Vol. 507: 197–206, 2014
doi: 10.3354/meps10815

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published July 17

Omnivory dampens trophic cascades in estuarine communities

Keith D. Johnson[1,*], Jonathan H. Grabowski[2], Delbert L. Smee[3]

[1]Department of Biological Sciences, Stevenson University, 1525 Greenspring Valley Road, Stevenson, MD 21153, USA
[2]Marine Science Center, Northeastern University, 430 Nahant Road, Nahant, MA 01908, USA
[3]Department of Life Sciences, Texas A&M University – Corpus Christi, 6300 Ocean Dr., Corpus Christi, TX 78412, USA

ABSTRACT: Predators often have large effects on prey populations and entire communities, but the nature of top-down control in speciose food webs is often difficult to assess due to consumer interactions such as complementarity, predator interference, and omnivory. To assess how top and intermediate predators affect community structure, we used predator exclusion experiments designed to isolate predator effects at different trophic levels in a species-rich community. Using oyster *Crassostrea virginica* reefs as a model system, predators were excluded using mesh-covered cages with openings of 1.0 cm^2 (small mesh) to exclude all potential oyster predators, 5.0 cm^2 (large mesh) to allow intermediate consumers but not large predators to access oyster reefs, and controls with complete predator access. Natural oyster settlement and survival were greatest in the small mesh cage when oysters were completely protected from consumers. Meanwhile, abundances of adult *Panopeus herbstii*, the Atlantic mud crab, an intermediate consumer and known oyster predator, were an order of magnitude greater in the large-mesh cage than in the other treatments. Oyster survival did not differ between the large-mesh cage and controls, suggesting that top predators such as blue crabs *Callinectes sapidus* and sheepshead *Archosargus probatocephalus* are likely consuming mud crabs (or inducing mud crabs to avoid controls) and consuming juvenile oysters on these oyster reefs. Top-down processes are known to be important on oyster reefs, but in this system, omnivory can overwhelm density-mediated cascading effects of top predators. We also found mud crabs to induce oysters to grow heavier shells and less soft tissue. Efforts to model the direct and indirect effects of predators on ecological communities will benefit from a more thorough understanding of the relative strength of omnivory on cascading effects of top predators.

KEY WORDS: *Crassostrea virginica* · Indirect effects · Lethal and non-lethal effects · Mud crabs · Predator–prey interactions · Food web · Top-down

INTRODUCTION

Many communities are structured by top-down forces, so that one species or a guild of consumers controls the populations of lower trophic levels (Paine 1966, Estes & Palmisano 1974, Menge 2000, Trussell et al. 2003, Grabowski 2004). Predators may also affect the abundance and distribution of organisms at several trophic levels by initiating trophic cascades (Carpenter et al. 1985). Trophic cascades occur when predators prey on intermediate consumers, thereby alleviating predation pressure on lower trophic levels that intermediate consumers prey on. Trophic cascades have been demonstrated in a wide array of terrestrial and aquatic ecosystems (Carpenter et al. 1985, Beckerman et al. 1997, Schmitz et al. 1997) and are thought to be particularly strong in marine benthic systems (Shurin et al. 2002). Yet, experiments that manipulate the presence of entire trophic levels are needed to augment our under-

---

*Corresponding author: kdjohnson@stevenson.edu standing of the degree to which top-down forces and trophic cascades structure communities (Stachowicz et al. 2007).

Predators mediate community structure via 2 distinct mechanisms: lethal or consumptive effects where predators consume prey (Paine 1966, Estes & Palmisano 1974, Trussell et al. 2003) and non-lethal or non-consumptive effects where predators alter prey traits such as foraging behavior or habitat selection (Trussell et al. 2003, Werner & Peacor 2003, 2006). Both lethal and non-lethal effects can have large effects on community structure and function (Grabowski 2004, Okuyama & Bolker 2007). For instance, when a predator induces prey to move less or emigrate from one field patch or stream section to another, both local and remote communities are influenced (Orrock et al. 2008). Developing a more holistic understanding of how lethal and non-lethal effects of top predators collectively influence intermediate and basal trophic levels remains a central challenge to community ecology, particularly in speciose systems when top-down forcing is maintained by multiple predator species and/or when these predators feed at multiple trophic levels. Most food webs are species rich, and examining the direct and indirect effects of predators in these systems is of particularly importance.

In situations where top-down forces are maintained by multiple predator species, top-down forces may be strengthened if predators complement one another to more effectively reduce populations of lower trophic levels (Nilsson et al. 2006, Huhta et al. 1999, Burkepile & Hay 2008). Trophic cascades could be dampened if top consumers themselves are omnivorous and feed at multiple trophic levels (O'Connor et al. 2008). Interestingly, the effects of predator interference on trophic cascades may differ depending upon whether the cascade results from direct consumption or from an alteration of prey behavior. Trophic cascades that are driven by lethal or density-mediated interactions would be dampened when predators interfere with each other and predation is reduced (Sih et al. 1998, Grabowski et al. 2008). In contrast, prey responses to multiple predator species and subsequent behaviorally mediated trophic cascades would perhaps be less likely to change regardless of whether predators interfere with or complement each other (O'Connor et al. 2013). These types of interactions are best tested in speciose communities so that effects of predators on multiple trophic levels can be assessed.

We selected oyster reefs as a model to test the strength of top-down forcing and trophic cascades on basal resources because oyster reef fauna are diverse and include numerous top predators, several of which are omnivorous (feeding at multiple trophic levels). Oyster reefs have been used as a model system to study the relative importance of non-lethal and lethal predator effects and to demonstrate the importance of animal behavior in mediating trophic cascades (Grabowski 2004, Grabowski et al. 2005, O'Connor et al. 2008). Specifically, higher-order consumers such as toadfish *Opsanus tau* and blue crabs *Callinectes sapidus* cause Atlantic mud crabs *Panopeus herbstii*, an abundant intermediate consumer on oyster reefs, to seek refuge and forgo foraging on juvenile oysters *Crassostrea virginica* and other bivalve species (Grabowski 2004, Grabowski et al. 2005). However, these trophic cascades may be dampened when consumers such as blue crabs or stone crabs *Menippe mercenaria* exhibit omnivory (feed at multiple trophic levels) and intra-guild predation (O'Connor et al. 2008; but see Grabowski et al. 2008) as well as in systems where more selective predators such as toadfish are less prevalent.

We manipulated oyster reefs in the field to test if excluding top and intermediate predators influenced the strength of trophic cascades and affected oyster reef community structure. The experiment had 2 goals: (1) to determine how access by different trophic levels of predators would affect juvenile oyster abundance and (2) to determine if a change in the abundance of intermediate predators would affect oyster growth and resource allocation.

MATERIALS AND METHODS

The experiments were performed in Corpus Christi Bay near Port Aransas, Texas, on intertidal oyster reefs. The reefs are bordered by salt marsh and seagrass habitats and are typical of oyster reefs in the general area. These reefs receive little freshwater input, and the water is exchanged by tides (~0.5 m) through the nearby Port Aransas ship channel. The average water temperature during the experiments was 28.6°C, and the average salinity was 31 as measured on the practical salinity scale.

Exclusion experiment

We used a predator exclusion experiment to ascertain how the absence of higher-order consumers would influence the prevalence of mud crabs and the settlement and survival of juvenile oysters *Crass-*

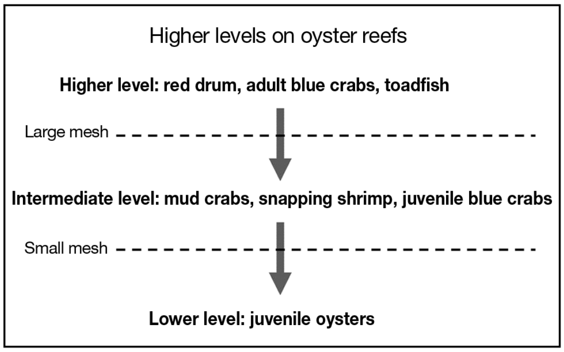

Fig. 1. Diagram of expected exclusion of predators by cage mesh size (large: 5 cm^2; small: 1 cm^2)

ostrea virginica. Predator exclusion cages were constructed from 2 × 2 inch (1 inch ≈ 2.54 cm) lumber, were 0.5 m × 0.5 m × 0.25 m tall, and were completely covered (i.e. top, bottom, and sides) with Vexar mesh of 1 of 2 mesh sizes (1.0 cm^2 and 5.0 cm^2) to exclude different sizes of predators (Fig. 1). Ten liters of sun-bleached oyster shells were placed inside each cage and control to create reef habitat and mimic the structural complexity of natural oyster reefs in the study area. Cages with only 2 perpendicular sides covered in mesh were used as controls, and we placed 1 cage control along with 1 cage covered with each mesh size in the field within existing oyster reefs to create an experimental block of 3 treatments (2 cages + 1 control = 1 block). We cleared 0.25 m^2 sections of oyster clumps and loose shells within natural oyster reefs to create openings for the cages and controls. The cages and controls were anchored flush with the sediment using rebar. Within blocks, cages or controls were spaced ~5.0 m apart, and their placement relative to each other was randomly assigned. Ten blocks were placed in the field, and the blocks were separated by at least 100 m. The exclusion experiment was in the field from August through November 2008.

Oyster reefs in the Western Gulf of Mexico, including those used in this study, are inhabited by a wide diversity of resident and transient top predators, such as adult blue crab, red drum *Sciaenops occelatus*, black drum *Pogonias cromis*, toadfish, and sheepshead *Archosargus probatocephalus*. All of these species are abundant in the study system and routinely collected by the Texas Parks and Wildlife Department as part of their monitoring of coastal fisheries populations (www.tpwd.state.tx.us/landwater/land/maps/gis/ris/catch_rate/). Both the large and small mesh-covered cages excluded these larger predators, so that they could only access the uncaged control treatment. Several intermediate predators such as mud crabs, snapping shrimp *Alpheus heterochaelis*, juvenile blue crabs, and juvenile Gulf stone crabs *Menippe adina* also inhabit oyster reefs. The small mesh cage excluded the majority of these intermediate predator species, but they were capable of accessing the control and larger mesh cages. By excluding both intermediate and top predators, the small mesh cage allowed us to quantify the survival of juvenile oysters free from predation pressure (Fig. 1). Meanwhile, the large mesh cage tested whether intermediate predators that are unchecked by top predators suppress survival of juvenile oysters. Finally, the uncaged control tested if top predators indirectly benefited oyster survival by suppressing intermediate predators or, alternatively, if top predators were omnivorous and consumed both intermediate predators and basal oyster prey. The cage treatments were unable to exclude some potential oyster predators, such as the flatworm *Stylochus* sp. as well as parasites, including *Perkinsus marinus*. However, we would not expect their abundance to differ among caging treatments within blocks.

We controlled for cage artifacts using a 2-sided cage. In spring 2008, we performed a preliminary experiment to determine if the 2-sided cage was an appropriate control for cage artifacts. In this experiment, we placed 10 l of sun bleached oyster shells into cages with 2 perpendicular sides covered with small mesh and onto trays without cages and deployed those within existing oyster reefs in pairs. Within pairs, the 2-sided cage and control were ~5 m apart, and pairs were separated by at least 100 m. Ten pairs of 2-sided cages and controls were placed into the field from April until June 2008. Oyster recruitment and reef fauna collected in 2-sided controls and control cages without sides were not significantly different, indicating that the 2-sided control is appropriate to control for caging artifacts (see 'Results').

At the conclusion of the cage deployment, the number of oyster spat and other sessile species (e.g. mussels) were counted and the associated reef fauna collected using a modified throw trap (for similar methods, refer to Rozas & Minello 1997). The throw trap was constructed using a 1.0 m^2 metal frame covered with fine mesh and fitted with a sharp metal skirt. Immediately prior to cage retrieval, we placed the throw trap over the cage and pressed it into the sediment to trap all mobile organisms. We then removed the cage or tray and jostled it in the water to dislodge mud crabs and other organisms. All shell material was thoroughly searched by hand, and any remaining organisms were collected. Then, we swept the throw trap with nets (0.5 mm mesh size) until no organisms were retrieved for 3 consecutive net passes. Organisms were then placed in 10% formalin and transported to the lab for sorting, identification, measurement, and enumeration. We also counted the number of oyster spat that naturally settled on the shells. Since our treatments were deployed in the field in a block design, we were concerned that this sampling could disturb other treatments in the block. To account for this potential artifact, we used multiple throw traps so that all cages within blocks or pairs were covered by a trap simultaneously. This technique was performed in June 2008 to collect organisms inside the 2-sided cages and control trays and again in November 2008 to sample fauna in cages with different mesh sizes and controls.

In the caging experiment, mud crabs were the most common intermediate predator collected (Fig. 2) and are known to be important predators of newly settled oysters and other bivalves (Grabowski 2004, Grabowski et al. 2005). Abundance of mud crabs and other intermediate predators collected were compared using separate 1-way blocked ANOVAs with cage treatment as a fixed factor in the model (Sokal & Rohlf 1995). Tukey-Kramer post hoc tests were used to compare pairwise differences among treatments (Day & Quinn 1989). We divided Atlantic mud crabs *Panopeus herbstii* into 2 size classes: <10 mm carapace width and >10 mm carapace width and compared abundances of these different size classes using separate ANOVAs. We analyzed *P. herbstii* abundance in this manner because larger mud crabs are known predators of oysters and other bivalves and smaller mud crabs did not consume juvenile oysters in preliminary experiments (K. D. Johnson unpubl. data).

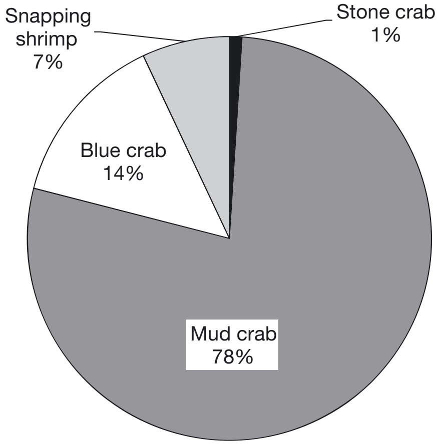

Fig. 2. Relative abundance of intermediate predators collected. Percentages reflect the total of each species collected in all caging treatments combined. Mud crab: all species of mud crab

In addition to intermediate predators, we counted the number of juvenile oysters (<10 mm) that were found on the 10 l of shells in each treatment. The number of juvenile oysters per treatment was compared using a 1-way blocked ANOVA with cage treatment as a fixed factor (Sokal & Rohlf 1995). Tukey-Kramer post hoc tests were used to compare pairwise differences among treatments (Day & Quinn 1989).

Oyster predation experiment

We performed a mark-recovery cage experiment to determine how predation on pre-settled juvenile oysters would be influenced by predator access resulting from each mesh size. Oyster larvae were purchased from a local supplier and settled onto sun-bleached oyster shells. After the larvae settled, they were given ambient seawater and allowed to grow until they reached ~2 mm in diameter. We then removed excess oyster larvae from each shell to reduce the number of juveniles to 10. These shells were then individually attached to rebar and deployed onto existing oyster reefs in our study site. The rebar was pressed into the sediment so that the shells were at a similar height as other shells on the reef. We placed individual shells in a block design with 3 treatments to correspond to the caging study: no cage (control), 1.0 cm^2 mesh cage (small) and 5.0 cm^2 mesh cage (large). Ten blocks were deployed so that treatments within blocks were ~5.0 m apart and blocks were ~100 m apart. The shells were recovered after 1 wk, and the number of juvenile oysters remaining was counted and compared between caging treatments using a 1-way blocked ANOVA with cage treatment as a fixed factor in the model (Sokal & Rohlf 1995). Tukey-Kramer post hoc tests were used to compare pairwise differences among treatments (Day & Quinn 1989). The study was performed once in September 2009.

Non-lethal effects of mud crabs on juvenile oysters

We performed a field experiment to elucidate the non-lethal effects of mud crabs on juvenile oysters. Oysters produce heavier shells and less soft tissue in the presence of Atlantic mud crabs (Johnson & Smee 2012), and we wanted to know if an increase in mud

Table 1. Intermediate predator abundance and average size by treatment. No. of ind. indicates total number of individuals collected. Atlantic mud crabs *Panopeus herbstii*, values in **bold**, are the only intermediate predator whose abundance differed significantly between caging treatments. Ten replicates of each caging treatment were performed

Common name	Species	Control		Small mesh		Large mesh		Total	
		No. of ind.	Avg. size (mm)	No. of ind.	Avg. size (mm)	No. of ind.	Avg. size (mm)	No. of ind.	Avg. size (mm)
Snapping shrimp	*Alpheus heterochaelis*	77	21.4	170	21.9	102	21.4	349	21.6
Blue crab	*Callinectes sapidus*	186	4.9	222	5.6	313	4.9	721	5.2
Stone crab	*Menippe adina*	1	28.3	11	14.5	2	9.7	14	17.5
Atlantic mud crab	***Penopeus herbstii***	**5**	**23.5**	**12**	**23.9**	**98**	**14.6**	**115**	**20.7**
Ridgeback mud crab	*Eurypanopeus turgidus*	171	12.1	268	15.5	138	14.1	577	12.9
Flatback mud crab	*Eurypanopeus depressus*	2	9.2	39	13.2	0		41	11.2
Small mud crab	Xanthidae	656	6.7	1102	7.2	1298	6.2	3056	6.7

crab density would exacerbate this non-lethal effect. We used juvenile oysters settled onto oyster shells as described in the previous subsection. When they reached 2 mm in diameter, these juveniles oysters were placed inside a cage in 1 of 3 treatments: a control with no mud crab predators, a treatment with 2 Atlantic mud crabs, and a treatment with 6 Atlantic mud crabs. This design permitted us to determine if oysters alter their morphology in the presence of mud crabs and if increasing the amount of predator cue induces greater morphological changes.

Mud crabs were caged on both sides of the cage containing the juvenile oysters to ensure that the oysters received predator cues regardless of flow direction. Mud crabs were fed weekly, and any dead crabs were replaced. The experiment lasted for 45 d as previous work indicated this time was sufficient to observe morphological changes in oysters.

After 45 d, the oysters were recovered and returned to Texas A & M University – Corpus Christi. Individual oysters were placed in a drying oven for 2 d at 90°C and then weighed to the nearest 0.001 g to determine total dry weight. The oysters were then transferred into a muffle furnace and baked at 500°C for 2 h and reweighed to determine the ash-free dry weight. We then divided the ash-free weight from the total dry weight to obtain a percentage of shell mass. This estimate represents the relative allocation of growth to shell vs. soft tissue and accounts for growth or size differences among individual oysters (Johnson & Smee 2012). A greater percentage of shell mass indicates greater production of shell and less allocation of resources to tissue mass.

Percentage of shell mass was compared among controls and treatments using a 1-way blocked ANOVA with number of mud crabs (0, 2, or 6) as the fixed factor in the model (Sokal & Rohlf 1995). Tukey-Kramer post hoc tests were used to compare pairwise differences among treatments (Day & Quinn 1989). All statistical analyses were performed using JMP® PRO (v. 9).

RESULTS

Exclusion experiment

We identified several species of intermediate predators that could potentially prey on oysters in our cage and control treatments (Table 1, Fig. 2). Four of the 6 predators were mud crabs, which were the most abundant intermediate consumers present (Fig. 2). We also found a large number of mud crabs (Xanthidae) that we were unable to identify to species but that were small (<8 mm carapace width) and equally distributed among the cage treatments (Tables 1 & 2). With the exception of the Atlantic mud crab *Panopeus*

Table 2. ANOVA table for intermediate predator abundance by cage treatment (control; small mesh; large mesh). Atlantic mud crabs *Panopeus herbstii*, values in **bold**, are the only intermediate predator whose abundance differed significantly between caging treatments

Common name	Species	df	Error	*F*	p
Snapping shrimp	*Alpheus heterochaelis*	2	28	2.87	0.07
Blue crab	*Callinectes sapidus*	2	28	0.82	0.45
Stone crab	*Menippe adina*	2	28	0.92	0.41
Atlantic mud crab	***Panopeus herbstii***	**2**	**28**	**6.11**	**0.004**
Ridgeback mud crab	*Eurypanopeus turgidus*	2	28	2.68	0.08
Flatback mud crab	*Eurypanopeus depressus*	2	28	1.23	0.30
Small mud crab	Xanthidae	2	28	0.94	0.39

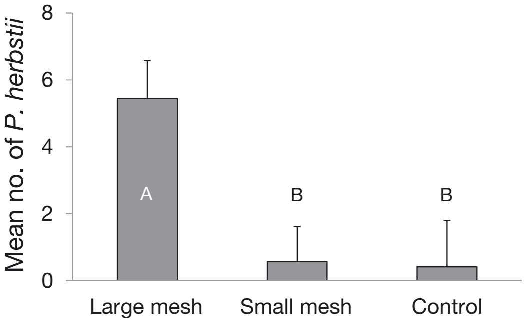

Fig. 3. Mean (±1 SE) abundance of *Panopeus herbstii* (>10 mm) by caging treatment. Different letters represent significant differences between treatments ($p < 0.05$) based on a Tukey-Kramer post hoc test

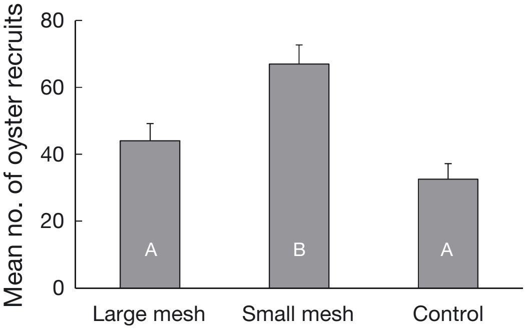

Fig. 4. Mean (±1 SE) abundance of naturally settled juvenile oysters by caging treatment. Different letters represent significant differences between treatments ($p < 0.05$) based on a Tukey-Kramer post hoc test

herbstii, the abundance of all potential oyster predators was not significantly different among cage treatments and controls. Significantly more *P. herbstii* were present in the 5.0 cm^2 mesh cage than in the other treatments (Table 2, Fig. 3), and the *P. herbstii* collected in all treatments were >10 mm carapace width and capable of consuming juvenile oysters. Stone crabs, flatback mud crabs *Eurypanopeus depressus*, ridgeback mud crabs *Eurypanopeus turgidis*, and snapping shrimp were more abundant in the small mesh cage, but their abundance was not significantly different among caging treatments (Tables 1 & 2). The blocking factor was not significant ($F_{20,60}$ = 1.48, p = 0.12; Fig. 4) and indicates that these species are ubiquitous in this habitat. Oyster spat was highest in the small mesh cage treatment where these species were most abundant, suggesting that their abundance was not related to oyster spat survival. We did not find significant differences in the abundance of fish, crabs, shrimp, mollusks, or oysters between the 2-sided cage and the tray without a cage (Table 3).

Table 3. Mean abundances (±1 SE) for cage control with 2 sides and the control without sides (tray) to examine possible cage artifacts. Significant differences between 2-sided cages and trays without sides were not found

Group	2-sided cage control	Control (tray)	*t*	p
Diversity (Simpson's index)	0.68 ± 2.8	0.69 ± 2.8	0.42	0.68
Juvenile oysters	8.33 ± 4.5	6.3 ± 3.2	0.36	0.72
Shrimp	130.7 ± 25.1	98.7 ± 23.2	0.94	0.36
Crab	68.2 ± 9.4	72.2 ± 10.4	0.28	0.78
Fish	32.3 ± 2.8	31.7 ± 2.1	0.15	0.88
Mollusk	130.7 ± 31.7	83.1 ± 12.3	1.4	0.18
Total	361.7 ± 42.7	285.7 ± 33.4	1.41	0.17

The 1.0 cm^2 mesh cages had a significantly greater number of newly settled oysters than the 5.0 cm^2 mesh cage and the control ($F_{2,28}$ = 6.12, p = 0.02; Fig. 4). The blocking factor was significant ($F_{2,28}$ = 6.01, $p < 0.01$), and we attribute the significant block effect to patchy settlement and survival of oysters across the study site. The number of surviving, newly settled oysters was not significantly different between controls and cages covered with 5.0 cm^2 mesh.

Oyster predation experiment

Mesh size significantly influenced juvenile oyster survival, with oyster survival significantly greater in the 1.0 cm^2 mesh treatment than in the uncaged control or the 5.0 cm^2 mesh treatment ($F_{2,27}$ = 19.96, $p < 0.001$; Fig. 5), suggesting that predation on oyster spat most likely accounted for differences in the

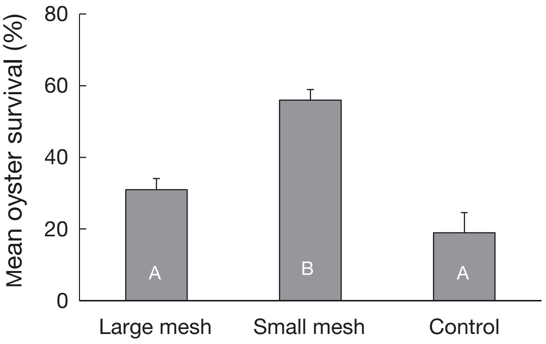

Fig. 5. Mean (±1 SE) percentage of juvenile oysters that survived for 1 wk by mesh size. Different letters represent significant differences between treatments ($p < 0.05$) based on a Tukey-Kramer post hoc test

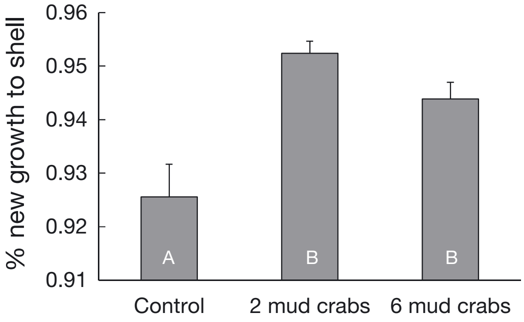

Fig. 6. Mean percentage of new growth devoted to shell (±1 SE) by treatment. Different letters represent significant differences between treatments ($p < 0.05$) based on a Tukey-Kramer post hoc test

abundance of newly settled oysters in the caging experiments.

Non-lethal effects of mud crabs on juvenile oysters

The presence of Atlantic mud crabs influenced how oysters allocate tissue vs. shell growth. When caged near Atlantic mud crabs in the field, oysters produced significantly more shell mass relative to overall mass compared to control oysters ($F_{2,84} = 10.28$, $p < 0.001$; Fig. 6); however, we did not find a significant difference in shell mass growth for the treatments with 2 vs. 6 mud crabs.

DISCUSSION

In this study, we were able to ascertain how predators influence oyster reef community structure by excluding top and intermediate predators from oyster reefs based upon predator size. When both top and intermediate predators were excluded using a small mesh cage, the number of surviving oyster spat significantly increased. We propose 3 possible explanations for this finding. First, protection from Atlantic mud crabs, blue crabs, and sheepshead might have reduced the consumption of oysters and led to a greater number of surviving spat. Second, snapping shrimp and other small crabs in the small mesh cage treatment consumed other oyster spat predators, such as oyster drills or flat worms (e.g. *Stylochus* spp.), that we were unable to exclude and subsequently might have alleviated predation on oyster spat. Third, the small mesh cage treatment might have altered the localized flow patterns and induced greater oyster settlement.

Several pieces of evidence suggest that protection from crabs and omnivorous fishes accounted for a greater number of oyster spat. First, we performed a mark and recovery experiment in which oysters were placed in the field at a known density and protected from predators using the same large, small, or no-mesh control. This experiment was designed to determine if predation alone would produce significant differences in oyster survival as observed in the predator exclusion (i.e. caging) experiment. More oysters survived when protected from predators using a small mesh cage, which mirrored the finding of greater oyster survival in the small mesh cage. This finding suggests that predator access alone could produce differences in the exclusion study if settlement were equal among caging treatments. With the exception of Atlantic mud crabs, other potential oyster spat predators were equally distributed among the caging treatments, and their abundance did not coincide with oyster spat survival. We collected few oyster drills in the study. *Stylochus* sp. worms often cause high mortality of newly settled oysters, but mortality caused by these parasites should not have differed among caging treatments. Therefore, we do not think these organisms are influencing our results even though our cages may not have excluded them.

Although oyster settlement can be variable, we used a block design and placed our caging treatments within blocks ~1.0 m apart to intentionally expose each treatment within blocks to similar levels of oyster recruitment as well as similar abiotic conditions. We cannot verify if oyster larvae recruited differently among our caging treatments. However, we controlled for changes in flow produced by our cages by using a control cage that was covered on 2 perpendicular sides with small mesh. The cage with 2 sides did not have significantly different levels of oyster recruitment compared to a control tray that lacked sides or mesh. If flow caused by the cage was having significant effects on oyster recruitment, we should have found evidence of it when comparing trays to 2-sided control cages, but we did not. Thus, we do not expect differences in flow to explain preferential oyster recruitment in our predator exclusion experiment. It is not known if oyster larvae avoid settling in areas where predators are present, but mud crabs were ubiquitous on the reef and present in all cage treatments. The results from our mark and recovery experiment where oysters were protected from predators using different mesh sizes, the rarity of oyster drill and worm predators from our field site and similarity in abundance of very small mud crabs between caging treatments, and the use of a control treatment with small mesh on 2 sides to disrupt flow without finding an increase in oyster spat abundance together suggest that predator access is the most likely explanation for differences in oyster survival in the exclusion experiment.

In cages covered with the larger mesh, only top-predators were excluded, and adult Atlantic mud crab abundances were much greater than in either of the other 2 treatments. Thus, the small mesh cage successfully excluded this important predator. The absence of Atlantic mud crabs in controls resulted from either direct predation by higher-order consumers or an avoidance of controls because higher-order consumers were present in them. Although stone crabs, ridgeback and flatback mud crabs, and snapping shrimp were more abundant in the small mesh cage, the number of oyster spat was highest in this treatment, suggesting that these predators do not prey heavily on newly settled oysters at the sizes present in our treatments. Further, Atlantic mud crabs were the only intermediate predators whose abundance differed significantly among caging treatments. Our results imply that top predators in this system exert strong top-down control on Atlantic mud crabs, the most abundant intermediate consumer in oyster reef communities.

Our study design was aimed at testing whether excluding whole predator trophic levels would reveal whether oyster reef communities are dominated by trophic cascades or whether top predators are omnivorous and capable of suppressing both intermediate predators and basal prey on oyster reefs. Although Atlantic mud crabs were over an order of magnitude more abundant in the large mesh cage when only top predators were excluded, oyster survival did not differ between the large mesh cage treatment and the uncaged controls that were accessible to both top and intermediate predators. Counter to our hypothesis that top predators would indirectly benefit juvenile oyster survival, there was no statistical difference in oyster survival in controls vs. large mesh cages containing mostly mud crabs as the primary oyster consumer. This finding indicates that top predator consumption of oysters more than compensated for any indirect benefits derived from top predators consuming or intimidating intermediate predators such as mud crabs. Our results indicate that predators exert significant top-down influence on oyster reefs, but they are omnivorous, and thus, trophic cascades are dampened.

Collectively, predators can increase top-down forcing in communities when predators have complementary diets or facilitate one another, or predators may decrease top-down forcing when predators interfere with one another (Sih et al. 1998, reviewed by Stachowicz et al. 2007). In speciose communities, consumers routinely feed at multiple trophic levels, which can dampen trophic cascades (Strong 1992, Polis & Strong 1996, Sih et al. 1998, Casula et al. 2006). In oyster reef systems, toadfish have been shown to exert strong trophic cascades on oyster reefs, even when omnivorous top predators such as blue crabs are present (Grabowski 2004, Grabowski et al. 2008). We attribute the lower oyster survival in our control treatments to the omnivorous predators that are common on oyster reefs in Texas, including adult blue crabs, black drum, and sheepshead that feed on oysters and on intermediate predators such as mud crabs (Dittel et al. 1996). Previous studies have shown that toadfish, a predator that does not consume oysters, can benefit oysters by suppressing foraging of both blue crabs and mud crabs (Grabowski 2004, Grabowski et al. 2008). Thus, toadfish have a more positive effect on oysters than do omnivorous predators. Our results suggest that omnivorous predators have larger effects on oyster reefs than do toadfish in this system. This finding may result from stronger effects emanating from omnivorous predators or from a lower abundance of toadfish in our study sites. Further investigation is required to ascertain the separate and combined effects of individual predator species.

Our study demonstrated that consumptive effects of top and intermediate predators on oysters were largely equivalent, but non-consumptive effects can also influence prey communities. In particular, oyster survival did not differ between the uncaged treatment open to top predators and the large cages that had high densities of adult mud crabs. Yet we found that mud crabs induced oysters to allocate more energy to shell than to tissue growth, which likely lowers their fecundity, since gonad size is positively correlated to soft tissue mass in bivalves (Peterson 1986, D. L. Smee unpubl. data). Oysters in particular produce relatively less soft tissue per body size in the presence of mud crab exudates (Johnson & Smee 2012, Robinson et al. 2014), which lowers their fecundity but increases their survival in the presence of mud crabs by making their shells harder to break (Robinson et al. 2014). Therefore, even though transient predators such as blue crabs and sheepshead consume oysters, they may also benefit juvenile oysters by consuming mud crabs, thereby reducing both the lethal and non-lethal effects of mud crabs on oysters. We did not test whether these transient predators induce morphological changes in oysters. However, they are far less common on oyster reefs than mud crabs and would thus have to induce much stronger effects on oyster tissue allocation to compensate for lower effective densities on reefs to match the non-consumptive effects induced by mud crabs. Furthermore, many of these transient predators are active pursuit predators, a foraging modality that typically does not induce strong anti-predator behavior in prey (Schmitz et al. 2004). Mud crabs are one of the most abundant resident species on oyster reefs (Wells 1961, Bahr & Lanier 1981); however, top predators suppressed large mud crab densities in our experiment by 90%.

The loss of consumer diversity globally remains a central challenge for conservation biologists (Duffy et al. 2001) and is common in marine habitats as a consequence of over-harvesting (Botsford et al. 1997, Hutchings 2000, Jackson et al. 2001). Our results reveal that top predator loss can have important but subtle effects on oyster reef communities by increasing the abundance of intermediate predators that exert both lethal and non-lethal effects on oysters. Whether these non-consumptive effects have long-term effects on oyster fitness, population size, and reef complexity when top predators are removed from the system requires further research.

In addition to this precipitous decrease in predator populations, oyster populations have declined by 1 to 2 orders of magnitude over the past century in many regions of the USA (Rothschild et al. 1994, Kirby 2004, Ermgassen et al. 2013), and it is estimated that oyster reefs have decreased 85% worldwide (Beck et al. 2011). Conservation efforts to sustain and rebuild oyster reefs will likely be influenced by how we manage and conserve the predators that forage on them. For instance, changes in predator abundance can contribute to declines in bivalve fisheries (Myers et al. 2007) and may also contribute to a decline in oyster populations (O'Connor et al. 2008). Moreover, predator identity is extremely important in predicting how predator removals will influence juvenile oyster survival. For instance, the removal of omnivorous predators, such as blue crabs, that feed on multiple trophic levels will have more subtle effects than removing predators such as toadfish that largely prey on crustaceans. Conservation efforts should consider how predator identity influences oysters via both lethal and non-lethal processes to anticipate the consequences of future predator removals for restoration success.

Acknowledgements. This research was supported by Texas Sea Grant, the Texas Research Development Fund, the Harvey Weil Sportsman Conservationist Award, the Ruth A. Campbell Professorship to D.L.S. and the National Science Foundation grant no. OCE-12-03859 to J.H.G. The Texas AgriLife Research Mariculture Laboratory in Port Aransas, TX, and the TAMU-CC Center for Coastal Studies provided facilities that made the work possible. The Marine Ecology Lab at Texas A & M University – Corpus Christi, especially P. Torres, E. Robinson and J. Lunt, provided valuable assistance in both the lab and field. Comments from J. Pollack greatly improved the manuscript.

LITERATURE CITED

Bahr LM, Lanier WP (1981) The ecology of intertidal oyster reefs of the south Atlantic Coast: a community profile. FWS/OBS-81/15, US Fish Wildl Service, Washington, DC

Beck MW, Brumbaugh RD, Airoldi L, Carranza A and others (2011) Oyster reefs at risk and recommendations for conservation, restoration, and management. Bioscience 61: 107–116

Beckerman AP, Uriarte M, Schmitz OJ (1997) Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. Proc Natl Acad Sci USA 94: 10735–10738

Botsford LW, Castilla JC, Peterson CH (1997) The management of fisheries and marine ecosystems. Science 277: 509–515

Burkepile DE, Hay ME (2008) Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. Proc Natl Acad Sci USA 105: 16201–16206

Carpenter SR, Kitchell JF, Hodgson JR (1985) Cascading trophic interactions and lake productivity. Bioscience 35: 634–639

Casula P, Wilby A, Thomas MB (2006) Understanding biodiversity effects on prey in multi-enemy systems. Ecol Lett 9:995–1004

Day RW, Quinn GP (1989) Comparisons of treatments after an analysis of variance in ecology. Ecol Monogr 59: 433–463

Dittel A, Epifanio CE, Natunewicz C (1996) Predation on mud crab megalopae, *Panopeus herbstii* H. Milne Edwards: effect of habitat complexity, predator species and postlarval densities. J Exp Mar Biol Ecol 198: 191–202

Duffy JE, Macdonald KS, Rhode JM, Parker JD (2001) Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test. Ecology 82: 2417–2434

Estes JA, Palmisano JF (1974) Sea otters: their role in structuring nearshore communities. Science 185:1058–1060

Grabowski JH (2004) Habitat complexity disrupts predator-prey interactions but not the trophic cascade on oyster reefs. Ecology 85:995–1004

Grabowski JH, Hughes AR, Kimbro DL, Dolan MA (2005) How habitat setting influences restored oyster reef communities. Ecology 86:1926–1935

Grabowski JH, Hughes AR, Kimbro DL (2008) Habitat complexity influences cascading effects of multiple predators. Ecology 89:3413–3422

Huhta A, Muotka T, Juntunen A, Yrjonen M (1999) Behavioural interactions in stream food webs: the case of driftfeeding fish, predatory invertebrates and grazing mayflies. J Anim Ecol 68:917–927

Hutchings JA (2000) Collapse and recovery of marine fishes. Nature 406:882–885

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA and others (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–637

Johnson KD, Smee DL (2012) Size matters for risk assessment and resource allocation in bivalves. Mar Ecol Prog Ser 462:103–110

Kirby MX (2004) Fishing down the coast: historical expansion and collapse of oyster fisheries along continental margins. Proc Natl Acad Sci USA 101:13096–13099

Menge BA (2000) Top-down and bottom-up community regulation in marine rocky intertidal habitats. J Exp Mar Biol Ecol 250:257–289

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

Nilsson E, Hertonsson P, Stenberg M, Brodersen J and others (2006) Facilitation and interference among three predators affect their consumption of a stream-dwelling mayfly. Freshw Biol 51:1507–1514

O'Connor NE, Grabowski JH, Ladwig LM, Bruno JF (2008) Simulated predator extinctions: predator identity affects survival and recruitment of oysters. Ecology 89:428–438

O'Connor NE, Emmerson MC, Crowe TP, Donohue I (2013) Distinguishing between direct and indirect effects of predators in complex ecosystems. J Anim Ecol 82: 438–448

Okuyama T, Bolker BM (2007) On quantitative measures of indirect interactions. Ecol Lett 10:264–271

Orrock JL, Grabowski JH, Pantel JH, Peacor SD and others (2008) Consumptive and nonconsumptive effects of predators on metacommunities of competing prey. Ecology 89:2426–2435

Paine RT (1966) Food web complexity and species diversity. Am Nat (1966):65–75

Peterson CH (1986) Quantitative allometry of gamete production by *Mercenaria mercenaria* into old age. Mar Ecol Prog Ser 29:93–97

Polis GA, Strong DR (1996) Food web complexity and community dynamics. Am Nat 147:813–846

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

Rothschild BJ, Ault JS, Goulletquer P, Héral M (1994) Decline of the Chesapeake Bay oyster population: a century of habitat destruction and overfishing. Mar Ecol Prog Ser 111:29–39

Rozas LP, Minello TJ (1997) Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: a review of sampling design with focus on gear selection. Estuaries 20:199–213

Schmitz OJ, Beckerman AP, Obrien KM (1997) Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. Ecology 78:1388–1399

Schmitz OJ, Krivan V, Ovadia O (2004) Trophic cascades: the primacy of trait-mediated indirect interactions. Ecol Lett 7:153–163

Shurin JB, Borer ET, Seabloom EW, Anderson K and others (2002) A cross-ecosystem comparison of the strength of trophic cascades. Ecol Lett 5:785–791

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

Sokal R, Rohlf F (1995) Biometry: the principles and practice of statistics in biological research. WH Freeman, New York, NY

Stachowicz JJ, Bruno JF, Duffy JE (2007) Understanding the effects of marine biodiversity on communities and ecosystems. Annu Rev Ecol Evol Syst 38:739–766

Strong DR (1992) Are trophic cascades all wet: differentiation and donor-control in speciose ecosystems. Ecology 73:747–754

Trussell GC, Ewanchuk PJ, Bertness MD (2003) Trait-mediated effects in rocky intertidal food chains: predator risk clues alter prey feeding rates. Ecology 84:629–640

Wells HW (1961) Fauna of oyster beds, with special reference to the salinity factor. Ecol Monogr 31:239–266

Werner EE, Peacor SD (2003) A review of trait-mediated indirect interactions in ecological communities. Ecology 84:1083–1100

Werner EE, Peacor SD (2006) Lethal and nonlethal predator effects on an herbivore guild mediated by system productivity. Ecology 87:347–361

Zu Ermgassen PSE, Spalding MD, Grizzle RE, Brumbaugh RD (2013) Quantifying the loss of a marine ecosystem service: filtration by the eastern oyster in US estuaries. Estuaries Coasts 36.1:36–43

Editorial responsibility: Kenneth Heck Jr.,
Dauphin Island, Alabama, USA

Submitted: August 27, 2013; Accepted: April 3, 2014
Proofs received from author(s): June 30, 2014