Journal of Experimental Marine Biology and Ecology 501 (2018) 74–82

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Size-dependent predation and intraspecific inhibition of an estuarine snail feeding on oysters

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ARTICLE INFO

Keywords:
Consumer front
Gastropod
Oyster reef
Predator outbreak

ABSTRACT

Predator outbreaks have increased in the past two decades in many ecosystems and are predicted to become more common with climate change. During these outbreaks, predator densities increase rapidly, and can cause large reductions in prey populations or shifts in prey size structure. However, unexpected interactions may occur at high predator densities, necessitating a mechanistic understanding of how increased predator density affects predator-prey dynamics. In the northern Gulf of Mexico, outbreaks of southern oyster drill, *Stramonita haemastoma* (Linnaeus, 1767), occur during high salinity events, and can greatly reduce eastern oyster, *Crassostrea virginica* (Gmelin, 1791), populations. A large outbreak of drills occurred from 2013 to 2015 in Apalachicola Bay, FL which corresponded with an oyster fishery collapse in that bay. To improve our mechanistic understanding of predation during such a high-density outbreak, laboratory experiments based on field observations were used to quantify the prey size selection by drills and the drill functional response, as a function of drill abundance. Drills fed on medium-sized oysters (50–75 mm) more often than small and larger-sized oysters, and often formed aggregations during feeding events. However, despite this aggregative response, there was a negative relationship between per capita feeding rates and drill abundance. Indeed, the Crowley-Martin functional response model had the most parsimonious fit to the data, suggesting that predator-predator inhibition reduced attack rates and increased handling times. Due to an increase in regional drought conditions and water usage in the southeastern United States, drill outbreaks will likely increase in frequency and duration. A greater understanding of how predation rates change with predator densities during outbreaks will improve predictions of oyster mortality, and strengthen the scientific framework for oyster fishery decisions.

1. Introduction

Predation can be a key factor structuring benthic marine communities (Paine, 1966; Estes and Palmisano, 1974; Menge, 1976; Steele and Anderson, 2006; Hixon, 2015). Accurately predicting the effects of predation begins with a quantitative understanding of how predators affect the abundance of their prey. Specifically, it is useful to characterize the predator functional response, which is the relationship between the instantaneous per-predator feeding rate and prey density (Murdoch, 1973; Hunsicker et al., 2011). The most commonly used functional response model is the Holling Type II (Holling, 1959; Skalski and Gilliam, 2001). It models the feeding rate as a function of both the search (or attack) rate of a randomly foraging predator and the handling time per captured prey. Under this model, the per capita feeding rate initially increases rapidly with prey density, then asymptotes as predators become limited by handling time (Holling, 1959). While useful as a first approximation, this model does not account for some important ecological realities, such as predator-predator interactions and size-selective predation, both of which may alter consumption rates and ultimately prey population dynamics (Sih et al., 1998; Skalski and Gilliam, 2001; Arditi and Ginzburg, 2012).

Predator-predator interactions are particularly important to consider when predator densities are unusually high. Examples include the crests of predator-prey cycles (Hassell and Varley, 1969) or during

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https://doi.org/10.1016/j.jembe.2018.01.005
Received 11 August 2017; Received in revised form 3 January 2018; Accepted 19 January 2018

biological invasions when the populations of novel predators can grow exponentially at the expense of native prey. Two notable invasions are the lionfish (*Pterois spp.*) in the tropical western Atlantic (Morris Jr. and Whitfield, 2009; Côté et al., 2013) and the European green crab (*Carcinus maenas*) in the northwestern Atlantic (Grosholz and Ruiz, 1995; Klassen and Locke, 2007). Similarly, native predators can undergo rapid population growth during atypical shifts in abiotic conditions (e.g., Brodie et al., 2005) or following depletion of higher-trophic-level predators (e.g., Silliman and Bertness, 2002). In many cases, high local concentrations of predators can form consumer fronts, which may cause rapid declines in the prey populations by locally overwhelming the renewal capacity of the prey (reviewed by Silliman et al., 2013). In these situations, it is reasonable to question whether the Type II functional response is appropriate because it does not account for predator-predator interactions, which can alter the per-capita feeding rate either through inhibition, e.g., inter- or intraspecific competition (Soluk, 1993; Kratina et al., 2009; de Villemereuil and López-Sepulcre, 2011; Stier and White, 2014), or facilitation, e.g., group hunting (Stallings and Dingeldein, 2012; Thiebault et al., 2016). Consequently, improving the ability to predict variation in the duration, magnitude, and consequences of predator outbreaks fundamentally depends on understanding how the density of predators influence its functional response (Sih et al., 1998; Skalski and Gilliam, 2001; Arditi and Ginzburg, 2012).

The effect that predators have on prey may also be influenced by size-structured interactions between predators and prey (Werner and Gilliam, 1984; Aljetlawi et al., 2004). Predation in marine communities is often strongly size-selective: predators generally prefer larger prey items, but very large prey are not easily consumed due to gape limitation (Persson et al., 1996), escape behavior (Scharf et al., 1998), or improved defenses (e.g., bivalve shell thickness; Boulding, 1984). As a result, there is typically a hump-shaped relationship between prey size and foraging profitability for predators of a particular size (Scharf et al., 1998; Stephens and Krebs, 1986). As predators grow, they shift foraging towards larger prey, such that their diet breadth is described by the ratio of predator:prey sizes (Scharf et al., 2000). Accounting for predator size-selectivity is particularly important when the predator population is increasing (or declining) rapidly. Those changes are usually associated with shifts in the predator size distribution (Rudolf, 2012; White et al., 2013; Eisenlord et al., 2016), which can translate into size-dependent changes in the overall effect on the prey population (de Roos et al., 1990; Andersen and Pedersen, 2010).

Along the coast of the northern Gulf of Mexico (GOM), the predatory southern oyster drill, *Stramonita haemastoma* (Linnaeus, 1767, hereafter ‘drill’), is an important predator of the eastern oyster, *Crassostrea virginica* (Gmelin, 1791, hereafter ‘oyster’; Butler, 1954). During prolonged periods of high salinity, outbreaks of drills have been observed in the northern GOM (Menzel et al., 1966; FFWCC, 2013) with up to 222 drills per m^2 (May, 1971). These outbreaks begin when typically mesohaline locations increase in salinity to levels suitable for drills, typically above a salinity of 15 (Garton and Stickle, 1980; Roller and Stickle, 1989). The drills respond by moving up the estuary into those areas to take advantage of previously inaccessible oyster reefs. The initial outbreak is an aggregative response to improving environmental conditions and an abundant food source, although a secondary numerical response may also occur due to increased reproduction. Predation on oysters by drills during high-salinity outbreaks has been associated with the loss of oyster reefs (Livingston et al., 2000; Petes et al., 2012; Kimbro et al., 2017). Oysters are a foundation species because they filter water, sequester carbon, and create reefs that buffer coastal erosion and provide habitat for other economically and ecologically important species (Bruno and Bertness, 2001; Grabowski et al., 2005; Jackson et al., 2001; Piehler and Smyth, 2011). Therefore, any increase in mortality may have profound ecological and economic effects.

There already exists some preliminary research of how predation rates may differ at different stages of a drill outbreak. For instance, at low densities drills feed individually, but at higher densities they often exhibit aggregative feeding with two or more drills consuming a single oyster (Butler, 1985; Brown and Alexander Jr., 1994; Fodrie et al., 2008). While it is assumed that aggregations enhance the mortality of oysters, the effect on the per capita predation rate has not been thoroughly described (but see: Brown and Richardson, 1987; Brown and Alexander Jr., 1994). Similarly, there also exists a basic understanding of how variation in the size distribution of drills may affect prey populations. Brown (1997) found that feeding rates and prey size preferences increased with drill size, but that large oysters (i.e., those over 150 g wet mass or 95–100 mm in total length) benefitted from a size refuge from drill predation. However, this previous study examined drill sizes from 23 to 60 mm, which does not include the largest drills (up to 84 mm) observed in more recent outbreaks in the northern GOM. Finally, no study to date has quantitatively described the functional response of drills and how per capita feeding rates change with drill abundance. Thus, several knowledge gaps inhibit accurate modeling of how oyster populations respond to changes in drill abundance and size structure.

This study addressed these knowledge gaps about drill predation by estimating the effect of increasing predator abundance on prey populations. Two separate laboratory experiments were used to test the following questions: (1) Do drills exhibit size-selective feeding? (2) Does drill abundance affect their aggregate and daily per capita predation rates on oysters? (3) Do higher abundances of drills facilitate or inhibit the consumption of oysters? and (4) Which functional response model best describes the instantaneous per capita feeding rate with increasing drill abundance? The two controlled experiments each described a specific predator effect: individual drill predation (Experiment I) and the effect of drill abundance on predation rates (Experiment II).

2. Methods

2.1. Experimental setup

Two separate experiments used drills and oysters that were collected from subtidal habitats in Apalachicola Bay, FL USA (both collections occurred around 29° 40′ 32.56″ N, 84° 51′ 36.76″ W and 29° 42′ 7.2″ N, 84° 49′ 31.76″ W). Feeding trials were conducted at both the Florida State University Coastal and Marine Laboratory in St. Teresa, FL (FSUCML, Experiment I) and the University of South Florida, College of Marine Science in St. Petersburg, FL (USFCMS, Experiment II). At FSUCML two filtered flow-through seawater systems were used. Both the first system (volume = 216 l; dimensions = 240 × 60 × 15 cm) and the second system (1105 l; 302 × 60 × 61 cm) were partitioned into eight equal-sized areas (using vinyl-coated wire mesh of 12 × 12 mm), while still allowing for water flow. These isolated replicates had similar base areas of 0.18 m^2 and 0.22 m^2 respectively. Filtered seawater from the adjacent bay was used in these systems. At USFCMS three separate, closed-seawater systems, each comprising ten experimental tanks (47.3 l; 68 × 40 × 27.5 cm), were constructed for a total of 30 tanks. The base area of these tanks was similar to the first experiment, 0.27 m^2. Within each system, approximately 950 l of artificial seawater was recirculated through the experimental tanks and a large sump (633 l; 76 × 45.5 × 183 cm). During Experiment I at FSUCML, the salinity (29) and temperature (29 °C) reflected ambient estuarine conditions. In Experiment II at UFSCMS, salinity was maintained at 25 by mixing deionized water with Instant Ocean sea salt (Instant Ocean Spectrum Brands, Blacksburg, VA, USA), and checked daily with a YSI 85 (Xylem Inc., Yellow Springs, OH, USA). Water temperature was maintained between 20 and 22 °C using Finnex TH-800 Plus, 800-watt titanium heating rods (Finnex, Chicago IL, USA) with a Reef Octopus Heater Controller (Honya Co. Ltd., Shenzhen, China). The temperature and salinity were chosen based on conditions that occurred during an outbreak in the northern GOM (Menzel et al., 1966; FFWCC, 2013). During both experiments and the one week holding prior to Experiment

II, oysters were fed Instant Algae Shellfish Diet 1800 (Reed Mariculture Inc., San Jose, CA) daily, following the manufacturer's instructions of 3.6 ml per 100 g of oyster wet weight.

2.2. Experiment I: size-selective predation

In the seawater system at FSUCML, the feeding rate and size-selective predation of individual drills ($n = 63$) that ranged in size from 41 to 84 mm were characterized. Oysters ranged in size from 25 to 99 mm, longest umbo-lip distance (also sometimes referred to as shell height), and were assigned to one of three size classes: small (25–49 mm), medium (50–74 mm), or large (75–99 mm). The break between the medium and large size class was chosen based on the legal-size limit for oyster harvest in Apalachicola Bay, which is 76.2 mm (3 in.). Immediately after collection from the field, each drill was placed in a tank with a total of fifteen oysters, five from each size class. Equal numbers of prey size classes were used so that selection was not confounded with encounter rates. Oysters were checked every two days for the first eight days of the experiment and then every four or five days, for a total trial duration of 13–17 days. Oysters were classified as either live or dead (i.e., valves remained open with some to no tissue present). If a drill was actively consuming an oyster, then the size of the oyster was noted, but it was left in the tank until drill feeding ended. All dead oysters were replaced with a live one from the same size class to preserve a constant density and size structure of prey. From these data, the mean size and number of oysters that each drill consumed per oyster size group and the average feeding rate (total number of oyster consumed per day) were calculated.

Linear regression was used to test the relationship between drill size and mean size of oysters consumed, as well as drill size and daily feeding rate. A Chi-squared test was also used to investigate whether drills consumed any of the three size classes of oysters more than would be expected by equal chance.

2.3. Experiment II: aggregate predation and predator functional response

In the seawater system at USFCMS, six drill abundances (2, 3, 4, 6, 8, and 12 drills per tank) were orthogonally crossed with five oyster abundances (3, 4, 6, 8, and 12 per tank), yielding two replicates for each orthogonal cross. The wide range of abundances reflects a response-surface approach to the regression analysis, improving the chances of detecting interactions between experimental factors despite low replication at any one combination of treatments. The treatment abundances were equivalent to densities ranging from 7 to 44 m^{-2} (drills) and 16–65 m^{-2} (oysters), both within the natural range observed for each species during and after outbreak conditions (See Supplemental Fig. 1). In this second experiment, drills ranged in size from 30 to 81 mm and were separated into small (30–55 mm) and large (56–81 mm) size classes. Oysters ranged in size from 25 to 99 mm and were separated into small (25–49 mm), medium (50–74 mm), and large (75–99 mm) size classes, as in Experiment I. Abundances of drills and oysters were split equally among each size class. To quantify oyster mortality in the absence of drills, each level of oyster abundance was paired with a corresponding control treatment ($n = 2$) that lacked an oyster drill; no oysters died in these controls. After collection from the field, drills were held for one week and allowed to feed ad libitum on oysters before the start of the experiment to reduce any transportation effect to USFCMS from Apalachicola Bay, FL. The experiment began with a 5-day starvation period, based on the feeding rate of individual-housed drills from Experiment I, to standardize predator hunger. During feeding trials, tanks were checked twice daily for dead oysters, and the number of drills on each oyster was counted. Any dead oysters were replaced with a live oyster from the same size class to preserve a constant prey density, as assumed in predator functional response models that quantify the instantaneous feeding rate as opposed to the integrated feeding rate. After the 15-day experimental period, both the per capita feeding rate and the aggregate feeding rate (oysters consumed per replicate) were calculated.

The results of Experiment II were analyzed in three ways. First, to test whether more drills fed as an aggregation than expected by chance, a Chi-squared goodness-of-fit test was performed. The null expectation followed a Poisson distribution with a mean equal to the overall mean number of drills per oyster observed in the experiment. This distribution is typically used for count data such as found in this experiment. Next, the null expectation was compared to the observed counts of aggregation sizes, from zero to the specific drill treatment abundance on days 3, 8, and 13. The analysis was restricted to these days to reduce any possible effect from the pre-experiment starvation period and to prevent double-counting any feeding events that occurred on any one day, based on the single-drill feeding rate results from Experiment I.

Second, a traditional hypothesis-testing analysis was used to quantify feeding rates as a function of predator and prey abundance. Specifically, regression analyses described the aggregate and daily per capita feeding rate as a function of drill and oyster abundance. For both the aggregative and per capita feeding rate we compared linear (full and reduced) and a non-linear model using Akaike Information Criterion corrected for small sample size ($\mathrm{AIC_c}$) (Burnham and Anderson, 2002). The model with the lowest $\mathrm{AIC_c}$ score was selected as the most parsimonious model. These analyses were conducted using the base, *nlme*, and *AICcmodavg* packages in R version 3.2.2 (R Core Team, 2013).

Third, an information-theoretic approach was used to identify the most appropriate functional response model to describe the effects of variation in predator density on prey consumption. Five possible functional response curves were fit to the data (Table 1). The null model was the Holling Type-II functional response (H2; Holling, 1959), which assumes no interaction among predators. The four other models that were used included some form of predator-dependence (Skalski and Gilliam, 2001): (1) the Beddington-DeAngelis model (BD; Beddington, 1975; DeAngelis et al., 1975), in which the predator attack rate, but not handling time, is affected by predator density; (2) the Crowley-Martin model (CM; Crowley and Martin, 1989), in which both the predator attack rate and handling time are affected by predator density; (3) the Hassell-Varley model (HV; Hassell and Varley, 1969), which is similar to the BD model but allows for a nonlinear effect of predator density on attack rate; and (4) ratio-dependent predation (RD, reviewed in Arditi and Ginzburg, 2012) where the attack rate depends on the ratio of predators to prey.

The maximum likelihood fit of each model was estimated using the *fmincon* function with interior-point algorithm in the Matlab 8.4 (R2014b) optimization tool box. Likelihoods were calculated assuming a normal error distribution and constrained functional response parameters to be nonnegative when appropriate. Handling times were constrained to be positive and non-zero. The model that produced the most parsimonious fit was determined by $\mathrm{AIC_c}$.

3. Results

3.1. Experiment I: size-selective predation

There was a slight positive relationship between the sizes of drills and consumed oysters ($F\text{-stat}_{1,60} = 4.49$ p-value $= 0.03$ Fig. 1a, Supplemental table1). However, the feeding rate did not change as a function of predator size, with drills consistently consuming approximately one oyster every five days, or 0.2 oysters day^{-1}, regardless of drill size ($F\text{-stat}_{1,60} = 1.23$; p-value $= 0.27$; Fig. 1b, Supplemental table 1). Drills were found to consume more oysters between 50 and 74 mm in length, and fewer oysters > 74 mm than expected by chance ($\chi^2_{\mathrm{df}=2} = 17.38$, $p = 0.0002$, Fig. 1c).

Table 1

Five functional response models that described how predator density affected the number of prey consumed per predator. For each model, we report the difference between the Akaike Information Criterion (corrected for small sample size, AIC$_c$) score and that of the most parsimonious model (ΔAIC$_c$) and the AIC$_c$ weights (w). All models included a variable for the attack rate (a, units: day^{-1} [no. predators 0.25 m^{-2}]$^{-1}$), handling time (b, units: [no. prey 0.25 m^{-2}]$^{-1}$) for a given predator density (P, units [no. 0.25 m^{2}]$^{-1}$), and prey density (N, units [no. 0.25 m^{2}]$^{-1}$). In the BD, CM, and HV models the parameters c (units: [no. predators 0.25 m^{-2}]$^{-1}$), and m (dimensionless) described the magnitude of predator facilitation ($c < 0, m < 1$) or interference ($c > 0$, $m > 1$). The parameter s was the residual error term.

Model	Formula	Parameter	Estimate	SD	AIC$_c$	w
Holling type II (H2)	$f_{H2}(N,P) = \frac{aN}{1+bN}$	a	0.0171	0.0357	42.8	< 0.001
		b	0.5142	0.2434		
		s	0.3703	0.0338		
Beddington-DeAngelis (BD)	$f_{BD}(N,P) = \frac{aN}{1+bN+cP}$	a	6.424×10^4	3.344×10^7	9.9	0.007
		b	2.614×10^5	1.361×10^8		
		c	1.862×10^5	9.692×10^7		
		s	0.2762	0.0246		
Crowley-Martin (CM)	$f_{CM}(N,P) = \frac{aN}{1+bN+cP+bcNP}$	a	0.2068	0.0532	0	0.965
		b	0.5142	0.1690		
		c	0.2162	0.0519		
		s	0.2544	0.0234		
Hassell-Varley (HV)	$f_{HV}(N,P) = \frac{aN}{bN+P^m}$	a	0.3385	0.1445	9.9	0.007
		b	1.3785	0.7236		
		m	0.9908	0.1867		
		s	0.2762	0.0260		
Ratio-dependent (RD)	$f_{RD}(N,P) = \frac{a(N/P)}{1+b(N/P)}$	a	0.3453	0.7881	7.7	0.021
		b	1.411	3.8323		
		s	0.2762	0.0310		

3.2. Experiment II: aggregate predation

Multiple aggregations were observed during feeding events in all six drill-abundance treatments (Fig. 2). The occurrence of a feeding event that involved two or more drills across all daily observations and treatments ranged from 32% to 54%. In one case a feeding event that involved an aggregation of ten drills on a single oyster was observed. Across all treatment abundances, drills were observed feeding as an aggregation more often than would be expected by chance, as described by a Poisson distribution: 2-drill ($\chi^2_{df=2} = 23.8$, $p < 0.001$), 3-drill ($\chi^2_{df=3} = 58.2$, $p < 0.001$), 4-drill ($\chi^2_{df=4} = 167.2$, $p < 0.001$), 6 drill ($\chi^2_{df=6} = 791.8$, $p < 0.001$), 8-drill ($\chi^2_{df=8} = 560.15$, $p < 0.001$), and 12-drill ($\chi^2_{df=12} = 81{,}698$, $p < 0.001$). During the experiments, higher frequencies of drill-free oysters (no aggregation) and aggregations of 3 to 8 drills per feeding event were observed, compared to aggregations with 1 or 2 drills (Supplemental Fig. 2).

The relationship between both the aggregate and per capital feeding rates and drill abundances followed a non-linear relationship (Fig. 3a,b, Supplemental table 1). The aggregate feeding rate increased with drill abundnace, but this rate declined as drill abundance increased, especially at lower oyster abundance treatments (Fig. 3a), and the per capita feeding rate declined following a negative exponential relationship (Fig. 3b). The per capita feeding rates also showed larger differences among oyster treatments at low drill abundances compared to high drill abundances when the per capita feeding rate was the lowest (Fig. 3b).

Each aggregate feeding rate was compared to an additive model, which predicted no interference among drills and a linear increase in the feeding rate (dashed line Fig. 4) based on the feeding rate of a single drill (open square Fig. 4). Points above the predicted relationship indicate facilitation, and points below the line indicate inhibition. While all aggregate drill feeding rates were higher than the single drill feeding rate of ~0.20 oyster/day^{-1}, at the higher drill abundances there were larger departures from the predicted additive model (Fig. 4). Across all oyster abundances, the mean group feeding rate for the 2-drills treatment was 0.50 (95% CI: 0.38–0.62) oysters day^{-1}. The 95% CI of this estimate included the prediction from an additive feeding model of 0.40 oysters day^{-1}. The observed mean feeding rate for the 8-drill treatment was 0.77 (95% CI: 0.66–0.88) oysters day^{-1}, and the 12-drill treatment was 1.3 (95% CI: 1.04–1.52). While these rates were higher than the 2-drill treatment, they were significantly lower (i.e. no overlap with the 95% CI's) than the expected aggregate feeding rates under an additive model, 1.6 and 2.4 oysters day^{-1} respectively (Fig. 4).

3.3. Experiment II: predator functional response

The CM model was the most parsimonious description of the predator functional response, compared to the predator-independent H2 model and the alternative predator-dependent models, BD, HV, and RD (AIC$_c$ weight = 96.5%, Table 1, Fig. 5a–f). The maximum likelihood fit of the model had parameter $c > 0$ (maximum likelihood value 0.22, standard deviation 0.05), indicating a negative effect of predator density on the attack rate and handling time (Table 1). As is typical for functional response models, there was a strong correlation ($r = 0.89$) between the attack rate (parameter a in Table 1) and handling time

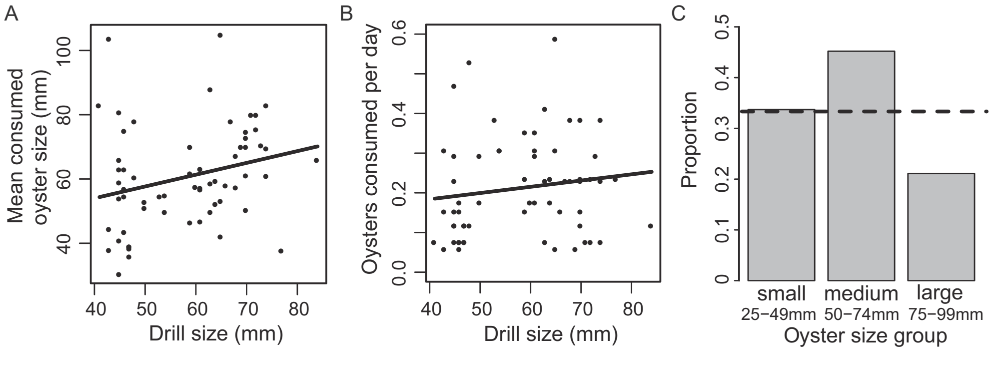

Fig. 1. Predation characteristics of a single predatory drill with multiple oyster prey. (a) The linear relationship of mean size (mm) of consumed oysters as a function of drill size (mm). (b) The linear relationship of the drill feeding rate (oysters day^{-1}) as a function of drill size (mm). (c) The proportion of oyster consumed by oyster size group (gray bars) with expected proportion (dashed line).

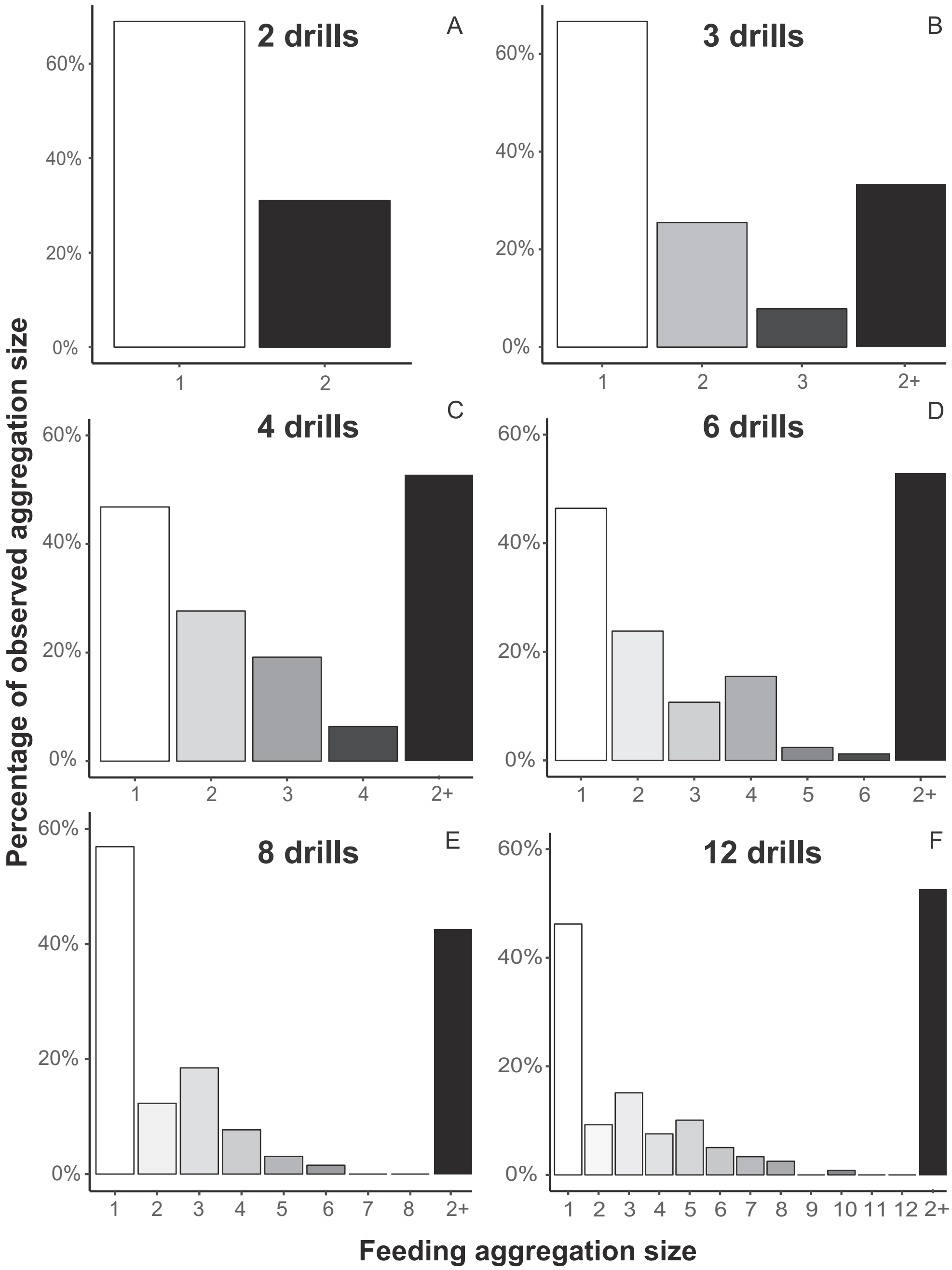

Fig. 2. The percentage of observed drill aggregation sizes during all daily observations of drills on oysters. Panels correspond to treatments with (a) two, (b) three, (c) four, (d) six, (e) eight, and (f) twelve drills. In (b)-(f) the black bar represents the cumulative aggregative feeding events that included 2 or more drills. Data are pooled across all oyster abundance treatments.

(parameter *b* in Table 1, Supplemental Fig. 3a). While maximum likelihood estimates for these two parameters were strongly correlated, their values were also jointly constrained by the value of the predator-dependent parameter (*c* in Table 1, Supplemental Fig. 3b,c).

4. Discussion

This study demonstrated that drills, a major predator of oysters in the northern Gulf of Mexico, disproportionately consumed oysters just below legal harvest size (50–74 mm in length). Drills at higher densities were likely to feed in aggregations on fewer oysters and at higher drill numbers per oyster than expected by chance. Although this aggregative feeding behavior accelerated the loss of oysters (relative to treatments with fewer drills), the per capita feeding rates of drills were reduced, likely due to intraspecific inhibition. This observation was supported by the fact that variation in the functional response of drill densities was best described by the Crowley-Martin (CM) model, which can describe intraspecific interference in both predator attacks rates and prey handling times. The feeding rates may have been elevated due to increased encounter rates that occur in mesocosms, but all experimental tanks had similarly sized base areas, allowing for reasonable comparisons between experiments and among treatments. Future field experiments would improve the description of the intraspecific interaction of drills when feeding on oysters at high drill densities. The effect of future drill outbreaks on oyster populations will depend on the density and size of drills in the outbreak, and the ability to predict and mitigate such intense predation events will require accounting for both prey size selectivity for sub-legal oysters and intraspecific predator inhibition.

Drills have been documented as an important predator of oysters in the northern Gulf of Mexico (Butler, 1954) and previous studies have provided some insight on this predator-prey dynamic. Our study builds

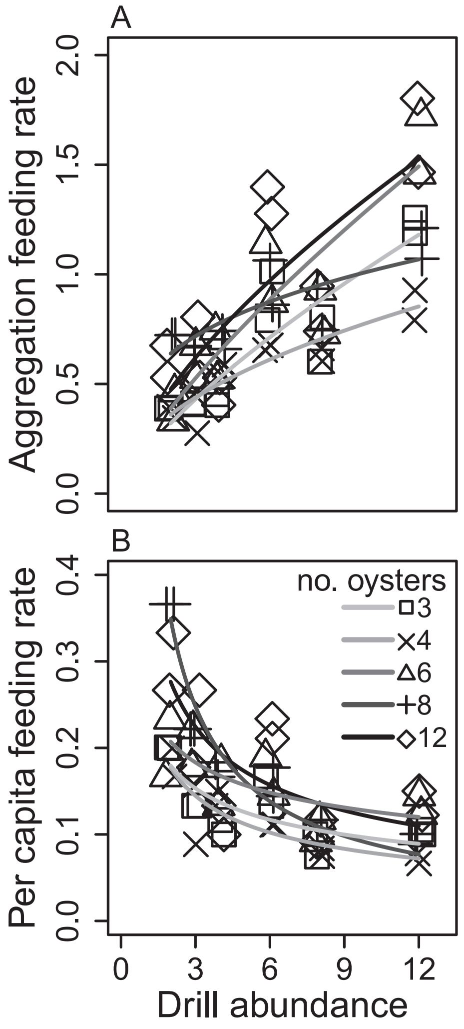

Fig. 3. The aggregation (a) and per capita (b) feeding rates of drills on oysters. The shapes, jittered for visualization, represent different oyster abundances: squares, 3 oysters; circle, 4 oysters; triangles, 6 oysters; upside down triangle, 8 oysters; diamond, 12 oysters. In (b), each of the oyster abundances is modeled (solid line) using a negative exponential model, $= a \times x^b$. The gray scale ranges from the lowest abundances (3 oysters) the lightest gray to the highest abundance (12 oysters) darkest gray (see Supplemental table 1).

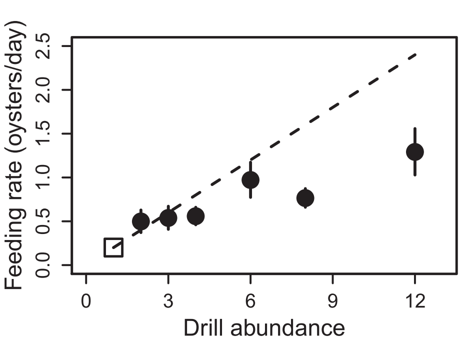

Fig. 4. The aggregation feeding rate of drills on oysters compared to the prediction of an additive relationship of the per capita feeding rate of one drill, 0.2 oysters day^{-1}(dashed line) for each drill abundance treatment level. Points indicate mean (± 95% confidence intervals) aggregate feeding rates (summed across all oyster treatments) of drills at different abundances. The open square is the daily feeding rate of one drill.

on this understanding by describing some novel details about the drill's functional relationship. Similar to other studies, a single drill consumed approximately one oyster every five days (Brown and Alexander Jr., 1994; Garton, 1986), albeit with some minor variation probably due to differences in temperature and salinity (Garton and Stickle, 1980). The more striking and biologically meaningful result that emerged from our study was that drills selectively consumed more medium-sized oysters (50–74 mm) relative to both large and small ones. This result differs from Brown (1997) who did not detect a difference in the number of oysters consumed based on size. Brown's (1997) size bins were larger than the ones in this study, e.g. 50–95 mm vs. 50–74 mm and > 74 mm, (based on conversions from wet weight, see Supplemental table 2). The finer resolution of size bins in the present study indicated a pattern not previously documented and could have been the reason for the difference compared to Brown's (1997) study. Because drills were found to feed more than expected on sub-legal-sized oysters, predation could negatively affect the number of oysters entering the fishery. Incorporating this information could promote a more strategic management of oyster harvesting.

In the second experiment, drills were often observed in feeding aggregations, which occurred between ~30–50% of the time when an oyster was being eaten, similar to field observations on natural oyster reefs in Louisiana (Brown and Alexander Jr., 1994). Lower per capita feeding rates have also been reported (Brown and Richardson, 1987; Brown and Alexander Jr., 1994), but these studies did not use a regression-based design to describe the relationship over a range of drill densities. By using multiple densities, the present study showed that increasing drill density caused a larger departure from the predictions of an additive model. This result suggested interference among drills occurred as the density increased. Combined with the functional response analysis, these results suggest that inhibition occurred among drills at high densities and reduced drill predation on oysters. This study is the first to quantitatively describe the inhibition of drill feeding rates at high densities and incorporating this information will also promote a more strategic management of oyster harvesting.

Drills, like other estuarine and marine whelks, have been the subject of many predation studies (e.g., Brown and Alexander Jr., 1994; Garton, 1986; Fairweather et al., 1984; Hughes and Dunkin, 1984; Fairweather, 1988a, 1988b; Burrows and Hughes, 1989, 1991; Sr Vadas et al., 1994; Hughes and Grabowski, 2006). This study was the first to quantify the functional response of drills at different densities, and found that the Crowley-Martin (CM) functional response model was overwhelmingly the best fit. Out of the four predator-dependent models compared, the CM model was the only one that included an effect of predator density on both the attack rate and handling time (the others only included effects on attack rate). The handling time sets the asymptotic maximum predation rate, so whereas the other four models eventually converge on the same asymptote, the CM model (and the data) exhibits substantially higher maximum per-capita feeding rates at lower drill densities (Fig. 5). As a good comparison, the H2 model multiplied by predator density overestimates the consumption rate (Fig. 5b) compared to the fit of CM (Fig. 5f). This suggests it is not just the number of predators but predator-predator interactions that affects the consumption rate. It is good practice to compare the fit of different models that incorporate predator dependence (Skalski and Gilliam, 2001) to describe how predator interactions affect the per capita mortality more accurately. For this predator-prey interaction, the use of an additive functional response model would not have accounted for predator interactions during drill outbreaks.

In addition to including predator dependence, adding size-dependent parameters could improve the predictive accuracy of functional response models (McCoy et al., 2011). There have been a few studies that have incorporated prey size into the predator functional response, detecting subtle changes in the functional response of the predators for different prey sizes (McCoy and Bolker, 2008; McCoy et al., 2011) or for different ratios of predator:prey biomass (Aljetlawi et al., 2004). Although we detected a relative preference of drills for medium-sized oysters, logistical considerations prevented estimation of a functional response that included both size-dependence and predator-dependence

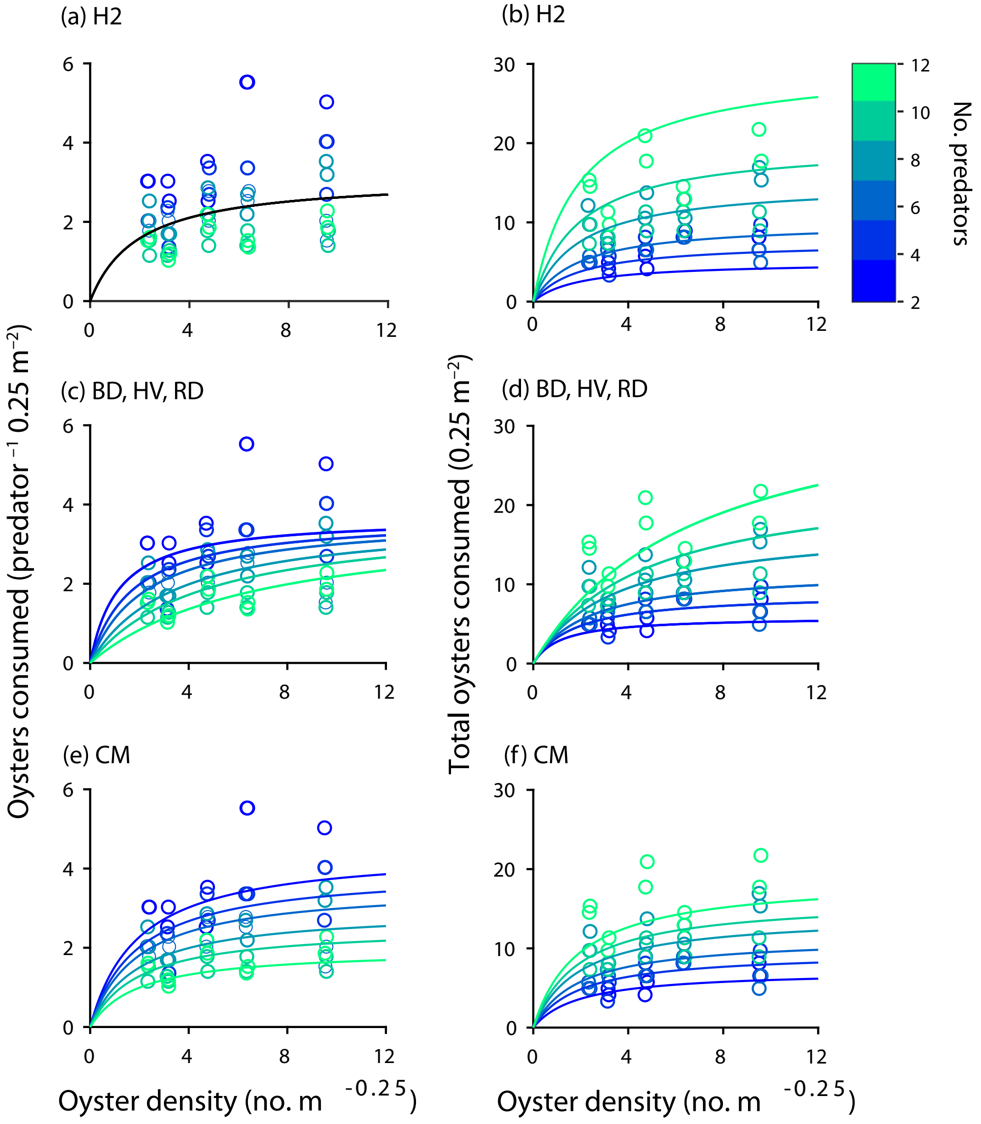

Fig. 5. Fitted functional response curves for multiple densities of drills on oysters. Each circle is a per predator feeding rate, and the densities of drills range from 2 to 12 drills indicated by the blue to green gradient. Left panels (a, c, e) display the per-predator feeding rate; right panels (b, d, f) display the overall feeding rate in each treatment. Panels (a,b) show the Holling Type II (H2) functional response curve (in panel (a) this is a single black line because the per-predator prediction is the same across all predator densities). Panels (c,d) show the Beddington-DeAngelis (BD), Hassell-Varley (HV), and the ratio-dependent (RD) curves, all of which reduced to the same prediction. Panels (e,f) show the Crowley-Martin functional response (CM). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(in short, it was difficult to distinguish which drill consumed which oyster in multiple-predator treatments and the width of our prey size bins was too large to precisely quantify prey-size-dependence). The primary goal of our size-dependent experiment was to determine whether drills disproportionately feed on oysters above or below the legal-size limit, in order to understand possible interactions with the oyster fishery. However, follow up experiments specifically focused on describing the effect of prey size could allow for a more nuanced description of drill predation on oysters and the effect that occurs during these predator outbreaks.

Although evidence of inhibition among drills was found, how it manifests itself among aggregations of drills is still unknown. Drills locate prey using chemical cues (Smith, 1983) and then attack oysters using a combination of radula scraping and acid secretions to penetrate the valves (Butler, 1985; Brown and Richardson, 1987). Finally, the drill releases a toxin and proteolytic enzyme to paralyze the oyster abductor muscle and consume the soft tissue (Brown and Alexander Jr., 1994). Aggregations of drills could inhibit each other through a variety of possible mechanisms during the search and handling times. Further investigation during both these periods is needed to describe the mechanism that is occurring. For example, chemical cues of an attacked oyster may trigger other drills to pursue the injured oyster; however, energy could have been better expended on searching for viable oysters without other drills present. Additionally, multiple oyster drills may interfere with one another for the optimal feeding position. Alternatively, there may be a negative effect of multiple drills releasing toxins and proteolytic enzyme on nearby drills leading to longer handling times. From an evolutionary perspective, it appears counterintuitive that drills would preferentially aggregate to feed when per capita consumption is reduced in aggregations. However, one should consider that the present study examined consumption purely from the perspective of prey mortality; it is possible that energetic or other types of fitness benefits accrue to aggregating drills. In any case, drills exhibit this aggregative behavior at high densities both in the field (Brown and Alexander Jr., 1994) and in the lab (Brown and Richardson, 1987; Brown and Alexander Jr., 1994), a similar phenomenon as other invertebrate predators that form consumer fronts during outbreaks (Silliman et al., 2013). Thus, further investigation is warranted to describe the nature of inter-drill interference and any possible fitness benefits to aggregation.

Although the specific mechanism(s) of the inhibition remains unknown, documenting the per capita feeding rates of drills is important to understand the long-term persistence of oyster populations and the reef communities that they support. Oyster drills are believed to be one of the most influential predators on oysters in the northern Gulf of Mexico (Butler, 1954). They have frequently been observed to feed in aggregations on natural reefs (Brown and Alexander Jr., 1994). The ability to model their feeding rates, based on fluctuations in drill density, is important for predicting how strongly oyster populations will be altered by predator outbreaks. Drill outbreaks are likely to occur more often due to regional drought conditions in the southeast United States (Silliman et al., 2005; FFWCC, 2013) and increased freshwater usage due to urban development, agriculture, and industry (Marella and Fanning, 2011; Lawrence, 2016). As a result, there has been a reduction in freshwater input into estuaries and longer durations of higher salinity events (Petes et al., 2012). The oyster fishery within the Apalachicola Bay, FL estuary has recently collapsed from what is believed to be a result of poor juvenile survivorship (Pine III et al., 2015). In tandem with low oyster recruitment, there was a large increase in the drill population and increased predation on mature (adult) oyster populations and elevated oyster mortality more than expected from drought alone (Kimbro et al., 2017). Our functional response research will help subsequent efforts to model the degree to which this predator outbreak and anthropogenic stressors that elevated water salinity caused the collapse, as opposed to just the recruitment failure or over-fishing. Because the frequency and persistence of drought conditions are projected to increase in the southeast United States throughout the next century (Hanson and Weltzin, 2000), increased densities of drills may occur more frequently, and for longer durations, throughout northern GOM estuaries, potentially increasing mortality of oysters. Gaining a better understanding of how drills successfully feed at these higher densities will provide more accurate information for management plans that will support the preservation and growth of eastern oyster reefs.

4.1. Conclusions

This study highlights the importance of incorporating ecological reality into laboratory experiments, specifically using multiple predators to accurately describe predators-prey dynamics (Sih et al., 1998). We have shown that manipulating biotic variables such as predator density can improve functional response models. Including these types of effects may be particularly important for systems experiencing rapid increases in predator density –such as invasive species – because these species might experience some degree of self-regulation. Additionally, future experiments with the goal of describing predator-prey dynamics should also incorporate abiotic variables to improve descriptions of the mechanisms that produce natural patterns. Incorporating findings from such laboratory studies can then be used to parameterize mechanistic models (Boettiger and Hastings, 2013), which can predict how ecosystems may change under different environmental conditions and anthropogenic actions.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2018.01.005.

Acknowledgments

We thank Nikkie Cox, Megan Christopher, and Samantha Yuan for assistance with field collections. We thank Matthew Farnum and Owen Stokes-Cawley for daily maintenance of laboratory experiments, and Andrea Jerabek, Zach Osteroff, Kara Wall, and Bethany Williams for additional assistance during experiments. Two anonymous reviewers provided constructive suggestions on the manuscript. This work was supported by the Florida Department of Environmental Protection [grant number: OGC071].

References

Aljetlawi, A., Sparrevik, E., Leonardsson, K., 2004. Prey-predator size-dependent functional responses: derivation and rescaling to the real world. J. Anim. Ecol. 73, 239–252.

Andersen, K.H., Pedersen, M., 2010. Damped trophic cascades driven by fishing in model marine ecosystems. Proc. R. Soc. B 277, 795–802.

Arditi, R., Ginzburg, L.R., 2012. How Species Interact: Altering the Standard View on Trophic Ecology. Oxford University Press, New York.

Beddington, J.R., 1975. Mutual interference between parasites or predators and its effect on searching efficiency. J. Anim. Ecol. 44, 331–340.

Boettiger, C., Hastings, A., 2013. Tipping points: from patterns to predictions. Nature 493, 157–158.

Boulding, E.G., 1984. Crab-resistant features of shells of burrowing bivalves: decreasing vulnerability by increasing handling time. J. Exp. Mar. Bio. Ecol. 76, 201–223.

Brodie, J., Fabricius, K., De'ath, G., Okaji, K., 2005. Are increased nutrient inputs responsible for more outbreaks of crown-of-thorns starfish? An appraisal of the evidence. Mar. Pollut. Bull. 51, 266–278.

Brown, K.M., 1997. Size-specific aspects of the foraging ecology of the southern oyster drill *Stramonita haemastoma* (Kool 1987). J. Exp. Mar. Biol. Ecol. 214, 249–262.

Brown, K.M., Alexander Jr., J.E., 1994. Group foraging in a marine gastropod predator: benefits and costs to individuals. Mar. Ecol. Prog. Ser. 112, 97–105.

Brown, K.M., Richardson, T.D., 1987. Foraging ecology of the southern oyster drill *Thais haemastoma* (gray): constraints on prey choice. J. Exp. Mar. Biol. Ecol. 114, 123–141.

Bruno, J., Bertness, M.D., 2001. Positive interactions, facilitations and foundation species. In: Bertness, M.D., Gaines, S.D., Hay, M. (Eds.), Marine Community Ecology. Sinauer Associates, Sunderland, pp. 201–218.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer, New York, NY.

Burrows, M.T., Hughes, R.N., 1989. Natural foraging of the dogwhelk, *Nucella lapillus* (Linnaeus); the weather and whether to feed. J. Molluscan Stud. 55, 285–295.

Burrows, M.T., Hughes, R.N., 1991. Variation in foraging behavior among individuals and populations of dogwhelks, *Nucella lapillus*: natural constraints on energy intake. J. Anim. Ecol. 60, 497–514.

Butler, P.A., 1954. The southern oyster drill. Proc. Nat. Shellfish. Assoc. 44, 67–75.

Butler, P.A., 1985. Synoptic review of the literature on the southern oyster drill *Thais haemastoma floridana*. NOAA Technical Report NMFS 35, 1–9.

Côté, I.M., Green, S.J., Hixon, M.A., 2013. Predatory fish invaders: insights from Indo-Pacific lionfish in the western Atlantic and Caribbean. Biol. Conserv. 164, 50–61.

Crowley, P.H., Martin, E.K., 1989. Functional responses and interference within and between year classes of a dragonfly population. J. NA. Benthol. Soc. 8, 211–221.

DeAngelis, D.L., Goldstein, R.A., O'Neill, R.V., 1975. Model for trophic interaction. Ecology 56, 881–892.

Eisenlord, M.E., Groner, M.L., Yoshioka, R.M., Elliott, J., Maynard, J., Fradkin, S., Turner, M., Pyne, K., Rivlin, N., van Hooidonk, R., Harvell, C.D., 2016. Ochre star mortality during the 2014 wasting disease epizootic: role of population size structure and temperature. Phil. Trans. R. Soc. A 371, 20150212.

Estes, J.A., Palmisano, J.F., 1974. Sea otters: their role in structure nearshore communities. Science 185, 1058–1060.

Fairweather, P.G., 1988a. Correlations of predatory whelks with intertidal prey at several scales of space and time. Mar. Ecol. Prog. Ser. 45, 237–243.

Fairweather, P.G., 1988b. Movements of intertidal whelks (*Morula morginalba* and *Thais orbita*) in relation to availability of prey and shelter. Mar. Biol. 100, 63–68.

Fairweather, P.G., Underwood, A.J., Moran, M.J., 1984. Preliminary investigations of predation by the whelk *Morula marginalba*. Mar. Ecol. Prog. Ser. 17, 143–156.

Florida Fish and Wildlife Conservation Commission (FFWCC), 2013. 2012–2013 Florida Gulf Coast Oyster Disaster Report.

Fodrie, F.J., Kenworthy, M.D., Powers, S.P., 2008. Unintended facilitation between marine consumers generates enhanced mortality for their shared prey. Ecology 89, 3268–3274.

Garton, D.W., 1986. Effect of prey size on the energy budget of a predatory gastropod, *Thais haemastoma canaliculata* (gray). J. Exp. Mar. Biol. Ecol. 98, 21–33.

Garton, D.W., Stickle, W.B., 1980. Effects of salinity and temperature on the predation rate of *Thais Haemastoma* on *Crassostrea virginica* spat. Biol. Bull. 158, 49–57.

Grabowski, J.H., Hughes, A.R., Kimbro, D.L., Dolan, M.A., 2005. How habitat setting influences restored oyster reef communities. Ecology 86, 1926–1935.

Grosholz, E.D., Ruiz, G.M., 1995. Spread and potential impact of the recently introduced European green crab, *Carcinus maenas*, in central California. Mar. Biol. 122, 239–247.

Hanson, P.J., Weltzin, J.F., 2000. Drought disturbance from climate change: response of United States forests. Sci. Total Environ. 262, 205–220.

Hassell, M.P., Varley, G.C., 1969. New inductive population model for insect parasites and its bearing on biological control. Nature 223, 1133–1137.

Hixon, M.A., 2015. Predation: piscivory and the ecology of coral-reef fishes. In: Mora, C. (Ed.), Ecology and Conservation of Fishes on Coral Reefs: The Functioning of an Ecosystem in a Changing World. Cambridge University Press, Cambridge, pp. 41–52.

Holling, C.S., 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Can. Entomol. 91, 293–320.

Hughes, R.N., Dunkin, S. de B., 1984. Behavioral component of prey selection by dogwhelks, *Nucella lapillus* (L.) feeding on mussels, *Mytilus edulis* L., in the laboratory. J. Exp. Mar. Biol. Ecol. 77, 45–68.

Hughes, R.N., Grabowski, J.H., 2006. Habitat context influences predator interference interactions and the strength of resource partitioning. Oecologia 149, 256–264.

Hunsicker, M.E., Ciannelli, L., Bailey, K.M., Buckel, J.A., White, J.W., Link, J.S., Essington, T.E., Gaichas, S., Anderson, T.W., Brodeur, R.D., Chan, K.S., Chen, K., Englund, G., Frank, K.T., Freitas, V., Hixon, M.A., Hurst, T., Johnson, D.W., Kitchell, J.F., Reese, D., Rose, G.A., Sjodin, H., Sydeman, W.J., van der Veer, H.W., Vollset, K., Zador, S., 2011. Functional responses and scaling in predator–prey interactions of marine fishes: contemporary issues and emerging concepts. Ecol. Lett. 14, 1288–1299.

Jackson, J.B., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Stenck, R.S., Tegner, M.J., Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293, 629–638.

Kimbro, D.L., White, J.W., Tillotson, H., Cox, N., Christopher, M., Stokes-Cawley, O., Yuan, S., Pusack, T.J., Stallings, C.D., 2017. Local and regional stressors interact to drive a salinization-induced outbreak of predators on oyster reefs. Ecosphere 8 (11), e01992.

Klassen, G.J., Locke, A., 2007. A biological synopsis of the European green crab, *Carcinus maenas*. Can. Manuscr. Rep. Fish. Aquat. Sci. 2818, 1–75.

Kratina, P., Vos, M., Bateman, A., Anholt, B.R., 2009. Functional responses modified by predator density. Oecologia 159, 425–433.

Lawrence, S.J., 2016. Water use in the Apalachicola-Chattahoochee-Flint River Basin, Alabama, Florida, and Georgia, 2010, and water-use trends, 1985 –2010. In: U.S. Geological Survey Scientific Investigations Report 2016–5007. 72http://dx.doi.org/10.3133/sir20165007.

Livingston, R.J., Lewis, F.G., Woodsum, G.C., Niu, X.F., Galperin, B., Huang, W., Christensen, J.D., Monaco, M.E., Battista, T.A., Klein, C.J., Howell, R.L., Ray, G.L., 2000. Modelling oyster population response to variation in freshwater input. Estuar. Coast. Mar. Sci. 50, 655–672.

Marella, R., Fanning, J., 2011. Water withdrawals, wastewater discharge, and water consumption in the Apalachicola-Chattahoochee-Flint River basins, 2005, and water-use trends, 1970–2005. US Geol. Surv. Sci. Investig. Rep. 2011, 5130.

May, E.B., 1971. A survey of the oyster and the oyster shell resources of Alabama. Ala. Mar. Resour. Bull. 4, 53.

McCoy, M.W., Bolker, B.M., 2008. Trait-mediated interactions: influence of prey size, density and experience. J. Anim. Ecol. 77, 478–486.

McCoy, M.W., Bolker, B.M., Warkentin, K.M., Vonesh, J.R., 2011. Predicting predation through prey ontogeny using size-dependent functional response models. Am. Nat. 177, 752–766.

Menge, B.A., 1976. Organization of the new England Rocky Intertidal Community: role of predation, competition, and environmental heterogeneity. Ecol. Monogr. 46, 355–393.

Menzel, R.W., Hulings, N.C., Hathaway, R.R., 1966. Oyster abundance in Apalachicola Bay, Florida in relation to biotic associations influenced by salinity and other factors. Gulf. Res. Rep. 2, 73–96.

Morris Jr., J.A., Whitfield, P.E., 2009. Biology, ecology, control and management of the invasive Indo-Pacific lionfish: an updated integrated assessment. In: NOAA Technical Memorandum NOS NCCOS. 99. pp. 1–57.

Murdoch, W.W., 1973. The functional response of predators. J. Appl. Ecol. 14, 335–341.

Paine, R.T., 1966. Food web complexity and species diversity. Am. Nat. 100, 65–75.

Persson, L., Andersson, J., Wahlström, E., Eklöv, P., 1996. Size-specific interactions in lake systems: predator gape limitation and prey growth rate and mortality. Ecology 77, 900–911.

Petes, L.E., Brown, A.J., Knight, C.R., 2012. Impacts of upstream drought and water withdrawals on the health and survival of downstream estuarine oyster populations: reduced freshwater input effects on oysters. Ecol. Evol. 2, 1712–1724.

Piehler, M.F., Smyth, A.R., 2011. Habitat-specific distinctions in estuarine denitrification affect both ecosystem function and services. Ecosphere 2 art 12.

Pine III, W.E., Walters, C.J., Camp, E.V., Bouchillon, R., Aherns, R., Sturmer, L., Berrigan, M.E., 2015. The curious case of eastern oysters *Crassostrea virginica* stock status in Apalachicola Bay, Florida. Ecol. Soc. 20, 46.

R Core Team, 2013. R: A Language and Environment for Statiscial Computing. In: R Foundation for Statistical Computer. Austria. URL, Vienna. http://www.R-project.org/.

Roller, R.A., Stickle, W.B., 1989. Temperature and salinity effects on the intracapsular development, metabolic rates, and survival to hatching of Thias haemastoma canaliculata (gray)(Prosobranchia: Muricidae) under laboratory conditions. J. Exp. Mar. Biol. Ecol. 23, 235–251.

de Roos, A.M., Metz, J.A.J., Evers, E., Leipoldt, A., 1990. A size dependent predator-prey interaction: who pursues whom? J. Math. Biol. 28, 609–643.

Rudolf, V.H.W., 2012. Seasonal shifts in predator body size diversity and trophic interactions in size-structured predator-prey systems. J. Anim. Ecol. 81, 524–532.

Scharf, F.S., Buckel, J.A., Juanes, F., Conover, D.O., 1998. Predation by juvenile piscivorous bluefish (*Pomatomus saltatrix*): the influence of prey to predator size ratio and prey type on predator capture success and prey profitability. Can. J. Fish. Aquat. Sci. 55, 1695–1703.

Scharf, F.S., Juanes, F., Rountree, R.A., 2000. Predator size-prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. Mar. Ecol. Prog. Ser. 208, 229–248.

Sih, A., Englund, G., Wooster, D., 1998. Emergent impacts of multiple predators on prey. Trends Ecol. Evol. 13, 350–355.

Silliman, B.R., Bertness, M.D., 2002. A trophic cascade regulates salt marsh primary production. Proc. Natl. Acad. Sci. U. S. A. 99, 10500–10505.

Silliman, B.R., van de Koppel, J., Bertness, M.D., Stanton, L.E., Mendekssohn, I.A., 2005. Drought, snails, and large scale die off of southern US salt marshes. Science 310, 1803–1806.

Silliman, B.R., McCoy, M.W., Angelini, C., Holt, R.D., Griffin, J.N., van de Koppel, J., 2013. Consumer fronts, global change, and runaway collapse in ecosystems. Annu. Rev. Ecol. Evol. Syst. 44, 503–538.

Skalski, G.T., Gilliam, J.F., 2001. Functional responses with predator interference: viable alternatives to the Holling type II model. Ecology 82, 3083–3092.

Smith, D.J., 1983. Chemoattraction of the Southern Oyster Drill *Thais haemastoma* towards the Oyster *Crassostrea virginica*, as a Function of Temperature and Salinity. Louisiana State University, Baton Rouge, Louisiana, M. SC. thesis.

Soluk, D.A., 1993. Multiple predator effects: predicting combined functional response of stream fish and invertebrate predators. Ecology 74, 219–225.

Sr Vadas, R.L., Burrows, M.T., Hughes, R.N., 1994. Foraging strategies of dogwhelks, *Nucella lapillus* (L.): interacting effects of age, diet and chemical cues to the threat of predation. Oecologia 100, 439–450.

Stallings, C.D., Dingeldein, A., 2012. Intraspecific cooperation facilitates synergistic predation. Bull. Mar. Sci. 88, 317–318.

Steele, M.A., Anderson, T.W., 2006. Predation. In: Allen, L.G., Horn, M.H., Pondella IID.J. (Eds.), Ecology of California Marine Fishes. U.C. Press, Los Angeles, pp. 428–448.

Stephens, D.W., Krebs, J.R., 1986. Foraging Theory. Princeton University Press, Princeton, NJ USA.

Stier, A.C., White, J.W., 2014. Predator density and the functional responses of coral reef fish. Coral Reefs 33, 235–240.

Thiebault, A., Semeria, M., Lett, C., Tremblay, Y., 2016. How to capture fish in a school? Effect of successive predator attacks on seabird feeding success. J. Anim. Ecol. 85, 157–167.

de Villemereuil, P.B., López-Sepulcre, A., 2011. Consumer functional responses under intra- and inter-specific interference competition. Ecol. Model. 222, 419–426.

Werner, E.E., Gilliam, J.F., 1984. The ontogenetic niche and species interactions in size-structured populations. Annu. Rev. Ecol. Syst. 15, 393–425.

White, J.W., Botsford, L.W., Hastings, A., Baskett, M.L., Kaplan, D.M., Barnett, L.A.K., 2013. Transient responses of fished populations to marine reserve establishment. Conserv. Lett. 6, 180–191.