

# Caged oysters still get scared: Predator presence and density influence growth in oysters, but only at very close ranges

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**ABSTRACT:** Two common forms of variation that may influence consumptive and non-consumptive effects differently are how the biomass of predators is allocated among individual predators (e.g. several small vs. few large predators) and how predators are spaced throughout a community. We analyzed how varying the presence, biomass (density, size, and total biomass), and distance to crown conchs *Melongena corona* impacted growth in eastern oysters *Crassostrea virginica* grown in field conditions. The presence of predators decreased growth (new shell added and mass) and increased shell thickness in a 58 d experiment. Although these effects were more pronounced as predator density increased, total predator biomass and predator size had limited impact on the strength of non-consumptive effects. The allocation of total oyster mass between shell and tissue was also not impacted by predator treatments. Results from a 96 d study examining the range of these effects indicated that they may exist only over short distances or change as oysters grow, as oysters at varying distances from a caged predator showed no differences in growth traits. These results show that non-consumptive interactions in oyster reef communities may be highly non-linear in regards to predator community structure and exposure distance and indicate these factors may be important in determining the impact of non-consumptive effects in other communities. Our growth data also show that non-consumptive effects may have major impacts on oyster growth under normal aquaculture conditions and suggest that these effects may need to be considered in management efforts.

**KEY WORDS:** Non-consumptive effects · Predator–prey interactions · Oyster reef ecology · Predator biomass · *Crassostrea virginica*

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## INTRODUCTION

The relationship between predators and their prey, and the impact these relationships have on ecological communities, has been and remains a dominant theme in ecology. Over the past decade a growing amount of attention has been directed toward the non-consumptive aspects of these interactions (Peckarsky et al. 2008). Non-consumptive effects (NCE) are characterized by changes in prey activity, behavior, morphology, and development in response to predator presence or cues (Orrock et al. 2008). The impacts of

NCE on prey and community dynamics are equivalent to or stronger than consumptive effects (CE) in many systems (Preisser et al. 2005). Given the ubiquity and strength of NCE, understanding how these effects change along multiple environmental gradients and how they influence species in conjunction with other interactions is essential to understanding how predators influence natural communities.

Although commonly overlooked in empirical studies and predator–prey models, both consumptive and non-consumptive predator–prey interactions are influenced by a variety of factors that may impact the

magnitude, direction, and even presence of CE and NCE differently. For example, use of complex habitats can reduce the CE of predators on prey, but non-consumptive interactions may still extend to these environments (Grabowski et al. 2005). Likewise, environmental conditions such as water temperature, pH, and salinity can influence predation rates (Whetstone & Eversole 1981, Held & Harley 2009). These conditions may also affect NCE by influencing the movement and detection of cues that trigger predator responses (Smee et al. 2008, Dixson et al. 2010, Kimbro 2012), thus changing the perceived risk of predation. Differences in the responses of NCE and CE to changing environmental factors may have major impacts on how predator–prey interactions and communities ultimately respond to environmental change.

Two major forms of variation that may influence CE and NCE in different ways include variation in the allocation of biomass among predators (e.g. several small vs. few large predators) and the spacing of predators throughout a community. Predator body size can physically limit the ability of individual predators to consume prey or impact overall consumption (Paine 1976, Eurich et al. 2014). Predator density is also positively correlated with consumption. Models and meta-analyses (Holt et al. 1994, Carbone & Gittleman 2002) indicate that larger predator populations should require more prey for survival. Natural examples include growing populations of reintroduced wolves leading to more elk kills (Smith et al. 2004) and declines in apex predator sharks leading to increases in the population sizes of their prey (Myers et al. 2007). The impacts of size and abundance on non-consumptive interactions, however, are less clear. While some prey species may respond more strongly to predator cues when the prey are small (Selden et al. 2009, Johnson & Smee 2012), responding to predator size would require prey to discern predation risk based on external cues.

Although evidence suggests prey may be able to identify and respond to different predators (Freeman 2007, Robinson et al. 2014), and prey may visually inspect predators to determine risk (Lima & Dill 1990), prey that evaluate risk through the use of chemical and auditory cues may or may not be able to distinguish the differing levels of risk posed by predators that differ in size (Chivers et al. 2001, Kusch et al. 2004). Similarly, prey may (Van Buskirk & Arioli 2002) or may not (Gosnell & Gaines 2012) be able to determine and respond to predator density based on cues. The inability to detect or respond to various sizes or densities of predators may lead to dif-

ferences in the relative impacts of CE and NCE as the size or abundance of predators changes. For example, mud crabs have been shown to exhibit the same predator-induced behavior whether in the presence of 1 large blue crab or several small blue crabs even though small blue crabs pose minimal predation risk (Hill & Weissburg 2013). Since NCE usually reduce prey growth or other traits in order to reduce predation rates, the inability of prey to accurately perceive risk based on predator size or density could lead to increased costs associated with NCE.

Besides distinguishing between a single large predator and several small predators, prey may be exposed to cues from predators at varying distances or threat levels (Turner & Montgomery 2003, Cresswell et al. 2010). For example, while consumptive interactions and the event of a predator actively pursuing a prey item require close contact, cues may emanate from a predator to prey that are out of its reach or search area, leading prey to overestimate risk. Predator proximity and size are also related, as cues from a small predator that is close to potential prey may be similar in concentration (e.g. chemical cues) or intensity (e.g. sound) to those from a larger predator at a distance. Similarly, dilute cues from multiple distant predators may be similar to those from fewer nearby threats (Ferrari et al. 2006). For these reasons, understanding how NCE are influenced by biomass allocation and distance to predators, along with the interactions between these factors, is critical in determining how non-consumptive interactions affect communities and relate to CE. The inability to differentiate threat levels may explain the non-linear relationships that have been observed (Gosnell & Gaines 2012) between predator density and non-consumptive responses and may enable small groups of predators (in size or number) to continually influence prey in ways far beyond what actual consumption would suggest. Alternatively, if prey can detect differences in the size, density, and distance of predators and accurately assess risk, the overall effects of predators on communities may be very different.

Unfortunately, limitations on space and the inability to replicate variation in water movement and water quality parameters means that recreating realistic variation in predator biomass and proximity (and associated impacts on cue production and detection) may be extremely difficult in lab settings. For this reason, we assessed the ability of prey to perceive variation in predator presence, size, density, biomass, and distance through a set of field-based mesocosm experiments focused on eastern oysters *Crass-*

*ostrea virginica*. Past work on NCE in oyster reefs has shown that small oysters grow more slowly in the presence of some predators (Johnson & Smee 2012) and may vary shell thickness due to predator presence (Garland 2014, Johnson & Smee 2014). However, work with other mollusks has demonstrated that prey may not demonstrate graded responses to predation risk (Gosnell & Gaines 2012).

Focusing on responses of oysters to predators also allowed us to consider the importance of non-consumptive interactions in a real-world management context. Hundreds of years of overfishing combined with coastal development and environmental degradation have caused an 85% loss of reefs globally (Beck et al. 2011), leading to efforts to rear oysters for future use in both restoration and food production. Off-bottom culture of oysters in floating cages is an increasingly common practice that is thought to benefit aquaculturists by increasing growth rates and reducing losses to predation compared to oysters grown without cages or bottom-caged oysters (Leonhardt 2013, Walton et al. 2013). Although predation and resulting mortality is a common concern for reared organisms (Griffin et al. 2000) that may be reduced by caging oysters, potential NCE of predators are often not considered by these programs. This is true in the use of floating cages for oyster aquaculture despite the fact that predators (e.g. blue crabs, mud crabs, drilling mollusks, toadfish) are commonly found in, on, or near cages (Marengi & Ozbay 2010, authors' pers. obs.).

Considering the non-consumptive interactions between cultured oysters and potential predators may be important for several reasons. Oysters exposed to predator cues may grow more slowly, meaning these interactions could impact aquaculture projects even without obvious impacts of consumption. Oysters exposed to predators may also develop traits that may or may not be desired by managers. Bivalves exposed to predator cues may increase shell thickness to lower the success of predators that break shells (Robinson et al. 2014), or they may increase muscular tissue used to keep shells closed in response to predators that pry open shells (Freeman 2007). However, these responses may not be species-specific or may seem counter-intuitive (Garland 2014). Changes in morphology that reduce future susceptibility to predation may benefit oysters being used to rebuild reefs (Robinson et al. 2014), but if the same changes reduce the amount of consumable tissue oysters produce or overall growth rate, they may be a negative consequence for oysters cultured for human consumption. For these reasons, we carried

out our experiments using procedures commonly employed by aquaculture and conservation groups to rear oysters. This design also allowed us to determine if non-consumptive interactions were noticeable in an environment characterized by natural variation in water movement, temperature, and other factors and in a setting where predators may realistically be caged next to prey for a number of weeks.

We conducted experiments to determine how size, density of, and distance from the predatory crown conch *Melongena corona* impacted non-consumptive interactions between the predator and its oyster prey. *M. corona* are part of a larger *Melongena* species complex of carnivorous gastropods that can be found intertidally in the USA from Alabama to the Atlantic coast of Florida (Hayes 2003). The species typically inhabits shallow protected intertidal sites and feeds on a variety of bivalves, gastropods, and horseshoe crabs (Hayes 2003), in addition to acting as scavengers. Crown conchs feed on oysters by inserting their proboscis between the shell valves (as opposed to drilling) (Bowling 1994), and the presence of conchs has been shown to have variable effects on shell thickness in oysters (Garland 2014, Garland & Kimbro 2015). Recent work has suggested that predation by conchs is an increasing cause of mortality for oysters in the region, potentially due to reduced freshwater flow (Florida Sea Grant 2013, Garland & Kimbro 2015). Conchs are negatively impacted by freshwater and also have a larger impact on stressed oyster populations (Hathaway & Woodburn 1961). Focusing on the impacts of crown conchs thus allowed us to consider a predator-prey interaction that may be particularly relevant for on-going conservation and aquaculture work. Considering non-consumptive interactions among these predators and their oyster prey may be important to understanding how reefs may change as human- and naturally-induced changes occur in water input, temperature, and salinity, especially as increasing predator abundances may alter the relative strength of CE and NCE.

## MATERIALS AND METHODS

### General experiment protocol

We conducted 2 studies to determine if the growth of oysters was influenced by the density and abundance of crown conchs and to determine the range of these effects. We carried out these experiments in waters offshore of the Florida State University Coastal

and Marine Laboratory (FSUCML, St. Teresa, Florida) between April and July 2014. Water temperature at the study site for these months ranged from 17.3 to 30°C, with an average temperature of 25.24°C, and salinity varied from 21.3 to 31.5 ppt, with a mean reading of 27.96 ppt (data collected daily by staff at the FSUCML). Oysters and predators were housed in cages constructed of 3.2 mm diamond plastic mesh cut to 30.5 × 45.7 cm pieces and used to construct semi-rigid cages that measured 9 cm tall, 37 cm long, and 18 cm wide. Two 25 cm floats were attached to the top of each cage so that the top of the cage would float even with the surface of the water. Both the cage design and location were motivated by common techniques used in off-bottom oyster aquaculture. Oysters used in all experiments were triploid seed purchased from a local hatchery. A random sample of 90 oysters measured prior to the experiment had a mean shell height (umbo to ventral shell margin) of 18.36 mm, ranging from 12.35 to 23.55 mm (interquartile range: 17.35 to 19.55 mm). Conchs were collected from oyster reefs adjacent to the FSUCML.

Since accurately measuring the shell height and thus growth of oysters can be difficult (Johnson & Smee 2012), we employed several methods to consider the effects of predators on growth and development. A subset of oysters was marked at the beginning of the experiment by filing a small triangular notch in the middle of their beak using an xx-slim taper file (Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m568p111\\_supp.pdf](http://www.int-res.com/articles/suppl/m568p111_supp.pdf)). This method, which allows one to measure the percent growth and daily specific growth rate of individual organisms by taking both initial and final shell height measurements, has previously been used for oysters and other mollusks (Robinson et al. 2007, Gosnell & Gaines 2012). Daily specific growth was calculated for shell height following equations used for area by Carroll & Finelli (2015). Although past work has demonstrated that an increased frequency of notching does not impact growth or mortality (Ford 1986), concerns that the method may impact growth still exist (Gosling 2003), and the method is not commonly used in NCE studies in oysters. For this reason, we compared final shell height, mass, and mortality in notched and unmarked oysters. Besides changes in shell height, we also measured the final total mass of each oyster and separate weights for shell and tissue. We then dried tissue and shell for 24 h in a 70°C drying oven to obtain weights of dry shell and dry tissue.

All analyses were conducted in R (R Core Team 2014). Data were manipulated and plotted using the reshape (Wickham 2007) and ggplot2 (Wickham

2009) packages. Geographic data were provided by Natural Earth ([www.naturalearthdata.com/about/terms-of-use/](http://www.naturalearthdata.com/about/terms-of-use/)) and read using the rgdal (Bivand et al. 2015) library.

### Impact of conch density, size, and biomass on oyster growth

In the first study, we explored how the size and density of crown conchs impacted oyster growth. To determine appropriate ranges for conch density and natural size variation, we sampled reefs adjacent to the FSUCML as well as reefs southeast of Wakulla Beach, Florida (Fig. 1) to determine natural variation. Sites were sampled at low tide to ensure all areas of oyster coverage, including sites that remained covered at low tide by less than 0.3 m of water, could be included. Approximately every 5 m along the entire length of each exposed reef during low tide a quadrat (1 m<sup>2</sup>) was haphazardly placed in regards to the width of the reef; reefs varied in width from 1 to 5 m wide. Care was taken to collect every crown conch within each quadrat. Using a Vernier caliper, the height (measured as the distance from the apex of the shell to the tip of the siphonal canal) of each conch shell was measured and recorded. Both oyster coverage and whether or not the area within the quadrat was submerged were also recorded.

Using these data, we decided to focus on five predator treatments: 1 small (<50 mm shell height, average biomass: 15.60 g) conch, 3 small (average total biomass: 44.81 g) conchs, 1 large (>70 mm shell

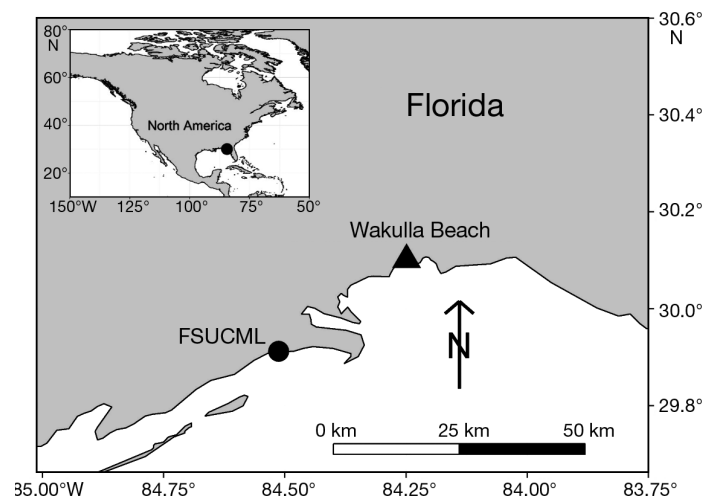


Fig. 1. Location of the field studies and predator (crown conch) survey sites on the northern coast of the Gulf of Mexico in Florida, USA. FSUCML: Florida State University Coastal and Marine Laboratory

height, average biomass: 99.48 g) conch, 3 large conchs (average total biomass: 185.42 g), and a no-conch control. This design allowed us to consider impacts of predator size (large vs. small), density, and biomass on oyster growth; a shell height–mass graph of conch data from conchs used in the experiment is also provided (Fig. S2 in the Supplement). Ten notched and 10 unmarked oysters were added to 20 floating cages that were subsequently attached to PVC pylons set in the local bay. Pylons were ~3 m long and were set in the sandy bottoms so that ~2 m extended above the water. Pylons were set in deep enough water so that all cages would remain submerged during normal tidal phases. All pylons were at least 3 m apart. A second cage (without floats) was attached to the bottom of each oyster cage (Fig. S3A in the Supplement). Predators were introduced into these cages (except for the no predator treatment). All bottom cages were also supplied with 5 oysters for predator consumption. A total of 4 replicate cages were constructed for each treatment (for a total of 20 cages).

Oysters were placed in the water on 1 April 2014, and predators were added a week later. The experiment lasted until 5 June 2014 for a total of 58 d of predator exposure. To reduce fouling on the cages, which can lead to reduced oyster growth and increased mortality, we followed standard aquaculture practice and removed all cages from the water for 24 h once per week. When fouling increased later in the summer months, we also lightly scrubbed the cages prior to removal from the water. Conchs were also checked for escape or mortality weekly and replaced as needed. Oysters in the cages with conchs were not replaced during the experiment in order to limit differences among cages in the amount of potential alarm cues or chemicals released during oyster consumption. However, oysters remained alive in most of the cages containing conchs, including cages associated with each treatment, suggesting conchs were not generally food-limited. Past work suggested impacts of conchs on caged oyster mortality are low (Hathaway 1958), possibly due to the difficulty conchs have in handling oysters that are not connected to a substrate. At the conclusion of the experiment, oysters were measured for final shell height, mass, and changes in shell height (or shell growth) for filed oysters. Tissue preparation was also carried out as noted above. Initial shell height was estimated by subtracting shell growth from final shell height, and we used this initial shell height to calculate a daily specific growth rate for filed oysters using the following formula:

$$\frac{\ln(\text{final shell height}) - \ln(\text{initial shell height})}{\text{Number of days exposure}} \quad (1)$$

We also calculated a shell thickness index for all oysters by dividing final shell height by oyster mass.

Initial shell heights for filed oysters were regressed against treatment and cage to determine if significant variation existed among treatments in initial oyster size. The impacts of treatment on oyster traits were analyzed in 2 ways. The overall effects of treatments (factors) were analyzed using linear mixed effect models to account for the potential for oysters in the same cage to have similar growth patterns (Zuur 2009). Impact of fixed factors was determined by comparing nested models fit by maximum likelihood using likelihood ratio tests in R using the lme4 and car packages (Fox & Weisburg 2011, Bates et al. 2012). If significant differences existed among treatments, planned post-hoc orthogonal contrasts focused on differences based on predator (1) presence (i.e. all treatments containing predators vs. control), (2) density (i.e. 3 predators vs. 1 predator), and (3) size (i.e. large predators vs. small predators) were carried out in the multcomp package (Hothorn et al. 2008). The impact of total predator biomass on traits was also considered in a separate model by regressing traits and mean predator biomass (average of predator masses in each set of cages at beginning and end of experiment). The impact of filing on oyster traits was also considered by including a variable to account for filed status into models comparing the final shell heights and masses of oysters; a similar binomial model was also employed to determine if filing influenced oyster mortality.

### Range of NCE

We used a similar experimental design to consider the potential distance at which predators may impact oyster growth. Four rows of 5 PVC pylons were deployed parallel to the shore. Pylons were spaced out by 0.5 m, meaning each row measured 2 m long (cages at 0, 0.5, 1.0, 1.5, and 2.0 m). Each row was at least 3 m from all other rows. We added 10 notched and 10 unmarked oysters to floating cages attached to each of these pylons. Separate floating cages containing 3 large (<70 mm total height) conchs were added to one end of each row (Fig. S3B,C in the Supplement). To ensure any differences in growth were not due to local circulation or other factors, predators were added to the alternating ends of adjacent rows.

Oyster cages were placed in the water on 8 April 2014, and predator cages were added on 10 April 2014. Cages were maintained as noted above. Oys-



ters were removed from the water on 14 July 2014 after 96 d. At the conclusion of the experiment, we again measured for final shell height, shell growth, and mass, and tissue preparation was carried out as noted above. We also calculated an initial shell height and daily specific growth rate for filed oysters and a shell thickness index for all oysters. To analyze the data, we used a linear mixed-effects model to regress distance from predators against oyster traits and compared this to a model that did not include distance using likelihood ratio tests. Random effects were included to consider similarities within cages and rows of the experiment. We also again considered the impact of filing oysters by including a variable to account for filed status into models focusing on changes in shell height and mass.

## RESULTS

### Predator surveys

Surveys conducted over 2 d at the FSUCML yielded over 100 crown conchs (2.79 per quadrat, mean shell height 53.1 mm), while surveys around Wakulla beach yielded only 7 crown conchs (0.128 per quadrat, mean shell height 59.1 mm). Conch sizes ranged from 31.3 to 79.5 mm (Fig. 2). Our size data were similar to earlier studies in the region (Bowling 1994).

### Biomass experiment

Oyster survival was high during the experiment (>89%), and oysters that died during the experiment were removed from all analyses. Linear models indicated no significant difference in initial oyster size among treatments ( $F_{4,159} = 1.234$ ,  $p = 0.298$ ) or cages ( $F_{19,144} = 1.528$ ,  $p = 0.0841$ ). Predator treatments had a substantial but not significant impact on final oyster shell height ( $\chi^2_4 = 8.977$ ,  $p = 0.062$ ) and percent dry mass in tissue ( $\chi^2_4 = 8.853$ ,  $p = 0.065$ ). For the planned post-hoc contrasts (impacts of predator presence, size, and density), significant negative impacts on final shell height were only noted based on predator presence, with predator density having a substantial but not significant effect. Shell height was not impacted by the size or biomass of predators (Table 1, Fig. 3). Percent dry mass in tissue did not differ among any of the planned contrasts.

All other examined traits, i.e. shell growth (calculated by measuring difference between filed mark and shell edge, Fig. S1 in the Supplement), daily spe-

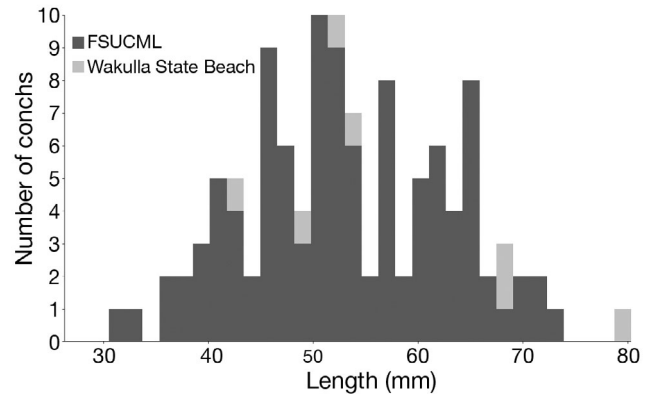


Fig. 2. Size distribution of crown conchs collected from the 2 survey sites. FSUCML: Florida State University Coastal and Marine Laboratory

cific growth rate, total mass, shell thickness index, shell dry mass, and tissue dry mass, differed significantly among treatments (Table 1, Fig. 3). Contrasts indicated that the presence of predators negatively impacted all traits except for shell thickness, which increased with predator presence (Table 1, Fig. 3). Increases in predator density led to significant decreases in shell growth, mass, dry shell mass, and dry tissue mass while significantly increasing shell thickness; predator density also had substantial but insignificant negative effects on shell height and daily growth rate. All other planned contrasts were insignificant, indicating predator size had no impacts (Table 1, Fig. 3). Higher total predator biomass led to significant increases in shell thickness indices and significant decreases in total mass and shell and tissue dry mass. There was no noticeable effect of filing the shell on height, mass, or mortality (respective results from these models:  $\chi^2_1 = 0.032$ ,  $p = 0.857$ ;  $\chi^2_1 = 0.0365$ ,  $p = 0.849$ ;  $\chi^2_1 = 0.8441$ ,  $p = 0.358$ ).

### Range of NCE

Minimal mortality was also observed in the range experiment, with only 1 out of 400 oysters dying. Linear models again indicated no significant difference in initial oyster size based on distance from predators ( $F_{1,176} = 1.9577$ ,  $p = 0.164$ ) or cages ( $F_{19,158} = 1.0467$ ,  $p = 0.4117$ ). The only measured trait that was significantly impacted by distance from predator was dry tissue mass, with dry tissue mass increasing with distance (impact of biomass; model coefficient = 0.043,  $\chi^2_1 = 0.4644$ ,  $p = 0.029$ ); all other traits were not impacted (shell height: coefficient =  $-0.946$ ,  $\chi^2_1 = 2.42$ ,  $p = 0.1174$ ; shell growth: coefficient =  $-0.1692$ ,  $\chi^2_1 = 0.024$ ,  $p = 0.878$ ; mass: coefficient =  $-1.599$ ,  $\chi^2_1 =$

Table 1. Impact of predator (crown conch) treatment on oyster traits. Significant relationships ( $p < 0.05$ ) are in **bold**. Units for estimates and coefficients indicated next to the trait name. Contrast estimates (Est.) are scaled to represent difference among group averages. Coefficients (Coef.) indicate relationship between biomass and traits

Trait	Treatment $\chi^2_4$	p	Presence (absent vs. present)		Size (large vs. small)		Density (multiple vs. single)		Biomass	
			Est.	z (p)	Est.	z (p)	Est.	z (p)	Coef.	$\chi^2_1$ (p)
Shell height (mm)	8.977	0.062	1.249	<b>2.126 (0.0335)</b>	0.747	1.351 (0.177)	-1.070	-1.936 (0.053)	-4.042 $\times 10^{-3}$	0.968 (0.325)
Shell growth (mm)	21.058	<b>&lt;0.001</b>	2.915	<b>4.119 (&lt;0.001)</b>	1.140	1.342 (0.089)	-1.597	<b>-2.380 (0.017)</b>	-7.302 $\times 10^{-3}$	2.335 (0.127)
Daily specific growth rate (ln(mm) d <sup>-1</sup> )	11.577	<b>0.021</b>	2.230 $\times 10^{-3}$	<b>23.101 (0.002)</b>	6.802 $\times 10^{-4}$	0.967 (0.333)	-1.298 $\times 10^{-3}$	-1.846 (0.065)	-6.886 $\times 10^{-6}$	2.011 (0.156)
Mass (whole, intact oysters) (g)	22.367	<b>&lt;0.001</b>	1.667	<b>5.564 (&lt;0.001)</b>	2.044 $\times 10^{-3}$	0.007 (0.994)	-0.907	<b>-3.277 (0.001)</b>	-7.467 $\times 10^{-3}$	<b>7.4847 (0.006223)</b>
Shell thickness index (mm g <sup>-1</sup> )	7.570	<b>0.011</b>	-0.543	-1.942 (0.052)	7.053 $\times 10^{-2}$	0.260 (0.794)	0.569	<b>2.102 (0.035)</b>	3.701 $\times 10^{-3}$	4.097 (0.043)
Shell mass (dry) (g)	23.281	<b>&lt;0.001</b>	1.263	<b>5.658 (&lt;0.001)</b>	-0.123	-0.586 (0.558)	-0.7195	<b>-3.446 (&lt;0.001)</b>	-6.447 $\times 10^{-3}$	10.032 (0.002)
Tissue mass (dry) (g)	13.388	<b>0.008</b>	2.032 $\times 10^{-2}$	<b>3.132 (0.002)</b>	-2.140 $\times 10^{-3}$	-0.347 (0.729)	-1.421 $\times 10^{-2}$	<b>-2.303 (0.021)</b>	-1.257 $\times 10^{-4}$	6.547 (0.011)
% dry mass in tissue	8.853	0.065	-1.178 $\times 10^{-3}$	1.765 (0.078)	1.960 $\times 10^{-4}$	0.303 (0.762)	3.910 $\times 10^{-4}$	0.605 (0.545)	3.964 $\times 10^{-6}$	0.968 (0.325)

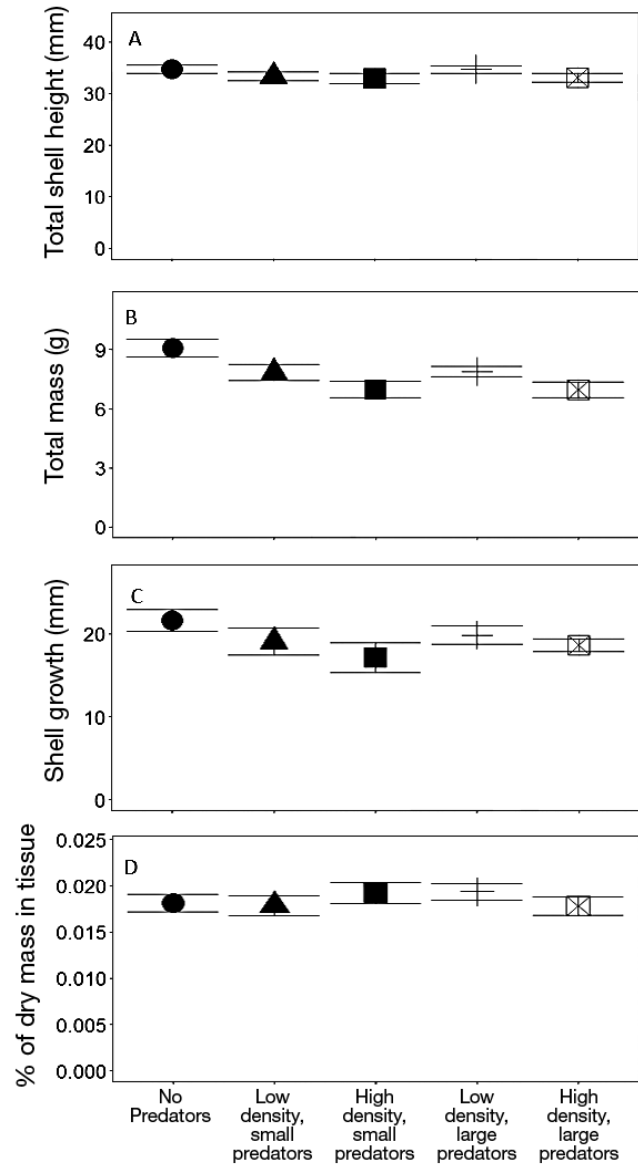


Fig. 3. Impact of predator treatments on oyster traits. Data points represent mean responses for each group; lines indicate 95% confidence intervals

1.440,  $p = 0.230$ ; shell thickness index: coefficient = 0.030,  $\chi^2_1 = 0.183$ ,  $p = 0.669$ ; daily growth rate: coefficient =  $2.84 \times 10^{-4}$ ,  $\chi^2_1 = 0.545$ ,  $p = 0.460$ ; dry mass of shells: coefficient =  $-0.488$ ,  $\chi^2_1 = 0.3471$ ,  $p = 0.558$ ; percent of dry mass in tissue: coefficient =  $-0.009$ ,  $\chi^2_1 = 0.231$ ,  $p = 0.631$ ). However, oysters did grow throughout the experiment. Analysis of notches indicated an average shell growth of 36.26 mm across the experiment, with an average final shell height of 49.86 mm. Filing of oysters was again found not to impact height ( $\chi^2_1 = 1.721$ ,  $p = 0.190$ ) or mass ( $\chi^2_1 = 1.651$ ,  $p = 0.120$ ). Mortality was not analyzed since only 1 individual died.

## DISCUSSION

These 2 studies examined how the NCE of predatory crown conchs on oyster growth varied based on (1) total predator biomass and how it was apportioned among individuals and (2) the proximity of prey to predators. In the study focusing on biomass, predator presence led to decreases in all measures of growth except for shell thickness, which increased in the presence of predators. These results indicate that the primary effect of predators was a decrease in growth. Changes in shell thickness due to predator presence have been observed in oysters and other bivalves (Freeman 2007, Johnson & Smee 2012), but past work on oysters and crown conchs have shown mixed impacts on shell thickness (Garland 2014, Garland & Kimbro 2015). Increasing shell thickness is also more commonly associated with a response to drilling predators as opposed to those that open bivalves, such as conchs. Contrary to predator density and total predator biomass, which had negative impacts on all traits except shell thickness, predator size had mixed impacts on measured growth traits and did not significantly impact any traits.

Since allocation of mass between shell and tissue did not change, it is possible the primary effect of conchs is to limit when oysters might open their valves to feed and thus reduce growth. Conchs may also cause oysters to alter the thickness of their shell, but since our index of shell thickness did not account for changes in shape, our results may be driven by changes in shell shape that occur as oysters develop. Future studies should incorporate direct measures of thickness and shape better than in our current project to consider these issues. Other studies of oyster responses to conchs have found limited evidence for reductions in shell mass (Garland 2014) that have also been attributed to changes in feeding patterns.

Other bivalves limit gaping in the presence of predators (Smee & Weissburg 2006). Limiting gaping may decrease feeding success of conchs and also may result in oysters filtering less water and thus growing less. Several traits of conchs may promote this behavioral response. Conchs (Hathaway & Woodburn 1961) and other predatory gastropods (Ferner & Weissburg 2005, Smee & Weissburg 2006) can locate prey even in turbid conditions, suggesting predator cues may be highly indicative to oysters of future predation risk. This may be especially true for crown conchs, which show high site fidelity to very specific, small areas (Hathaway 1958). Accordingly, we found the density of predators also impacted multiple oyster traits, with more predators leading to reduced

growth and mass in both shell and tissue, while the size of predators and total biomass impacted fewer traits.

Since the largest differences among treatments were based on the presence of predators as opposed to changes in density, our results indicate that NCE may operate primarily as a step-response, with the simple presence of predators leading to major changes that may be further modified by predator abundance. Predator density could have a large impact on NCE if it increased the number of close encounters between oysters and conchs. For example, contact with excretions released by conchs, as they move across substrates may be important cues, and an increasing number of close 'paths' would be expected when more conchs are present. Studies in other gastropods have also shown that mucus production does not scale linearly with size (Davies & Williams 1995) and that mucus constituents may play a role in chemical signaling (Kuanpradit et al. 2012). These hypotheses may explain why predator size and biomass had limited impacts.

Close encounters being important to the NCE of conchs on oysters could also explain the lack of difference in growth that we observed in the range experiment. While predator cages were housed beneath oyster cages in the biomass experiment, in the range study the predators were housed in a cage connected to the same pylon as the closest oysters (Fig. S3B). This setup was used to ensure movement did not differ among the various cages, since housing the predators on the bottom of one cage would have added extra weight to one cage and potentially impacted movement. This difference, however, also meant that the closest oysters were actually further from the predators than all oysters in the biomass experiment. If the chemical signal used to predict predation was quickly diluted over space or degraded in the environment, even these small changes in distances could have led to a lack of NCE.

An alternative explanation for our results in the range experiment may focus on the fact that oysters were caged for a longer period of time in the range experiment and thus may have reached a size refuge from which point growth was not impacted by predator presence. Oyster responses to predatory mud crabs are size-dependent. Oysters that are ~2 mm in shell height respond to these predators, while those 10–15 mm in shell height do not (Johnson & Smee 2012). We also found that the additional 38 d of growth for the range experiment led to mean final shell height differing among the experiments (33.80 in biomass experiment, 49.86 mm in range experi-



ment). However, crown conchs typically feed on and may prefer oysters that are larger than those used in our study (Garland & Kimbro 2015), suggesting that the oysters used in the 2 experiments would likely have the same response to conch predation cues despite their height differences. A third possibility is that the range of impact is greater than 2 m and all oysters were impacted similarly by the predator cages, but this seems unlikely given that we observed differences in growth in the first experiment with various treatment cages spread 3 m apart. The cage design used in the first experiment also may have allowed conchs to physically contact oysters with their proboscis, but given the small mesh size employed and 2 cage layers existing between predators and prey, in addition to the consistent movement of oysters by waves, we believe physical contact between the predators and prey was likely extremely limited. It should also be noted that while our treatments allowed us to control long-term, consistent exposure to predators, individual differences in growth may be due to the presence of other predators. For example, we have occasionally observed blue crabs *Callinectes sapidus* sitting on oyster cages in the bay and elsewhere along the coast, and small mud crabs (likely *Panopeus* sp.) may be found in cages. However, it again seems unlikely this was a major difference between the 2 studies.

We consider it most likely that NCE between oysters and conchs do not occur over large distances and require concentrated chemical cues to initiate. However, the changes in growth we observed suggest that NCE of conchs on oysters may reduce growth on reefs especially since conchs are known to remain in small areas on reefs (Hathaway 1958). These results add to current work on the impacts of conchs on reefs and increase our overall understanding of how NCE may structure oyster reef communities. If conchs slow the growth of oysters by limiting their ability to filter water and feed, NCE may directly reduce the growth of reefs and lead to oysters that are less prepared to deal with other environmental stressors. This may be extremely important given the water issues facing the region and could greatly increase the known impact of predatory conchs. Future studies may wish to more closely consider the range of these effects over very small scales to determine how far they extend from predators, the chemical identity of the cue used by oysters to estimate predation risk, and how NCE change throughout prey development and with predator exposure patterns (Trussell et al. 2011).

The noticeable impacts of predators on growth in our first study also suggest NCE may have ramifica-

tions for oyster aquaculture. For example, oysters reared in the presence of multiple predators (high density treatments) grew 3.53 mm less (shell height measured via notches) than those grown in the absence of predators. Oysters exposed to cues from multiple predators also added 2.12 g less in total mass during the 2 mo experiment. These changes could have major impacts on growth rates for both natural and aquacultured oysters. Although growth rate varies widely based on size, temperature, and other factors, rates of  $\sim 8 \text{ mm mo}^{-1}$  change in shell height were the maximum average growth rates observed in recent studies of off-bottom culture methods in the northern Gulf of Mexico (Leonhardt 2013, for oysters beginning in the 40–50 mm range), which closely matched our results for the biomass experiment. Similarly, recent summaries of growth in the region suggest initial growth rates may approach  $10 \text{ mm mo}^{-1}$  for newly settled spat (Florida Fish and Wildlife Commission 2013). If we assume  $10 \text{ mm mo}^{-1}$  is a high estimate for monthly growth rate, our changes in growth suggest consistent exposure to predators could reduce growth up to 18% and thus increase time needed for oysters to reach minimum size limits for harvesting wild oysters or optimal sizes preferred by aquaculturists. Losses in oyster mass would similarly impact the catch of fishermen and work of shucking houses relying on wild or planted bottom-cultured oysters.

While our combined studies suggest that predators may impact oyster growth only when they are extremely close, this is the scenario that exists when predators rest in or on cages, as we observed on both our study cages and at local aquaculture sites, or that occurs when conchs invade local reefs. Many aquaculture designs also house multiple cages together, similar to the design we used in our first experiment, meaning a predator invading one cage may cause NCE on oysters in adjacent cages until they are removed. Obviously, the extent of impact will depend on both the actual exposure time and how long NCE last when predators leave a cage, but this suggests that aquaculture operations should at least consider the influence of predators and potentially attempt to avoid areas near natural reefs that may harbor large predator populations in order to reduce exposure to predators that are commonly confined to reef areas. Sampling predator densities and occurrences at aquaculture sites would also be useful in understanding the impacts of NCE on aquaculture operations and build on work on quantifying diversity in oyster gardens (Marengi & Ozbay 2010). While predator presence only slows growth with minimal impacts on

mortality, longer growth times could increase mortality due to disease exposure or increase the chance of cages being lost in storms. Alternatively, these effects could prove useful in managing growth rates and future survival rates. Although work in other species (Jarvi & Uglem 1993, Gaudioso et al. 2011), including other cultured bivalves (Brokordt et al. 2011, Robinson et al. 2014), has shown that exposure to predator cues can induce traits that benefit survival in released organisms, we generally did not note changes in traits that support this NCE in oysters, especially given the noted issues with our shell thickness index and lack of difference in allocation among tissues based on predator treatments. However, we did not carry out predation trials following this work to fully assess if differences in predation rates existed based on exposure.

The impact of NCE may also differ based on available resources and base metabolic needs. For oysters in particular, NCE may differ between triploid oysters that do not produce gametes (such as those used in this project) and diploid populations. Triploid oysters typically grow faster than diploid oysters since energy is not expended on gamete production, but this could potentially lead to NCE having (1) a larger effect if predator presence led to a decrease in all growth or (2) a smaller effect if the larger availability of energy allowed triploid oysters to continue growing while simultaneously adjusting behavior or morphology to account for predator presence. Differences in energy allocation may also lead to diploid and triploid oysters employing different strategies for dealing with predation, with larger energy stores encouraging hurried growth in triploid oysters (Touchon et al. 2013) and limited energy availability instead favoring the development of defensive phenotypes or behaviors (e.g. shell thickening, reductions in gaping) in diploids. These issues may be essential to considering how NCE will affect natural and modified organisms.

These experiments also demonstrated that notching oyster shells to easily monitor and measure oyster growth has no significant impact on measured morphological traits or mortality. We suggest that notching can be used as an inexpensive, quick method of marking growth for oysters in studies of NCE and other areas where growth is important. Although not demonstrated here, use of sequential or systematic notches would enable growth to be measured over time and removes issues associated with the loss of tags or other markers used to identify organisms.

In conclusion, the results from our 2 studies add to the growing literature on how NCE are influenced by

common variation in predator communities and suggest that size- and density-specific responses for both predators and prey should be considered but may not always exist. Changes in the risk prey perceive may be impacted differentially by predator presence, size, density, and biomass, and these factors may need to be explored independently to understand what cues prey are using and how the size- and density-structure of predator populations impacts cue production. Recent work on identifying chemical cues suggests methods for pursuing these research questions (Decho et al. 1998, Ferrer & Zimmer 2007). Studies building upon this work could focus on changes in non-consumptive interactions throughout biological development and may wish to consider how impacts of biomass and range differ among predators. Past results suggest some responses may be predator-specific, possibly due to attack mode or change in predation risk based on density and size (Freeman 2007, Johnson & Smee 2012, Robinson et al. 2014). For example, crabs and fish may be faster than conch predators, and thus prey may be selected to respond to their presence at a greater distance (and thus be more responsive to biomass) using behavioral responses, while the threat of conchs and their speed may dictate responding to nearby threats only. Site fidelity of predators may also be important. Future studies should also consider how non-consumptive interactions change throughout biological development. Translating short-term measures, especially those observed in experimental settings, to real-world impacts remains the greatest challenge in determining the true importance of NCE. However, work in natural systems continues to suggest their importance (Berger 2007, Kuijper et al. 2013), and here we documented the existence of these effects in field conditions and demonstrated their potential impact on aquaculture programs.

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#### LITERATURE CITED

- Bates D, Maechler M, Bolker B, Walker S (2015). lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-9. <https://CRAN.R-project.org/package=lme4>
- Beck MW, Brumbaugh RD, Airolidi L, Carranza A and others (2011) Oyster reefs at risk and recommendations for conservation, restoration, and management. *Bioscience* 61: 107–116

- Berger J (2007) Fear, human shields and the redistribution of prey and predators in protected areas. *Biol Lett* 3:620–623
- Bivand R, Keitt T, Rowlingston B (2015) rgdal: bindings for the Geospatial Data Abstraction Library. R package version 1.0-7. <https://CRAN.R-project.org/package=rgdal>
- Bowling C (1994) Habitat and size of the Florida crown conch (*Melongena corona* Gmelin): why big snails hang out at bars. *J Exp Mar Biol Ecol* 175:181–195
- Brokordt KB, Núñez GA, Gaymer CF (2011) Improving escape responses of hatchery-reared scallops *Argopecten purpuratus*. *Mar Biol* 158:1311–1318
- Carbone C, Gittleman JL (2002) A common rule for the scaling of carnivore density. *Science* 295:2273–2276
- Carroll JM, Finelli CM (2015) Impacts of the ectoparasitic snail *Boonea impressa* on growth of postset juvenile oysters. *J Molluscan Stud* 81:161–163
- Chivers DP, Mirza RS, Bryer PJ, Kiesecker JM (2001) Threat-sensitive predator avoidance by slimy sculpins: understanding the importance of visual versus chemical information. *Can J Zool* 79:867–873
- Cresswell W, Lind J, Quinn JL (2010) Predator-hunting success and prey vulnerability: quantifying the spatial scale over which lethal and non-lethal effects of predation occur. *J Anim Ecol* 79:556–562
- Davies MS, Williams GA (1995) Pedal mucus of a tropical limpet, *Cellana grata* (Gould): energetics, production and fate. *J Exp Mar Biol Ecol* 186:77–87
- Decho AW, Browne KA, Zimmer-Faust RK (1998) Chemical cues: why basic peptides are signal molecules in marine environments. *Limnol Oceanogr* 43:1410–1417
- Dixon DL, Munday PL, Jones GP (2010) Ocean acidification disrupts the innate ability of fish to detect predator olfactory cues. *Ecol Lett* 13:68–75
- Eurich JG, Selden RL, Warner RR (2014) California spiny lobster preference for urchins from kelp forests: implications for urchin barren persistence. *Mar Ecol Prog Ser* 498:217–225
- Ferner MC, Weissburg MJ (2005) Slow-moving predatory gastropods track prey odors in fast and turbulent flow. *J Exp Biol* 208:809–819
- Ferrari MCO, Messier F, Chivers DP (2006) The nose knows: Minnows determine predator proximity and density through detection of predator odours. *Anim Behav* 72: 927–932
- Ferrer RP, Zimmer RK (2007) The scent of danger: arginine as an olfactory cue of reduced predation risk. *J Exp Biol* 210:1768–1775
- Florida Fish and Wildlife Commission (2013) 2012–2013 Florida Gulf Coast Oyster Disaster Report. [www.floridajobs.org/docs/default-source/2015-community-development/2015-cmyt-plan-acsc/20122013floridagulfcoast-oysterdisasterreport.pdf?sfvrsn=2](http://www.floridajobs.org/docs/default-source/2015-community-development/2015-cmyt-plan-acsc/20122013floridagulfcoast-oysterdisasterreport.pdf?sfvrsn=2)
- Ford SE (1986) Effect of repeated hemolymph sampling on growth, mortality, hemolymph protein and parasitism of oysters, *Crassostrea virginica*. *Comp Biochem Physiol Part A Physiol* 85:465–470
- Fox J, Weisburg S (2011) An R companion to applied regression, 2nd edn. Sage, Thousand Oaks, CA
- Freeman AS (2007) Specificity of induced defenses in *Mytilus edulis* and asymmetrical predator deterrence. *Mar Ecol Prog Ser* 334:145–153
- Garland HG (2014) Investigating the causes of sudden spatial shifts in oyster (*Crassostrea virginica*) abundance and traits in northeast Florida. Florida State University, Tallahassee, FL
- Garland HG, Kimbro DL (2015) Drought increases consumer pressure on oyster reefs in Florida, USA. *PLOS ONE* 10: e0125095
- Gaudioso VR, Sanchez-Garcia C, Perez JA, Rodriguez PL, Armenteros JA, Alonso ME (2011) Does early antipredator training increase the suitability of captive red-legged partridges (*Alectoris rufa*) for releasing? *Poult Sci* 90: 1900–1908
- Gosling E (2003) Bivalve molluscs: biology, ecology and culture, 1st edn. Wiley-Blackwell, Oxford
- Gosnell JS, Gaines SD (2012) Keystone intimidators in the intertidal: non-consumptive effects of a keystone sea star regulate feeding and growth in whelks. *Mar Ecol Prog Ser* 450:107–114
- Grabowski JH, Hughes AR, Kimbro DL, Dolan MA (2005) How habitat setting influences restored oyster reef communities. *Ecology* 86:1926–1935
- Griffin AS, Blumstein DT, Evans CS (2000) Training captive-bred or translocated animals to avoid predators. *Conserv Biol* 14:1317–1326
- Hathaway RR (1958) The crown conch, *Melongena corona* Gmelin; its habits, sex ratios, and possible relations to the oyster. *Proc Natl Shellfish Assoc* 48:189–194
- Hathaway RR, Woodburn KD (1961) Studies on the crown conch *Melongena Corona* Gmelin. *Bull Mar Sci* 11:45–65
- Havens K, Allen M, Camp E, Irani T and others (2013) Apalachicola Bay oyster situation report. Florida Sea Grant College Program, Technical Publication TP-200, Gainesville, FL
- Hayes KA (2003) Phylogeography and evolution of the Florida crown conch (*Melongena corona*). University of South Florida, Tampa, FL
- Held MBE, Harley CDG (2009) Responses to low salinity by the sea star *Pisaster ochraceus* from high- and low-salinity populations. *Invertebr Biol* 128:381–390
- Hill JM, Weissburg MJ (2013) Predator biomass determines the magnitude of non-consumptive effects (NCEs) in both laboratory and field environments. *Oecologia* 172: 79–91
- Holt RD, Grover J, Tilman D (1994) Simple rules for interspecific dominance in systems with exploitative and apparent competition. *Am Nat* 144:741–771
- Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. *Biom J* 50:346–363
- Jarvi T, Uglem I (1993) Predator training improves the anti-predator behaviour of hatchery reared Atlantic salmon (*Salmo salar*) smolt. *Nord J Freshw Res* 68:63–71
- Johnson KD, Smee DL (2012) Size matters for risk assessment and resource allocation in bivalves. *Mar Ecol Prog Ser* 462:103–110
- Johnson KD, Smee DL (2014) Predators influence the tidal distribution of oysters (*Crassostrea virginica*). *Mar Biol* 161:1557–1564
- Kimbro DL (2012) Tidal regime dictates the cascading consumptive and nonconsumptive effects of multiple predators on a marsh plant. *Ecology* 93:334–344
- Kuanpradit C, Stewart MJ, York PS, Degnan BM and others (2012) Characterization of mucus-associated proteins from abalone (*Haliotis*)—candidates for chemical signaling. *FEBS J* 279:437–450
- Kuijper DPJ, de Kleine C, Churski M, van Hooft P, Bubnicki J, Jędrzejewska B (2013) Landscape of fear in Europe: Wolves affect spatial patterns of ungulate browsing in Białowieża Primeval Forest, Poland. *Ecography* 36: 1263–1275

- ✦ Kusch RC, Mirza RS, Chivers DP (2004) Making sense of predator scents: investigating the sophistication of predator assessment abilities of fathead minnows. *Behav Ecol Sociobiol* 55:551–555
- Leonhardt JM (2013) An evaluation of oyster stocks, grow-out conditions, and off-bottom culture methods for increasing commercial production of eastern oysters (*Crassostrea virginica*) in the northern Gulf of Mexico. Master's thesis, Louisiana State University, Baton Rouge, LA
- ✦ Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640
- ✦ Marenghi F, Ozbay G (2010) Preliminary habitat assessment of floating oyster (*Crassostrea virginica*) gardens (Delaware). *Ecol Restor* 28:254–257
- ✦ Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH (2007) Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* 315:1846–1850
- ✦ Orrock JL, Grabowski JH, Pantel JH, Peacor SD, Peckarsky BL, Sih A, Werner EE (2008) Consumptive and non-consumptive effects of predators on metacommunities of competing prey. *Ecology* 89:2426–2435
- ✦ Paine RT (1976) Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. *Ecology* 57:858–873
- ✦ Peckarsky BL, Abrams PA, Bolnick DI, Dill LM and others (2008) Revisiting the classics: considering nonconsumptive effects in textbook examples of predator–prey interactions. *Ecology* 89:2416–2425
- ✦ Preisser EL, Bolnick DI, Benard MF (2005) Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology* 86:501–509
- R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- ✦ Robinson TB, Govender A, Griffiths CL, Branch GM (2007) Experimental harvesting of *Mytilus galloprovincialis*: Can an alien mussel support a small-scale fishery? *Fish Res* 88:33–41
- ✦ Robinson EM, Lunt J, Marshall CD, Smee DL (2014) Eastern oysters *Crassostrea virginica* deter crab predators by altering their morphology in response to crab cues. *Aquat Biol* 20:111–118
- ✦ Selden R, Johnson AS, Ellers O (2009) Waterborne cues from crabs induce thicker skeletons, smaller gonads and size-specific changes in growth rate in sea urchins. *Mar Biol* 156:1057–1071
- ✦ Smee DL, Weissburg MJ (2006) Clamming up: environmental forces diminish the perceptive ability of bivalve prey. *Ecology* 87:1587–1598
- ✦ Smee DL, Ferner MC, Weissburg MJ (2008) Alteration of sensory abilities regulates the spatial scale of nonlethal predator effects. *Oecologia* 156:399–409
- ✦ Smith DW, Drummer TD, Murphy KM, Guernsey DS, Evans SB (2004) Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995–2000. *J Wildl Manag* 68:153–166
- ✦ Touchon JC, McCoy MW, Vonesh JR, Warkentin KM (2013) Effects of plastic hatching timing carry over through metamorphosis in red-eyed treefrogs. *Ecology* 94: 850–860
- ✦ Trussell GC, Matassa CM, Luttbeg B (2011) The effects of variable predation risk on foraging and growth: Less risk is not necessarily better. *Ecology* 92:1799–1806
- ✦ Turner AM, Montgomery SL (2003) Spatial and temporal scales of predator avoidance: experiments with fish and snails. *Ecology* 84:616–622
- ✦ Van Buskirk J, Arioli M (2002) Dosage response of an induced defense: How sensitive are tadpoles to predation risk? *Ecology* 83:1580–1585
- Walton WC, Davis JE, Supan JE (2013) Off-bottom culture of oysters in the Gulf of Mexico. Southern Regional Aquaculture Center, Stoneville, MS
- ✦ Whetstone JM, Eversole AG (1981) Effects of size and temperature on mud crab, *Panopeus herbstii*, predation on hard clams, *Mercenaria mercenaria*. *Estuaries* 4:153–156
- ✦ Wickham H (2007) Reshaping data with the reshape package. *J Stat Softw* 21:1–20
- Wickham H (2009) ggplot2: elegant graphics for data analysis. Springer-Verlag, New York, NY
- Zuur AF (2009) Mixed effects models and extensions in ecology with R. Springer-Verlag, New York, NY

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