

# Intraspecific predator inhibition, not a prey size refuge, enables oyster population persistence during predator outbreaks

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**ABSTRACT:** Predators commonly structure natural communities, but predation effects can vary greatly. For example, increasing predator densities may not reduce prey populations as expected if intraspecific predator interactions suppress foraging efficiency or if prey size refuges exist. In northeastern Florida (USA), outbreaks of the predatory crown conch *Melongena corona* have contributed to declines in oyster populations and the commercial oyster fishery. However, despite expectations of oyster population collapse, reefs have persisted, albeit with reduced adult oyster size and living reef biomass. To investigate the mechanism(s) underlying this unexpected persistence, we used field observations and experiments to examine the effects of predator density and prey size on predation rates. Multi-year surveys indicated that large oysters did not experience a predation size refuge, and further suggested that predation rates declined with increased predator density. Consistent with field surveys, field experiments demonstrated that conchs selectively consumed larger oysters (potentially explaining the absence of large oysters on natural reefs) and that high conch densities suppressed per capita predation rates, likely due to intraspecific antagonistic interactions. A Type III ratio-dependent model best described the experimental conch functional response, explaining >50% of the variation in per capita prey consumption and including a signal of reduced attack rates at high predator densities. Thus, although large aggregations of predators have the potential to deplete prey populations, our study illustrates intraspecific predator interactions that possibly prevent the local extirpation of an important habitat-forming prey species.

**KEY WORDS:** *Crassostrea virginica* · Functional response · Gastropod · Interference · Predator outbreak

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## INTRODUCTION

Predation can strongly affect the trophic structure and ecosystem functioning of communities (Paine 1966, Estes & Palmisano 1974, Schmitz et al. 2000). However, the exact outcomes of predation can be highly context-dependent with variation in abiotic

and biotic factors (Sih et al. 1985, Chamberlain et al. 2014). Accounting for this variability requires understanding the relationship between predator and prey densities and predation rates. Per capita predation rates typically increase with prey density before saturating as a result of constraints of handling time (Holling 1959, Gross et al. 1993). However, variation

in predator density can alter predator functional responses (Skalski & Gilliam 2001, Arditi & Ginzburg 2012). Cooperative hunting between predators can lead to higher than predicted per capita feeding rates (e.g. Thiebault et al. 2016), but competitive interference between predators can reduce per capita feeding rates (Beddington 1975, Soluk 1993, Kratina et al. 2009, de Villemereuil & Lopez-Sepulcre 2011, Stier & White 2014, Pusack et al. 2018). Consequently, the development of several functional responses that simultaneously account for variation in the density of both predator and prey represents a major step toward a mechanistic understanding of predation effects (Hassell & Varley 1969, Beddington 1975, DeAngelis et al. 1975, Arditi & Ginzburg 1989, 2012, Crowley & Martin 1989, Skalski & Gilliam 2001, Novak et al. 2017).

Although variation in predation rates may depend on density, the size of predators and prey may be equally important (Werner & Gilliam 1984, Aljetlawi et al. 2004, Uiterwaal et al. 2017). Because predators must capture and subdue their prey, they typically exhibit size-selective foraging (Iriarte et al. 1990). For example, marine crabs selectively consume medium-sized mussels, often rejecting small and large individuals after a brief evaluation period (Jubb et al. 1983). This size-selective predation commonly occurs because a predator balances selection for larger, more profitable prey with the costly time and energy required to handle large prey (Stephens & Krebs 1986, Behrens Yamada & Boulding 1998). Predators cannot consume certain sizes of prey because of handling limitations (e.g. gape width [Persson et al. 1996, Mumby et al. 2006] and claw morphology [Behrens Yamada & Boulding 1998]), thus creating prey size refuges. These size refuges can be critical for the persistence of prey populations because larger prey typically produce more offspring (Turner & Trexler 1998). Thus, improving our ability to predict predator–prey dynamics likely requires a simultaneous focus on the effects of size as well as density.

Along the coast of northern Florida (USA), the crown conch *Melongena corona* is an important predator of the eastern oyster *Crassostrea virginica* (Wilber & Herrnkind 1982). In the Matanzas River Estuary (MRE; see Fig. 1), the combination of a regional drought and reduced tidal excursion elevated water salinities in the southern reach of the estuary starting in approximately 2006, creating a north–south salinity gradient across the estuary and facilitating the reproductive success and rapid population growth of the crown conch (Garland & Kimbro 2015). Concurrently, oyster reefs in the southern reach of

the MRE shifted into a degraded state that no longer supported a historically productive oyster fishery. In 2011 to 2012, Garland & Kimbro (2015) performed a multi-site predator-exclusion experiment across the MRE, and their results demonstrated that crown conch predation proximally caused this oyster reef degradation, rather than environmental stress or disease (Garland & Kimbro 2015).

In recent years, spatial and temporal variation in annual precipitation has weakened the estuary's north-south gradient in salinity (see Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m602\\_p155\\_supp.pdf](http://www.int-res.com/articles/suppl/m602_p155_supp.pdf)) but not in conch density (see Fig. 2a). Consequently, we expected further degradation of oyster reefs in the southern portion of the MRE. Such degradation would have produced significant ecosystem consequences because oysters provide essential services, including habitat provisioning for commercially important invertebrates and finfish, coastal water filtration, shoreline stabilization, and the removal of excess nitrogen (Grabowski et al. 2012, Zu Ermgassen et al. 2012). Surprisingly, despite the continued presence of an unusually large conch population, reefs in the southern reach of the MRE have persisted (Fig. 2b), albeit in an altered state of reduced oyster size and biomass that no longer supports commercial harvesting.

Because predation likely produced the original spatial gradient in oyster population reduction (Garland & Kimbro 2015), we sought to identify predator-centric mechanisms that could account for the unexpected persistence of oysters in the presence of high predator densities. To this end, we combined field observations with manipulative experiments to examine how the densities and sizes of predator and prey may influence conch predation rates. First, we conducted a multi-year survey of conchs and oysters throughout the MRE to test for the presence of a size refuge from predation (e.g. oyster size distributions are skewed towards larger sizes on reefs with high conch densities) and predator density-dependent saturation in feeding rates. Our observational results suggested 3 findings: large oysters do not experience a size refuge from conch predation, conchs frequently formed aggregations on reefs, and predation rates saturated as conch density increased. To experimentally identify the mechanisms responsible for these observed field patterns, we then conducted 2 field experiments that addressed the following questions: (1) Do conchs selectively consume certain sizes of oyster prey? (2) Do per capita predation rates of conchs depend on conch density, potentially decreasing as conch density increases?

## MATERIALS AND METHODS

### Study system

This research was conducted on oyster *Crassostrea virginica* reefs in the Guana Tolomato Matanzas National Estuarine Research Reserve, which is located within the MRE (29.67° N, 81.22° W; Fig. 1). This area of the MRE contains shorelines dominated by intertidal oyster reefs that border *Spartina alterniflora* salt marshes and mangroves (*Avicennia germinans* and *Rhizophora mangle*).

Crown conch gastropods *Melongena corona* are scavengers and predators of bivalves that occur intertidally along the Atlantic and Gulf coasts of Florida (Karl & Hayes 2012). They prey on bivalves by prying open the shells with their muscular foot and using their proboscis to consume the internal tissue (Menzel & Nichy 1958). Crown conchs are most active at high tide and during warmer seasons and can bury themselves in the sediment to survive colder winter temperatures and low tide exposure (Hathaway & Woodburn 1961, Loftin 1987). Whereas adult conchs can tolerate a wide range of salinities, crown conch larval mortality increases at salinities < 15 ppt (Hathaway & Woodburn 1961, Garland & Kimbro 2015), a likely factor driving increases in crown conch populations in the southern reach of the MRE following the north–south gradient in the estuary’s water salinity (Garland & Kimbro 2015).

### Field patterns

To examine the relationships among oyster size, oyster mortality, and conch density on natural reefs, we conducted annual surveys during the summer at 6 sites within the MRE from 2014 to 2016. These sites were the same as those used in the annual surveys of Garland & Kimbro (2015), encompassing a spatial gradient in salinity, conch abundance, and oyster reef condition (proportion of dead oysters out of total oysters on the reef). Within each site, we randomly selected and partitioned 6 reefs into a low and a high intertidal zone. Within each zone, we deployed a 20 m transect parallel to the shoreline, placed a 0.5 m × 0.5 m quadrat in the center of each transect, and collected all reef material within the quadrat for processing. In the laboratory, we measured the biomass of the entire sample before haphazardly selecting a subsample of 100 oysters and measuring their shell length (longest distance from the umbo to the tip of the shell). We then counted the remaining live adults (≥25 mm) and juveniles (<25 mm), as well as the number of ‘gaping’ oysters in the whole sample. Gaping oysters are dead adult oysters with both valves intact, but lacking tissue in the internal cavity. Gaping can indicate mortality due to stress, disease, or recent predation by a consumer that does not damage the shell, such as crown conchs. We used the proportion of gaping oysters relative to the total number of oysters (both gaping and alive) as a proxy for conch predation rate in our analyses of the observational data (e.g. Vucetich et al. 2011, Garland & Kimbro 2015). Whereas other sources of mortality could have caused gaping oysters, multiple experiments demonstrated predation as the dominant cause of oyster mortality at the southern MRE sites (Garland & Kimbro 2015). Therefore, we used the proportion of gaping oysters as a relative estimate of predation over space and time in this system. Conch densities were measured by walking the length of each 20 m transect and recording all individuals within a 0.5 m area on either side. At each of the same reefs, we also quantified the frequency and size of conch aggregations within 9 permanently marked circles (2 m diameter) on a monthly basis from March to August of 2015 and 2016 to evaluate local aggregation density. We quantified relative differences in environmental conditions between sites by collecting monthly point samples of water temperature, salinity, and dissolved oxygen with a handheld YSI meter (Xylem model no: 556, Yellow Springs, OH; see Fig. S1 in the Supplement).

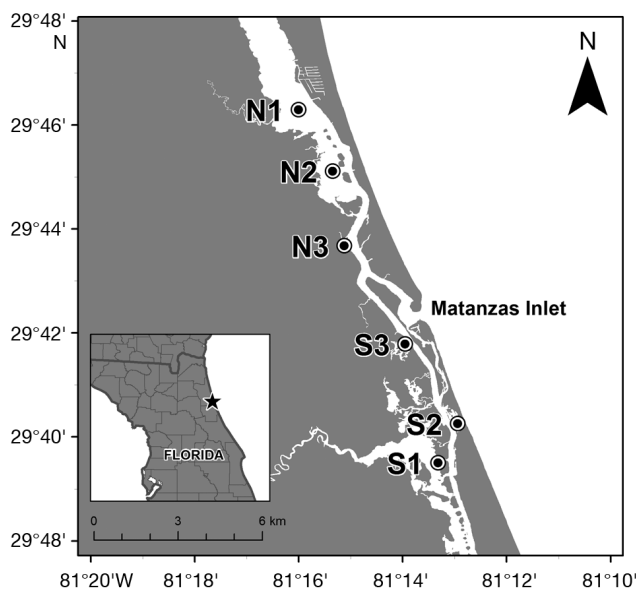


Fig. 1. Study locations (n = 6) in the Matanzas River Estuary (MRE); inset depicts the location of the MRE (star) within the Floridian ecoregion. Surveys spanned all sites, whereas field experiments occurred only at Site S2

### Size-selective predation

To test for crown conch size-selective predation on oysters, we conducted a field choice experiment in which adult-sized conchs (75–85 mm) were offered oysters ranging in size from 25 to 100 mm in shell length. We based the size range of conchs on the mean size of individuals from 2015 field surveys ( $78.8 \pm 10.0$  mm), and the oyster size range encompassed the smallest reproductively mature individuals (>25 mm) to the largest size that still commonly occurs on the reef (100 mm). Oysters were assigned to 1 of 3 size classes: small (25–50 mm), medium (51–75 mm), and large (76–100 mm), with the large size class approximately corresponding to the legal market size of oysters in the region.

At one site in the southern part of the MRE (S2; Fig. 1), we selected 2 reefs that were separated by 12 m and established 8 experimental units at the midpoint of the intertidal distribution of the oysters on each reef. Experimental units were spaced 2 m apart and consisted of a full 6-sided cage (0.5 m width  $\times$  0.5 m length  $\times$  0.3 m height, 0.075 m<sup>3</sup>) constructed of vinyl-coated wire mesh (5  $\times$  5 mm openings). The cages were dug 5 cm into the reef, and the bottoms were filled with mud and dead oyster shell to mimic the natural reef. Two 6.4 mm PVC pipes were driven into the reef, and each cage was secured with cable ties to the PVC pipes at 2 opposing corners of the plot.

All oysters and conchs used for the experiment were collected from local reefs and held in aquaria with flow-through seawater 4 to 5 d prior to the start of feeding trials. During this holding period, we fed oysters Instant Algae Shellfish Diet 1800 (Reed Mariculture, San Jose, CA) daily, following the manufacturer's instructions of 3.6 ml per 100 g of oyster wet weight. To standardize hunger levels, we held crown conchs without food for 3.5 d prior to the start of feeding trials. Prior to deployment in the field, we attached single oysters to small squares of plastic mesh with marine epoxy. To begin feeding trials, we deployed 1 conch in each cage and randomly selected 3 oysters from each size class (9 oysters total). We then secured the oysters with cable ties (via the small mesh squares) to the top of a brick that was dug into the center of the plot. We deployed an Onset HOBO conductivity logger (Onset model no: U24-002, Bourne, MA) near experimental plots to record water salinity and temperature at 30 min intervals. However, the instrument failed to collect consistent samples, so we report the monthly YSI data instead (Fig. S1 in the Supplement).

We conducted 2 choice experiment trials ( $n = 16$  total replicates) that lasted 7 d, and we used new

conchs for each feeding trial. Cages were checked daily at low tide, at which time we counted the number of gaping oysters. During the daily checks, we replaced all gaping oysters with live oysters within the same size class to maintain a constant prey density and size structure (Abrams & Ginzburg 2000). We measured and recorded the exact shell length of all gaping oysters and checked for cause of death. To examine oyster mortality in the absence of a conch, we deployed 3 control cages per trial that lacked a conch and had 1 oyster of each size class secured to a brick ( $n = 6$  total replicates). Over the course of both trials, a total of 3 control oysters died (1 from each size class), so we subtracted this mortality from the mortality in the predation cages to isolate mortality caused by predation from that associated with the environment.

### Functional response of crown conchs

To examine the effects of both conch and oyster density on predator functional response, we conducted a 3  $\times$  5 factorial experiment with conch density and oyster density as fixed factors. This experiment used the same reefs as the size-selection experiment, and followed immediately after the completion of the first experiment. The 3 treatment levels of conch density were 1, 3, and 5 conchs per reef, and the 5 treatment levels of oyster density were 2, 6, 10, 14, and 18 oysters per reef with an experimental reef area of 0.25 m<sup>2</sup>. The levels of experimental conch densities reflected the range of frequently observed conch aggregations in the southern portion of the MRE (see Fig. S2 in the Supplement). Meanwhile, the levels of experimental oyster densities reflected the lower range of oyster densities observed on natural oyster reefs (2 to 345 oysters 0.25 m<sup>-2</sup>) to facilitate checking as well as replacing experimental oysters during a single low tide period. In addition, preliminary observations of conch foraging rate suggested that our range of experimental oyster densities would not promote prey depletion. For the first trial, we randomly assigned treatments to 15 experimental plots (each 2 m apart) in a completely randomized design, using the same cages and plot set-up as in the size-selection experiment. For the second trial, however, we added an additional 15 cages to increase replication. These cages were set up in the same way, and we randomly assigned the 15 treatments among all 45 cages for a total of 3 replicates.

We used oysters from a subset of the medium and large size classes (50–80 mm) and the same size

range of conchs (75–85 mm) as in the size-selection experiment. The preparation and deployment of oysters mimicked the procedures used in the size-selection experiment, except that oysters were attached in pairs to the sides of 3 small bricks in each cage to reflect natural oyster clusters. At the beginning of both experimental trials, conchs were deployed in a consistent location in each cage. Each of the 2 trials lasted 7 d, and we used new conchs for each feeding trial. Cages were checked daily at low tide, at which time all gaping oysters were counted and replaced with living oysters within the target size range to maintain constant prey densities. We observed low background mortality in our control cages without conchs, and we multiplied the observed number of consumed oysters in each replicate by 1 minus the mean proportion of dead oysters in the controls to isolate mortality resulting from predation from that associated with the environment.

### Analysis

We present temporal and spatial trends in conch density and oyster biomass (mean, SE  $\text{g m}^{-2}$ ) for descriptive purposes only (Fig. 2). However, to analyze our observational survey data, we evaluated the relationship between prey size and predator density by using a nonlinear mixed model with site as a random effect (nlmer function within the R package lme4; Bates et al. 2014). We lacked sufficient replication to run a fully hierarchical model with year nested within site, so we tested models with each random effect separately and reported the model in which the random effect explained more of the variance. We included all 6 sites in the analysis because the 3 northern sites without conchs were necessary to estimate the zero-value for the non-linear regression (the random effects for the sites lacking conchs were approximately zero). We obtained a p-value by using the pt function in the base R package with the t-value generated from the nonlinear regression, estimating the appropriate degrees of freedom by subtracting the total number of random and fixed effects from the sample size minus one. We found the coefficient of determination ( $R^2$ ) by using the function r.squared-GLMM in the MuMIn package (Bartoń 2015); this function implements the method for finding the marginal  $R^2$  (i.e. variance explained by the fixed effects) described by Nakagawa & Schielzeth (2013). We used the same model structure and random effect of site for evaluating the relationship

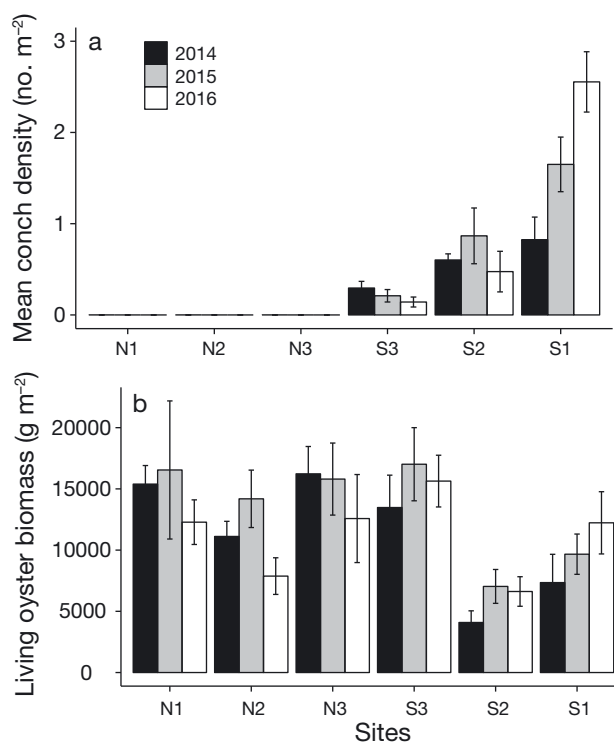


Fig. 2. Survey results showing trends in (a) the density of conchs  $\text{m}^{-2}$  (mean  $\pm$  SE) and (b) living oyster biomass ( $\text{g m}^{-2}$ , mean  $\pm$  SE) across all 6 sites in the MRE ( $n = 73$  replicates)

between predation rate (i.e. the proportion of gaping oysters out of total oysters) and predator density across all 6 sites.

For the size-selection experiment, we conducted a Chi-squared goodness-of-fit test to determine whether conchs consumed an equal number of oysters in each of the 3 size classes. We pooled the data over the replicates and feeding trials, finding the total number of consumption events for each size class and comparing these to the 'expected' values based on the number of samples in our experiment ( $df = 2$ ). All analyses were performed in R v.3.1.1 (R Core Team 2014).

For the functional response experiment, we used maximum likelihood estimation to fit a suite of 11 functional response models to the data, following the approach of Stier & White (2014; our Table 1). These included Holling's 3 prey-dependent models, which assume no predator interactions: Type I assumes no predator handling time and thus a linear increase in predation rates with increasing prey density; Type II includes a baseline predator attack rate and handling time that limits the predator at high prey densities; Type III is similar to Type II but as a sigmoid function in which the predation rate increases exponentially



Table 1. Results of model-selection approach to identify the functional response model that most parsimoniously describes how predator density influences the number of prey consumed per predator per unit time. We report the difference in AICc score to the most parsimonious model ( $\Delta\text{AICc}$ ), the AICc weight ( $w$ ), and the coefficient of determination ( $R^2$ ). All models included parameters of attack rate ( $a$ , units  $\text{time}^{-1} \text{ predator}^{-1}$ ), handling time ( $h$ , units  $\text{prey}^{-1}$ ), and the variable prey density ( $N$ , units  $\text{prey } 0.25 \text{ m}^{-2}$ ). Predator-dependent models also included the variable predator density ( $P$ , units  $\text{predators } 0.25 \text{ m}^{-2}$ ) and parameters  $c$  or  $m$ , which describe the magnitude of predator interference. Type III versions of models include parameter  $k$ , which allows a non-linear increase in predation rate at low prey densities

| Model                     | Formula                                  | $\Delta\text{AICc}$ | $w$    | $R^2$ |
|---------------------------|--|---------------------|--------|-------|
| Holling Type I            | $f(N) = aN$                              | 10.5699             | 0.0017 | 0.34  |
| Holling Type II           | $f(N) = \frac{aN}{1+hN}$                 | 12.7626             | 0.0006 | 0.34  |
| Holling Type III          | $f(N) = \frac{aN^k}{1+hN^k}$             | 12.2763             | 0.0007 | 0.38  |
| Crowley-Martin (CM)       | $f(N,P) = \frac{aN}{1+hN+cP+hcNP}$       | 3.5375              | 0.0581 | 0.49  |
| CM Type III               | $f(N,P) = \frac{aN^k}{1+hN^k+cP+hcN^kP}$ | 2.3193              | 0.1069 | 0.53  |
| Beddington-DeAngelis (BD) | $f(N,P) = \frac{aN}{1+hN+cP}$            | 3.5375              | 0.0581 | 0.49  |
| BD Type III               | $f(N,P) = \frac{aN^k}{1+hN^k+cP}$        | 2.4145              | 0.1019 | 0.53  |
| Hassell-Varley (HV)       | $f(N,P) = \frac{aN}{hN+P^m}$             | 3.368               | 0.0633 | 0.49  |
| HV Type III               | $f(N,P) = \frac{aN^k}{hN^k+P^m}$         | 2.3308              | 0.1063 | 0.53  |
| Ratio-dependent (RD)      | $f(N,P) = \frac{aN/P}{1+hN/P}$           | 1.4968              | 0.1613 | 0.49  |
| RD Type III               | $f(N,P) = \frac{aN^k/P}{1+hN^k/P}$       | 0                   | 0.3409 | 0.53  |

with prey density at low prey densities. The latter describes potential changes in predator behavior in which attack rate increases with prey density, which can arise from predators switching to alternative prey or simply reducing foraging activity to minimize search costs at low densities of the focal prey (Holling 1959, Murdoch & Oaten 1975, 1977, Hassell et al. 1977). The next 4 models incorporate some form of predator dependence (Skalski & Gilliam 2001): (1) the Beddington-DeAngelis model (BD; Beddington 1975, DeAngelis et al. 1975), in which predator density affects the predator attack rate, (2) the Crowley-Martin model (CM; Crowley & Martin 1989), in which predator density affects both attack rate and handling time, (3) the Hassell-Varley model (HV; Hassell & Varley 1969), which is similar to the BD model but allows for a non-linear effect of predator density on attack rate, and (4) a ratio-dependent model, in which the attack rate depends on the ratio of prey to predators (RD; Arditi & Ginzburg 1989,

Arditi & Ginzburg 2012). The Beddington-DeAngelis, Crowley-Martin, and Hassell-Varley models describe the dependence of predator density in different ways, but all reduce to either Holling Type II or Type III equations if their respective predator-dependent parameters are estimated as zero (i.e. BD and CM:  $c = 0$ ; HV:  $m = 0$ ) or if  $P = 1$  in the ratio-dependent model (see Table 1). The RD model is equivalent to the HV model with the exponent on predator density set to a value of one.

Finally, we created Type-III-like versions of the BD, CM, HV, and RD models by adding an exponent,  $k$ , to the prey density term, which allows the predation rate to increase nonlinearly at low prey densities. These models have a sigmoidal shape when  $k > 1$  and reduce to the original hyperbolic forms when  $k = 1$  (Okuyama & Ruyle 2011). While it is theoretically possible for  $k$  to be  $< 1$ , reflecting an attack rate that increases more slowly than linearly with prey density, our fitted values of  $k$  were all between 1 and 2,

consistent with our description of them as Type-III-like. Thus, we compared a full suite of functions allowing different interactions of prey and predator density on the predation rate.

We fit each model to our data (the number of prey consumed per predator per day as a function of prey density and predator density) using maximum likelihood, assuming a lognormal error structure for the response variable (as in Skalski & Gilliam 2001, Bolker 2008). We pooled all the data from both feeding trials to estimate an aggregate functional response across environmental conditions and multiple days of the trials. We calculated the instantaneous feeding rate for each model (instead of integrating the daily feeding rate over time) given that our experimental design replaced prey each day. Parameter estimation used the `sqp` (sequential quadratic programming) algorithm in the `fmincon` function in the Matlab 7.11 Optimization Toolbox (Mathworks, Natick, MA), and we restricted parameter estimates to biologically meaningful ranges (i.e. attack rate  $> 0$ , handling time  $> 0$ , variance  $> 0$ ). We inverted the Hessian matrix returned by `fmincon` to obtain the parameter covariance matrix. We then obtained estimates of the confidence intervals on the maximum likelihood model fits by simulating a distribution of  $10^4$  sets of parameter values by drawing from a multivariate normal distribution with the estimated covariance matrix, calculating the functional response curve for each parameter set, reweighting the curves by the log-likelihood of each parameter set, and then taking the middle 95% of the distribution of curves for each predator density (Bolker 2008). We determined which model produced the most parsimonious fit to the data using the Akaike information criterion, corrected for small sample sizes (AICc) (Burnham & Anderson 2002), and we calculated the coefficient of determination ( $R^2$ ) for these models using Nagelkerke's (1991) method.

## RESULTS

### Field patterns

In field surveys, mean adult oyster *Crassostrea virginica* size decreased with increasing conch *Melongena corona* density (nonlinear regression,  $t = 123.0$ ,  $df = 72$ ,  $p < 0.001$ , marginal  $R^2 = 0.92$ ; Fig. 3a). Additionally, the predation rate (based on the number of gaping oysters observed) increased with conch density only at the lowest conch densities and reached a

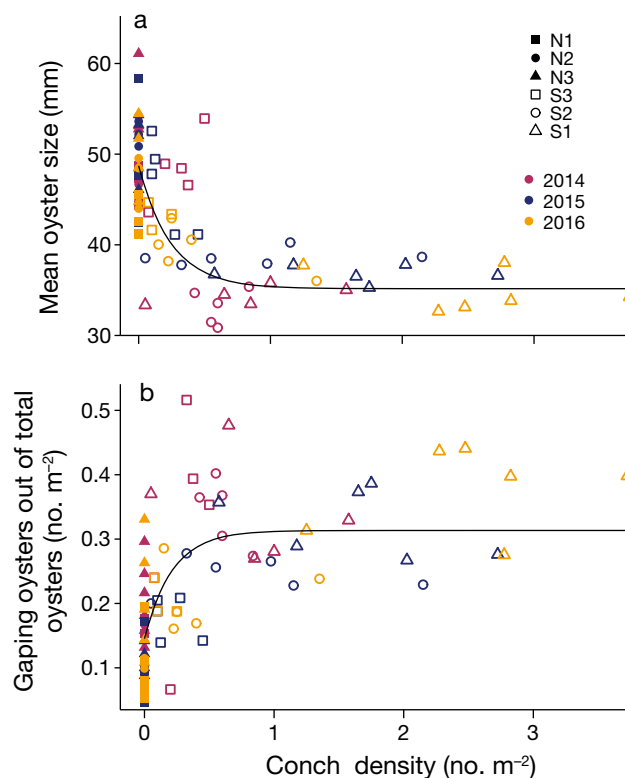


Fig. 3. Survey results showing the relationship between mean conch density  $m^{-2}$  and (a) mean adult oyster size (mm) and (b) the proportion of gaping oysters out of the total number of oysters  $m^{-2}$  (i.e. predation rate). Data were taken across all 6 sites from 2014, 2015, and 2016 ( $n = 73$  replicates)

saturation point at  $< 1$  conch  $m^{-2}$  (nonlinear regression;  $t = 68.36$ ,  $df = 74$ ,  $p < 0.001$ , marginal  $R^2 = 0.98$ ; Fig. 3b).

### Size-selective predation experiment

Conchs preferentially consumed oysters from the large size class (76–100 mm) more frequently than oysters from either the medium or small size classes ( $\chi^2 = 20.30$ ,  $df = 2$ ,  $p < 0.001$ ; Fig. 4).

### Functional response experiment

The conch functional response increased with oyster density, as expected, but per capita predation rates decreased significantly with increasing conch density (Fig. 5). The Type III ratio-dependent model best explained the predator functional response (AICc weight = 0.34;  $R^2 = 0.53$ ; Fig. 5c); however, the Type III versions of the BD, CM, and HV models were sim-

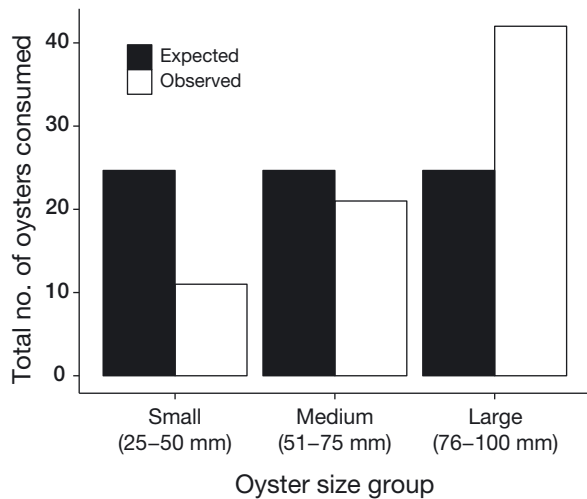


Fig. 4. Results of the size selection experiment showing observed and expected total number of oysters consumed by conchs based on oyster size group ( $n = 16$  replicates)

ilarly strong descriptors of predation rates (AICc weight  $\approx 0.11$ ;  $R^2 = 0.53$  for all 3 models; Fig. 5b, Table 1). All 8 predator-dependent models fit the data better than Holling's prey-dependent models, with each explaining  $\geq 48\%$  of the variation in per capita prey consumption (Table 1). Additionally, the positive parameter estimates that represent the magnitude of predator interference in the BD, CM, and HV models indicate that intraspecific conch interference both reduced predator attack rates and increased handling times in those models (depending on which terms in each model were predator-dependent; see Table S1 in the Supplement).

## DISCUSSION

Our study suggests that intraspecific inhibition among predatory conchs *Melongena corona*, rather than a size refuge from predation, may help northern Florida oyster *Crassostrea virginica* populations persist in the presence of high conch densities, albeit at a lower population size. In field experiments, conchs displayed strong size-selective predation by consistently consuming large, market-size oysters ( $>75$  mm) instead of smaller oysters ( $<75$  mm). This selection of larger prey, and thus lack of a predation size refuge, aligns with the multi-year field pattern showing significantly smaller adult oyster sizes at sites with abundant conchs. However, for that larger prey size class, we found observational and experimental evidence for intraspecific predator inhibition reducing predation rates at high

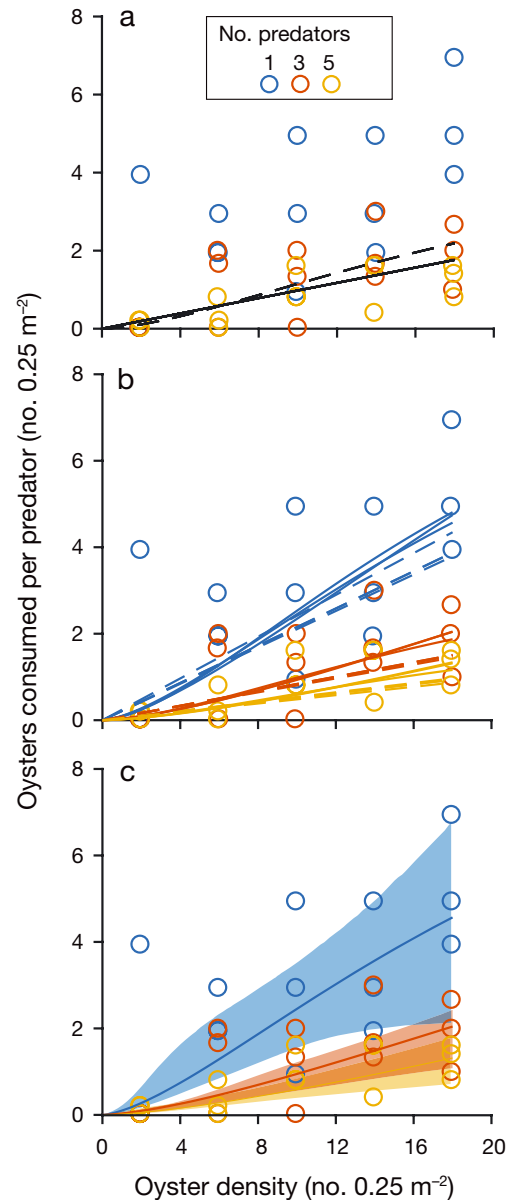


Fig. 5. Fitted functional response curves of (a) Holling Type II (dashed line) and Type III (solid line), (b) Type II versions of the Beddington-DeAngelis (BD), Crowley-Martin (CM), and Hassell-Varley (HV) models (dashed lines) and Type III versions of the BD, CM, and HV models (solid lines), and (c) Type III version of the best-fit ratio-dependent (RD) model with 95% confidence intervals (shaded regions) across multiple densities of oysters and crown conchs ( $n = 3$  replicates). Conch densities were 1, 3, and 5 ind.  $0.25 \text{ m}^{-2}$

densities. Whereas predation rates increased with oyster density, predator density influenced conch attack rates, decreasing as conch density increased in our experimental results and saturating at low predator densities in observational results. Thus, a prey size refuge does not help oysters persist in this



system, but inhibition of attack rates among conchs may lessen predation pressure and help maintain oyster populations.

### Size-selective predation

Size-selective predation or functional limitations in predators that produce a size refuge for large prey may stabilize population dynamics and promote persistence. For example, intertidal mussel populations can co-occur with predatory sea stars by growing out of vulnerable size classes (Paine 1976), and gape width differences in freshwater predatory fish alter prey habitat use and increase prey growth rates by releasing them from intraspecific competition (Persson et al. 1996). Although large oysters experience a predation refuge from another gastropod predator, the southern oyster drill *Stramonita haemostoma* (this predator is present on Gulf of Mexico oyster reefs but not in the Atlantic estuaries studied here; Pusack et al. 2018), as well as non-gastropod predators such as stone crabs (Brown & Haight 1992) and blue crabs (Eggleston 1990), our results show that conchs preferentially select the largest oysters, removing the potentially stabilizing size refuge in this species. Conch feeding mechanisms are unaffected by oyster size or defenses because large oysters pose no additional obstacles to conch feeding except potentially greater handling time; even the smallest adult conchs in our experimental size range (75 mm) preyed on large oysters. Additionally, the strong, effective shells of conchs protect them from most predators (Garland & Kimbro 2015), reducing any tradeoff in foraging time with predation risk (Werner et al. 1983).

A preference for larger oysters and increased tissue volume may have driven conch size selection. Alternatively, the encounter rate may increase linearly with oyster size and/or larger oysters may have produced more chemical cues within our experimental units. Regardless of the mechanism, conchs consumed large oysters more than expected in our experiments and apparently selected large individuals even when smaller oysters were available. Whereas the field pattern of reduced oyster size in areas with abundant conchs suggests the absence of a size refuge from predation, other mechanisms could explain the same field pattern. For example, high predation on small and mid-sized oysters could prevent oyster growth into large size classes (e.g. Botsford et al. 1994). However, our controlled mesocosm experiments confirmed size-selective predation

as the more likely mechanism underlying the field pattern in oyster size and conch density.

### Potential drivers of prey persistence

Given the absence of a size refuge from predation, why did oyster size and biomass not continue to decline further in recent years, despite consistent increases in conch populations (Fig. 2)? Persistence of oysters in the presence of abundant conchs could result from oyster recruitment from other source populations or from successful reproduction of the smaller oysters remaining on reefs. Because conch activity decreases during aerial exposure at low tide, oysters may also persist through a spatial refuge; although crown conchs are intertidal predators, prolonged low tides may slow their consumption on the highest elevation of an oyster reef. Similarly, colder months, when conchs are absent from reefs, may provide a temporal refuge. Additionally, our study suggests that foraging constraints at high predator densities could dampen the negative effects of conch predation. In many organisms, cooperative hunting behaviors may compensate for foraging restrictions (e.g. Macdonald 1983), but our results indicate a negative effect of conch density on predation rates. Predator dependence in trophic interactions can arise from factors such as aggressive social interactions or prey anti-predator behavior that increases with predator density (Arditi & Akçakaya 1990, Turchin 2003). Because oysters lack effective defenses against conchs (Garland & Kimbro 2015), we hypothesize that predator dependence in the conch functional response derives from antagonistic interactions that intensify with increased predator density, extending the time required to kill and ingest oysters and overwhelming the increased encounter rate at high prey densities.

### Intraspecific inhibition among predators

Although our results indicate an inhibitory effect of conch density on per capita predation rates, the exact nature of this inhibition remains unclear. Whereas other gastropods exhibit group feeding behavior (Butler 1985, Brown & Alexander 1994, Fodrie et al. 2008), such that per capita predation rates increase in dense aggregations of conspecifics, crown conchs do not appear to feed cooperatively. When conchs aggregate in high densities on reefs, they may indirectly interfere with each other by depleting their

shared prey resource (Free et al. 1977, Abrams & Walters 1996, Abrams 2015), although our experiment precluded this possibility by replenishing prey throughout feeding trials. Additionally, the low feeding rates of single conchs ( $0.7$  oysters  $d^{-1}$ ) suggest that 5 conchs could not have depleted the available prey resources over the course of the experiment. A more likely mechanism may be direct inhibition between conspecifics that reduces attack efficiency. Pusack et al. (2018) recently found that predation by the southern oyster drill on eastern oysters was best described by the Crowley-Martin functional response, suggesting predator-dependent effects that both reduce attack rates and increase handling times. In the present study, we found similar fits to the data for the various Type III predator-dependent models, and the lower-parameter ratio-dependent Type III model was most parsimonious. Thus, our study demonstrates a negative effect of predator density on attack rate and also contributes to the longstanding debate of whether functional responses are better described by prey-dependent models (i.e. Holling type classical forms) or ratio-dependent models (Abrams & Ginzburg 2000, Arditi & Ginzburg 2012). Our study supports the inclusion of predator-predator interactions as well as the strength of ratio-dependent models. However, whether a ratio-dependent model or more complex predator-dependent models best describes predator dependence requires further studies over natural and experimental species ranges (e.g. Novak et al. 2017).

While we could not directly assess the feeding behavior of conchs (they are most active during high tide when reefs are submerged), in treatments with high conch densities we often observed conch aggregations in a small section of the cage during low tide. This spatial clustering suggests that physical contact may cause interference between conchs by preventing efficient movement and feeding and that conch chemical cues may attract one another and intensify interactions as density increases (e.g. Cosner et al. 1999). Crown conchs respond to chemical cues from prey as well as each other (Hathaway & Woodburn 1961), so cues of an attacked oyster may potentially attract additional conchs, resulting in competitive interference between predators and/or longer search times as a result of conspecific encounters (e.g. Arditi & Akçakaya 1990, Kratina et al. 2009, Hossie & Murray 2016, Pusack et al. 2018). Density-driven mechanisms such as these could reduce attack efficiency in conchs at high densities, but confirmation of such interactions requires further behavioral studies.

Beyond a clear predator dependence in the form of reduced attack efficiency, sigmoid Type III versions of models better described the conch functional response than classic, hyperbolic, saturating Type II models. In Type III models, predation rates increase slowly for the lowest prey densities before rapidly increasing in the vicinity of an inflection point (Holling 1959). Detecting that subtle difference in curve shape at low densities is difficult; however, we found twice the Akaike weight for the sigmoid model compared to the hyperbolic version (despite the additional parameter), strongly supporting the sigmoidal shape. This functional form can indicate predator switching of prey at low densities or changes in predator behavior associated with predator learning or optimization of foraging rate (Holling 1959, Murdoch & Oaten 1975, 1977, Hassell et al. 1977). Because our experiment excluded alternative prey, the latter mechanism may be at play; a minimum density of oysters may be required to produce sufficiently strong chemical cues for a conch to alter its foraging rate. As oyster density increases, conchs may optimize their foraging behavior by spending proportionately more time searching for prey, as reflected in the sigmoid functional response. Predation rates accelerated just above the lowest oyster density ( $2$  oysters  $0.25$   $m^{-2}$ ), suggesting this threshold may occur around  $3$  to  $4$  oysters  $0.25$   $m^{-2}$ , but this threshold may also differ on natural oyster reefs.

### Experimental considerations

Ecological interactions can vary with scale, often creating mismatches between small-scale experiments and broad patterns in nature (Levin 1992, Ives et al. 1993, Abrams 2015). Although the manipulation of population densities and habitat resources within caging experiments does not always represent natural interactions accurately (Carpenter 1996, Schindler 1998), elucidating the mechanistic basis of observed patterns requires controlled experiments, as demonstrated by our study. Nonetheless, we acknowledge limitations in our experiment that may have influenced conch predation on oysters. First, our cages limited conch movement. In nature, conchs may redistribute themselves after foraging in a high-density patch, thus reducing their densities and sometimes masking the small-scale link between predator density and prey mortality. These movement restrictions may explain strong saturation in observational predation rates but its absence in experimental predation rates; conchs in nature may

simply disperse to find sufficient prey and reach satiation more quickly than conchs within cages. Tidal amplitude may also have influenced conch predation rates; we noticed differences in conch predation rates between feeding trials with reduced feeding during the trial with a longer low tide period. Given variation in conch activity levels with tidal period, future studies should examine the influence of tidal variation on conch predation and thus oyster survival. Finally, we did not evaluate the simultaneous effects of size and density on the conch functional response. Both of these factors were important in our separate experiments, but understanding the combined effects of predator density and prey size on predation rates represents a crucial next step.

## CONCLUSIONS AND IMPLICATIONS

Our study highlights several factors that may influence predation outcomes, an important consideration in accurately estimating functional responses as well as predicting predator–prey dynamics over time. By combining evidence of natural population variation in oysters and conchs across several years with controlled experimental manipulations, we found that intraspecific interactions may limit the negative effects of high predator densities by constraining per capita predation rates. This predator inhibition, in tandem with recruitment dynamics and environmental gradients, may help oyster populations persist in the absence of a size refuge and the resulting decrease in abundances of large oysters on natural reefs. Increases in predator outbreaks and climate-induced range expansion of species such as crown conchs (Hayes & Karl 2009, Silliman et al. 2013) amplifies the importance of understanding predator effects on both the size-distribution and overall dynamics of oyster populations as well as how management strategies should address these potential changes. Finally, our study demonstrates the importance of pairing observational data with controlled experiments in order to interpret large-scale field patterns accurately and better predict the outcomes of interspecific interactions in a changing environment.

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