prey demography, in the strictest sense (Abrams 2008). Consequently, we are unaware of previous studies that demonstrated a clear NCE on midtrophic level crabs in this system.

A second explanation concerns the life-history strategies and trophic position of the focal prey. In our study, we examined whether predator cues affected demographic rates of sessile prey occupying the basal trophic level of a food web. Sessile prey like oysters or terrestrial plants often respond to predator cues by changing traits. For example, in laboratory experiments, Scherer et al. (2016) exposed juvenile oysters to predator cues and observed differences in shell defensive metrics (thickness, crushing resistance) and growth. In fact, these shell trait responses—not quantified in the present study—may underlie the observed NCE on adult growth in our study. However, in natural settings, the energetic cost of these trait responses on growth and the associated NCE may be minimized or compensated for by the passive feeding strategy of suspension feeding invertebrates, particularly when changes in prey density due to CE alleviate competition for planktonic prey. In contrast, mobile prey and/or organisms occupying higher trophic levels must actively seek resources and may repeatedly experience greater energetic costs with each shift in habitat use and foraging behavior alteration, possibly without any reduction in competition, and thereby may experience stronger NCEs from predators (Heithaus et al. 2007). To understand how NCEs influence food webs, future research should explore whether the NCEs on prey vital rates differ deterministically across trophic levels and as a function of mobility.

Like all species interactions (Chamberlain et al. 2014), NCEs of predators are highly context-dependent and this variability may be deterministic along predictable environmental gradients (Kimbrow 2012). For example, recent work on rocky shores demonstrated that the NCE of a predatory snail on barnacle (prey) recruitment occurred on low energy shorelines but not on exposed high-energy shorelines, presumably because of site differences in the hydrodynamics of predator cue dissipation (Ellrich and Scrosati 2016). In the same system, shorelines with a moderate supply of barnacle larvae exhibited an NCE of the predatory snail on prey recruitment, but shorelines with high barnacle recruitment did not; barnacles are gregarious settlers and the cues of conspecific barnacles overwhelmed the predator cue at sites with high recruitment (Ellrich et al. 2015). Interestingly, in the current study, NCEs on oyster growth and larval recruitment occurred regardless of ambient growing conditions and larval

supply pool. Because of this conflicting evidence about the role of supply-side and bottom-up factors on the strength of NCEs, future NCE experiments must not only be conducted in the natural environment, but also across multiple sites that encompass environmental gradients. For example, we found that water flow was the most parsimonious explanatory variable describing among-site variability in growth. Although this result aligns with laboratory experiments showing a linear relationship between oyster growth and flow velocity (Lenihan et al. 1996), it is based on a regression across only three sites and must be interpreted with caution.

Surprisingly, NCEs on oyster vital rates were most consistently induced by the predator of adult oysters (conch) and not the voracious predator of juvenile oysters (mud crab; Grabowski 2004). It was also surprising that the mud crab cue at the juvenile stage did not interact with the conch cue at the adult stage to cause a multiple predator interaction through prey ontogeny, as Vonesh and Osenberg (2003) observed in amphibians. The absence of this multiple-predator interaction could be due to our decision to maintain equal predator densities but not predator biomass across our treatments, which may have created unequal concentrations in the cues of the conch (more biomass) and mud crab (less biomass; Hill and Weissburg 2012). However, equalizing biomass of the two predators would have created an unnaturally high concentration of mud crab cues (Kimbrow et al. 2017a). In addition, the lack of an NCE on oysters first exposed to mud crabs and then conchs suggests that the conch cue must not only be present, but it must be present during the juvenile stage. Further research is needed to evaluate the degree to which NCEs in this system are life stage and predator specific.

There are four limitations of our study to consider when interpreting its results. First, our simulated predation treatment did not precisely imitate the foraging behavior of a predator and therefore may not have created a realistic interaction between NCE and CE. For instance, prey may respond to tactile cues of the predator, cues of dying conspecifics, and/or cues of conspecifics being consumed, digested, and excreted along with biomolecules of the predator (Abrams 2008, Remington et al. 2018). A related second limitation exists because the predator cue may have been even stronger than real predator cues given that our predators were in close proximity to prey consistently for months. Although our study used ambient predator densities per unit area, we do not know the frequency and duration that an individual oyster is exposed to predator cues. Third, our simulated CE was not influenced by changes in prey traits as a real predator might be; that is, oysters that might have grown thicker shells in response to predator cues were no more or less likely to be removed in the experiment, possibly removing a benefit of the NCE. Finally, we lack a dynamic model to examine how the multivariate NCEs may combine to affect population dynamics over longer time periods (i.e., multiple generations) and if such a consideration actually improves

our understanding and predictive capability of prey population dynamics. Work currently underway will address that latter gap.

It has become increasingly apparent that in many ecological systems, predator NCEs can match or exceed the importance of CEs in their importance to prey demography. However, it has also become clear that much of this research involved risk cues with unnaturally simplistic sensory backgrounds, without consumption present, and focused on an individual trait response and assumed population level effects. Previously, we showed that reductions in mud crab (predator) foraging due to cue from a fish (top predator) affected oyster (prey) survival in short-, but not long-term experiments (Kimbrow et al. 2017a). But here we show that a predator NCE previously detected in the laboratory did not carry over through ontogeny in the way we had predicted, and also did not have a strong effect on prey demography in the field, where its importance appeared to be swamped by environmental variability and competitive release due to predator CEs. Thus, our findings serve as a cautionary tale for the importance of evaluating NCE processes over temporal scales and across environmental gradients relevant to prey demography.

ACKNOWLEDGMENTS

P. Langdon, M. Murdock, E. Pettis, T. Rogers, and B. Williams provided field assistance. The University of Florida Whitney Laboratory and the Guana Tolomato Matanzas National Estuarine Research Reserve granted access to their facilities, reserve, and system-wide water quality monitoring program. This work was funded by the National Science Foundation (awards OCE-1338372 and OCE-1736943 to DLK and OCE-1820540 to JWW). This is contribution 402 from the Northeastern University Marine Science Center. Author contributions: DLK and HGT conceived the idea and design for the study; HGT led and DLK assisted with the research; DLK and JWW analyzed and interpreted the data; DLK and JWW wrote the first draft of the paper; all authors made significant contributions to later drafts. All data and statistical code are available on Zenodo (see Data Availability section).

LITERATURE CITED

- Abrams, P. A. 2008. Measuring the impact of dynamic antipredator traits on predator-prey-resource interactions. *Ecology* 89:1640–1649.
- Barton, K. 2019. Multi-model inference. R package version 1.43.6. <https://CRAN.R-project.org/package=MuMIn>.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Benkwitt, C. E. 2017. Predator effects on reef fish settlement depend on predator origin and recruit density. *Ecology* 98:896–902.
- Booth, H. S., T. J. Pusack, J. W. White, C. D. Stallings, and D. L. Kimbro. 2018. Experimental evidence that oyster populations persist during predator outbreaks because of intraspecific predator inhibition, not a prey size refuge. *Marine Ecology Progress Series* 602:155–167.
- Chamberlain, S. A., J. L. Bronstein, and J. A. Rudgers. 2014. How context-dependent are species interactions? *Ecology Letters* 17:881–890.

- Ellrich, J. A., and R. A. Scrosati. 2016. Water motion modulates predator nonconsumptive limitation of prey recruitment. *Ecosphere* 7:e01402.
- Ellrich, J. A., R. A. Scrosati, C. Bertolini, and M. Molis. 2016. A predator has nonconsumptive effects on different life-history stages of a prey. *Marine Biology* 163:5.
- Ellrich, J. A., R. A. Scrosati, and M. Molis. 2015. Predator nonconsumptive effects on prey recruitment weaken with recruit density. *Ecology* 96:611–616.
- Garland, H. G., and D. L. Kimbro. 2015. Drought increases consumer pressure on oyster reefs in Florida, USA. *PLoS ONE* 10:e0125095.
- Gosnell, J. S., K. Spurgin, and E. A. Levine. 2017. Caged oysters still get scared: Predator presence and density influence growth in oysters, but only at very close ranges. *Marine Ecology Progress Series* 568:111–122.
- Grabowski, J. H. 2004. Habitat complexity disrupts predator-prey interactions but not the trophic cascade on oyster reefs. *Ecology* 85:995–1004.
- Grabowski, J. H., and D. L. Kimbro. 2005. Predator-avoidance behavior extends trophic cascades to refuge habitats. *Ecology* 86:1312–1319.
- Heithaus, M. R., A. Frid, A. J. Wirsing, L. M. Dill, J. W. Fourqurean, D. Burkholder, J. Thomson, and L. Beider. 2007. State-dependent risk-taking by green sea turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem. *Journal of Animal Ecology* 76:837–844.
- Hill, J. M., and M. J. Weissburg. 2012. Predator biomass determines the magnitude of non-consumptive effects (NCEs) in both laboratory and field environments. *Oecologia* 172:79–91.
- Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models. *Biometrical Journal* 50:346–363.
- Johnson, K. D., and D. L. Smee. 2012. Size matters for risk assessment and resource allocation in bivalves. *Marine Ecology Progress Series* 462:103–110.
- Kimbro, D. L. 2012. Tidal regime dictates the cascading consumptive and nonconsumptive effects of multiple predators on a marsh plant. *Ecology* 93(2):334–344.
- Kimbro, D. L., J. E. Byers, J. H. Grabowski, M. P. Piehler, and A. R. Hughes. 2014. The biogeography of trophic cascades on U.S. oyster reefs. *Ecology Letters* 1:845–854.
- Kimbro, D. L., J. H. Grabowski, A. R. Hughes, M. Piehler, and J. White. 2017a. Nonconsumptive effects of a predator weaken then rebound over time. *Ecology* 98:656–667.
- Kimbro, D. L., J. W. White, H. Garland, N. Cox, M. Christopher, O. Stokes-Cawley, S. Yuan, T. J. Pusack, and C. D. Stallings. 2017b. Local and regional stressors interact to drive salinization-induced outbreak of predators on oyster reefs. *Ecosphere* 8:e01992.
- Krebs, C. J., S. Boutin, R. Boonstra, A. R. Sinclair, J. N. Smith, M. R. Dale, K. Martin, and R. Turkington. 1995. Impact of food and predation on the snowshoe hare cycle. *Science* 269:1112–1115.
- Lenihan, H. S., C. H. Peterson, and J. M. Allen. 1996. Does flow speed flow speed also have a direct effect on growth of active suspension-feeders: An experimental test on oysters. *Limnology and Oceanography* 41:1359–1366.
- Nakagawa, S., P. C. D. Johnson, and H. Schielzeth. 2017. The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of the Royal Society Interface* 14:20170213.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* 100:65–75.
- Peacor, S. D., and E. E. Werner. 2001. The contribution of trait-mediated indirect effects to the net effects of a predator. *Proceedings of the National Academy of Sciences* 98:3904–3908.
- Peers, M. J. L., et al. 2018. Quantifying fear effects on prey demography in nature. *Ecology* 99:1716–1723.
- Preisser, E. L., D. L. Bolnick, and M. F. Benard. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* 86:501–509.
- R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Remington, P. X., S. Lavoie, K. Siegel, D. A. Gaul, M. J. Weissburg, and J. Kubanek. 2018. Chemical encoding of risk perception and predator detection among estuarine invertebrates. *Proceedings of the National Academy of Sciences of the United States of America* 115:662–667.
- Scherer, A. E., J. Lunt, A. M. Draper, and D. L. Smee. 2016. Phenotypic plasticity in oysters (*Crassostrea virginica*) mediated by chemical signals from predators and injured prey. *Invertebrate Biology* 135:97–107.
- Schmitz, O. J. 2008. Effects of predator hunting mode on grassland ecosystem function. *Science* 319:952–954.
- Sheriff, M. J., C. J. Krebs, and R. Boonstra. 2011. From process to pattern: how fluctuating predation risk impacts the stress axis of snowshoe hares during the 10-year cycle. *Oecologia* 166:593–605.
- Sih, A., G. Englund, and D. Wooster. 1998. Emergent impacts of multiple predators on prey. *Trends in Ecology and Evolution* 13:350–355.
- Smee, D. L., and M. J. Weissburg. 2006. Clamming up: environmental forces diminish the perceptive ability of bivalve prey. *Ecology* 87:1587–1598.
- Trussell, G. C., C. M. Matassa, and P. J. Ewanchuk. 2017. Moving beyond linear food chains: trait-mediated indirect interactions in a rocky intertidal food web. *Proceedings of Biological Sciences* 284:20162590.
- Vonesh, J. R., and C. W. Osenberg. 2003. Multi-predator effects across life-history stages: non-additivity of egg- and larval-stage predation in an African treefrog. *Ecology Letters* 6:503–508.
- Ward, D. M., K. H. Nislow, and C. L. Folt. 2011. Seasonal shift in the effects of predators on juvenile Atlantic salmon (*Salmo salar*) energetics. *Canadian Journal of Fisheries and Aquatic Sciences* 68:2080–2089.
- Weissburg, M., D. L. Smee, and M. C. Ferner. 2014. The sensory ecology of nonconsumptive predator effects. *American Naturalist* 184:141–157.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.3041/supinfo>

DATA AVAILABILITY

Data are available on Zenodo: <https://doi.org/10.5281/zenodo.3661419>