

Threat of Predation Does Not Affect *Crassostrea virginica* Filtration

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Abstract Biotic interactions can structure ecological communities and influence ecosystem functioning. As ecosystem engineers and filter feeders, bivalves often have disproportionately large effects on ecosystem functioning. They also utilize numerous morphological and behavioral responses to reduce predation, which can include changes in their filtration rates. To test the response of *Crassostrea virginica* filtration rates to the presence of predators, juvenile and adult oysters were separately exposed to varying types of predation risk from *Callinectes sapidus* and *Panopeus herbstii* in outdoor mesocosms. Water column chlorophyll *a* concentrations and crab behavior were measured over the duration of the experiment. Predation risk had no effect on oyster reef drawdown of chlorophyll *a*, which suggests that this important ecosystem function of oyster reefs is not mediated by behaviorally induced predator effects. Therefore, efforts to model how oyster predators influence filtration rates and associated ecosystem services should focus primarily on the factors that influence

oyster mortality rather than predator effects on oyster behavior.

Keywords *Crassostrea virginica* · Filtration · Non-consumptive effects · Predation

Introduction

Through indirect interactions, predators can influence not only community structure (Hairston et al. 1960; Paine 1966; Menge 1995; Grabowski and Kimbro 2005) but also ecosystem functioning (Chapin et al. 1997; Schmitz 2008; Schmitz et al. 2008). For instance, when in the presence of *Carcinus maenas* (green crab) effluent, the trophic efficiency of *Nucella lapillus* (dogwhelk) feeding on *Semibalanus balanoides* (acorn barnacle) is significantly reduced (Trussell et al. 2006). In this case, the predator induced reduced energy transfer from the basal resource (barnacle) to higher trophic levels. However, not all predator effects necessarily influence ecosystem functioning. Identifying and quantifying the effects that are of critical importance to ecosystem functioning are important for determining when biotic and physical processes are integrally coupled and to help inform efforts to manage these systems (Levin 1992; Kremen 2005).

As ecosystem engineers and filter feeders, bivalves perform a wide array of ecosystem functions (Jones et al. 1994; Grabowski and Peterson 2007). For instance, similar to herbivores, they promote trophic transfer and nutrient cycling. They also support aquatic-specific functions like enhancing benthic-pelagic coupling and water clarity. But some species, such as oysters and mussels, also influence a third suite of functions by creating habitat, which in turn promotes secondary and tertiary productivities and stabilizes sediments by baffling water flow. The vast majority of these functions stem

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directly or indirectly from oysters filtering the water because this process affects oyster growth and habitat provisioning (Grabowski and Peterson 2007). Therefore, factors that influence bivalve filtration are likely to have disproportionately large effects on the ecosystem functions that they provide.

Predation risk is one factor known to potentially affect filtration in bivalves (Kulakovskii and Lezin 2002; Smee and Weissburg 2006; Naddafi et al. 2007). Bivalves employ a wide range of behavioral and morphological responses to the risk of predation. Generally, induced morphological changes result in prey organisms that are more challenging for predators to capture and handle (Elner and Hughes 1978; Hughes and Seed 1995), and primarily include thicker or stronger shells and byssal threads (Côté 1995; Reimer and Harms-Ringdahl 2001; Newell et al. 2007b; Neo and Todd 2011; Johnson and Smee 2012), or behavioral changes that result in more cryptic or inaccessible individuals that are less likely to be identified and caught by predators (Griffiths and Richardson 2006; Smee and Weissburg 2006).

Bivalves respond to the threat of predation using a variety of predator avoidance behaviors. For instance, predators induce *Macoma balthica* (Baltic clam) to burrow deeper, thereby reducing their risk of being captured. The strength of this response changes with predator identity and predator diet, with the strongest response stemming from exposure to crab predators that have consumed *M. balthica* (Griffiths and Richardson 2006). Mussels also modify their behavior when exposed to predation risk: *Mytilus edulis* responds to the threat of lobster predators by aggregating (Côté and Jelnikar 1999), and *Brachidontes variabilis* (black mussel) occupies smaller shelters in the presence of injured conspecifics (Shin et al. 2008). In addition, bivalves alter their filtration rates to avoid being detected by predators. For instance, *M. balthica* decreases filter feeding when exposed to injured conspecifics or blue crabs, thereby decreasing the production of its odor plume (Smee and Weissburg 2006). Furthermore, exposure to predators induces *M. edulis* and *Dreissena polymorpha* (zebra mussel) to reduce filter feeding (Kulakovskii and Lezin 2002; Naddafi et al. 2007). Meanwhile, predation risk reduced *D. polymorpha* drawdown of phytoplankton biomass by 25% (Naddafi et al. 2007). When predators mediate prey filter feeding, they indirectly affect linkages between food web dynamics and ecosystem processes (Schmitz et al. 2008).

Crassostrea virginica is a reef-forming bivalve and a prominent provider of many ecosystem services such as removing excess nitrogen, providing habitat for commercially and recreationally valuable species, and stabilizing shorelines (Breitburg et al. 2000; Mann 2000; Coen and Luckenbach 2000; Newell et al. 2002; Peterson et al. 2003; Newell et al. 2007a; Piehler and Smyth 2011). *C. virginica* is capable of decreasing water column chlorophyll *a* concentrations by more than 75% (Dame et al. 1984) and can increase average denitrification rates two to six times the rate on unstructured

mudflats (Piehler and Smyth 2011). These and other water quality services have been estimated to contribute as much as half of the total ecosystem service value provided by *C. virginica* (Grabowski et al. 2012). If *C. virginica* responds in the same way to predator cues as the similarly conspicuous zebra mussel, predators could have a dramatic effect on several of the ecosystem functions and associated services that oysters provide.

To investigate the effect that predators have on the filtration rate of *C. virginica*, oyster removal of chlorophyll *a* from the water column was quantified when oysters were exposed to varying types of *Callinectes sapidus* (blue crab) and *Panopeus herbstii* (mud crab) predator cue treatments (physical contact only, chemical cues only, unrestricted blue crab, unrestricted mud crab, and unrestricted blue crab and mud crab together), the two dominant oyster predators in this system (O'Connor et al. 2008; Rindone and Eggleston 2011). The last three treatments involved predators at large in the tanks, thereby exposing the oysters to physical and chemical cues and the threat of being consumed. By measuring oyster drawdown of phytoplankton biomass across two oyster size classes in the presence and absence of predator cues, this study aimed to quantify the magnitude of consumptive and non-consumptive predator effects on oyster filtration and consequently their potential influence on associated ecosystem services.

Methods

Juvenile individual *C. virginica* (27.8 ± 5.1 mm) were obtained from the Horn Point Hatchery, MD, and adult *C. virginica* were collected from Hoop Hole Creek, NC (91.5 ± 11.4 mm). Adult oysters were separated, scraped clean, and then placed in a flow-through tank supplied with unfiltered seawater from Bogue Sound, NC, along with the juvenile oysters. *P. herbstii* (35 ± 4 mm) were obtained from intertidal oyster reefs at Hoop Hole Creek, NC, and *C. sapidus* (123 ± 12 mm) were caught in crab pots from Bogue Sound, NC. Individual juvenile oysters were obtained in May of 2013 and reared in flow-through tanks containing raw water from Bogue Sound until they were used in drawdown experiments. All crabs and adult oysters were collected in July of 2013 and maintained in flow-through tanks for at least 24 h before being used in experiments. All species were housed in separate tanks to prevent predation while acclimatizing. Crabs were fed shucked oysters ad libitum every other day with a final feeding ending approximately 12 h before the start of a trial. By feeding the crabs on oyster tissue prior to each experimental run and using relatively small mesocosms, the olfactory presence of the crabs in the mesocosms was maximized (Weissburg et al. 2014). All organisms were measured, and the crabs were sexed.

A total of seven treatments were used in this experiment: predator- and oyster-free (control), oysters with no other predator or cue manipulation (oyster only), physical manipulation

without chemical cues (physical manipulation), predator chemical cues without physical manipulation (chemical cues), unrestricted blue crab (blue crab), unrestricted mud crab (mud crab), and unrestricted blue crab and mud crab together (blue and mud crab). The treatment that contained no oysters or predators served as a control for the natural loss of chlorophyll *a* through settling. The oyster only and physical manipulation treatments contained only oysters, with the manipulation treatment also receiving physical disturbance without predator chemical cues to simulate tactile predatory stimuli. This was accomplished by lightly dragging a weighted polyester glove over all oysters, with manipulation rates determined from crab-oyster contact rates in preliminary trials. The chemical cues treatment contained both blue and mud crabs in the same mesocosm but caged separately for the duration of the experiment. These crabs were caged a minimum of 10 cm from the oysters, and thus were unable to consume them, so that this treatment isolated the effects of crab chemical cues on oyster filtration behavior. The mud crab, blue crab, and mud crab and blue crab consisted of uncaged crabs in the tank with oysters. Each treatment was replicated three times for each of the oyster size classes, resulting in a total of 42 individual trials.

Trials were conducted in tanks (90 cm × 90 cm × 22.5 cm) filled to a uniform depth of 14 cm. Tank bottoms were covered with a layer of clean oyster shell to provide shelter and a more natural substrate for the crabs. Oysters were secured to ceramic tiles (11 cm × 11 cm) with Z-Spar Marine Epoxy (Splash Zone A-788), which were then attached to cement pavers (15 cm × 15 cm) using silicone glue. This method was used to mimic how an oyster attaches to an oyster reef and avoid overestimating either the consumptive or non-consumptive effects of crab predators on filtration rates. The tiles were maintained in flow-through tanks while the epoxy cured for a minimum of 12 h. Crabs were placed in the experimental tanks approximately 12 h before the start of a trial to saturate the mesocosms with predator chemical cues. During this period, water flow through the tank was approximately 4 L min⁻¹. Blue crabs (1 replicate⁻¹, 1.2 m⁻²) were put in plastic mesh cages during this period to prevent predation on mud crabs, but released to roam freely within the tank at the inception of each trial. Mud crabs (8 replicate⁻¹, 9.9 m⁻²) were placed in their respective tanks. Large mud crab densities are consistent with local (high density ~9 m⁻²; average density ~4 m⁻²) (Grabowski *unpublished data*; Dodd *unpublished data*) and published values (McDonald 1982). For the chemical cues treatment, blue crabs and mud crabs were put into separate plastic mesh cages (approx. 20 cm × 10 cm × 5 cm) for the entire duration. Water flow was discontinued immediately prior to starting a trial, and an aquarium pump (606 L min⁻¹) was used to circulate and oxygenate water. Juvenile oyster trials contained 54 oysters in each replicate (66.7 m⁻²), whereas adult oyster trials contained 10 oysters in each (12.3 m⁻²).

Treatments were run concurrently for each oyster size class. Trials began approximately 30 min after sunrise. Oyster tiles were placed in their respective tanks, the appropriate crabs were released from their cages, and mesh coverings (2 cm stretch length) were clipped to the rim of the tanks to prevent blue crabs from escaping. While each treatment was running, a water sample was taken approximately 5 cm below the water surface every 60 min. The manipulation treatment was handled every 30 min, as determined by preliminary trials in which crab behavior was observed. When water sampling and manipulation were scheduled to occur at the same time, the water sample was collected first to reduce any effect of resuspension on the sample. After 4 h, the crabs were removed and oyster mortality was recorded.

Chlorophyll *a* drawdown was quantified through repeated water sampling of experimental trials throughout each experimental trial for a total of five samples per trial. Using a 0.7-μm GFF filter, 100 mL of each water sample was then filtered. Filters were extracted in 7 mL of 90% acetone solution and analyzed for chlorophyll *a* using a fluorometer (Welschmeyer 1994). Chlorophyll *a* concentrations were normalized to account for initial differences among tanks by converting them to proportion remaining from T_0 . A line was fitted through time for these points for each replicate, and the slopes (proportion chlorophyll *a* removed per hour) were analyzed in a two-way ANOVA with treatment and oyster size as fixed factors. Slopes were Box-Cox transformed to correct for heteroscedasticity, and the transformed data subsequently passed Levene's test ($p > 0.05$) for equality of variances. Orthogonal planned contrasts were established using the available degrees of freedom from the two-way ANOVA (Sokal and Rohlf 2012).

Results

Predator cues did not reduce removal of water column chlorophyll *a* by oysters (Fig. 1). The interaction between oyster size and predator treatment ($F_{6,28} = 2.28$, $P = 0.064$) and the main effect of oyster size ($F_{1,28} = 2.87$, $P = 0.101$) were not significant. There was a significant effect of treatment ($F_{6,28} = 21.28$, $P = <0.0001$) on chlorophyll *a* removal. Planned contrasts revealed a significant difference between the control treatment that had no oysters in it and all treatments with oyster present ($F_{1,28} = 126.49$, $P = <0.001$). However, following this first contrast, there was insufficient variation remaining to warrant conducting the remaining contrasts (approx. 1% for all five subsequent contrasts).

In the juvenile oyster treatments, oyster mortality as a result of predation occurred in three of the six predator treatments. Mean (SE) percent oyster mortality was 0.6% (±0.6) in the oyster only treatment, 0.6% (±0.6) in the blue and mud crab

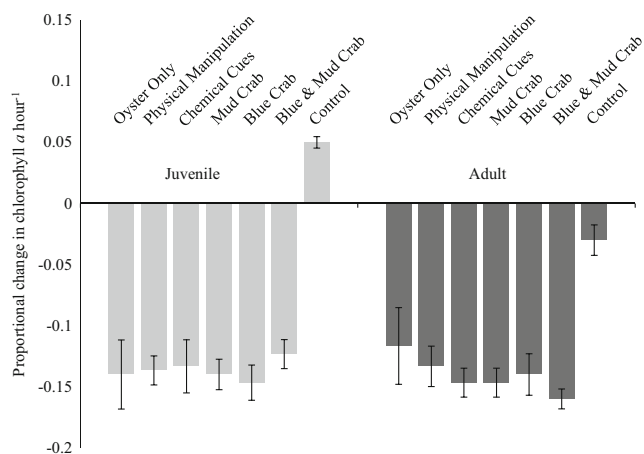


Fig. 1 Proportional change in chlorophyll *a* concentration per hour by oyster size and predator treatment. A priori contrasts indicate no difference between any treatments containing oyster

treatment, and 4.9% (± 0.6) in the mud crab treatment. There was no oyster mortality in the adult oyster treatments.

Discussion

Effects of predators on filtration rates have been demonstrated in several bivalve species including hard clams, blue mussels, and zebra mussels (Kulakovskii and Lezin 2002; Smee and Weissburg 2006; Naddafi et al. 2007). Contrary to this evidence, this study found that predators had no impact on oyster removal of chlorophyll *a* from the water column. This result suggests that oyster filtration rates, and hence the near-term delivery of ecosystem services by oyster reefs, may be at least directly decoupled from non-consumptive (i.e., predator avoidance behavior) predator-oyster interactions.

The normal feeding behavior of bivalves includes varying degrees of temporal variation. For instance, over a 26-h period in an environment with constant physical conditions and algal concentrations, *Argopecten irradians* (bay scallop) maintains a constant or steadily decreasing and then stabilizing filtration rate, characterized by minor variation and no periods when it ceases filter feeding (Palmer 1980). Alternatively, both *Crassostrea gigas* and *C. virginica* exhibit much higher variation, including periods of negligible filtration activity (Palmer 1980; Gerdes 1983). Hourly variation in mussel (e.g., *Choromytilus meridionalis* and *M. edulis*) filter feeding lies between these two extremes (Griffiths 1980; Kulakovskii and Lezin 2002). The cause of variation in oyster feeding rates is unclear but is hypothesized to be a consequence of alternating periods of increased feeding or digestion (Gerdes 1983). Detecting predator effects may be especially difficult under these circumstances, because if oysters do behaviorally respond to the presence of a predator, the response would likely mimic and may be functionally identical to a period of higher digestion. Similarly, following

the removal of the predator cue, the highly variable oyster feeding rates may allow for compensatory feeding, thereby increasing their filtration rates when predators are less proximal to account for any short-term feeding disruptions. Yet, we conducted the experiment in relatively small tanks where we would expect that oysters would be capable of detecting the presence of predators continually throughout the experiment and maximize the likelihood for disruption of oyster filtration. Thus, our results suggest that oysters likely do not alter their foraging rates in the presence of predators.

Predator and prey identities can determine the outcome of biotic interactions (O'Connor et al. 2008). For instance, the hard clam is cryptic and is typically found in low densities, so that a clam that responds to the threat of predation by reducing its filtration rate will likely enhance its chance of surviving (Smee and Weissburg 2006). Furthermore, although mussels are capable of forming reefs and are found in high densities, they are also more likely to occur in small aggregations and rely on their physical environment for protection (Uryu et al. 1996). In contrast, oysters are conspicuous and typically found in high densities. To realize an increase in survival by reducing their chemical cue profile, a large proportion of oysters, regardless of size, would have to stop filtering on a given section of reef. Given that the most abundant predators are not capable of consuming the largest oysters, this scenario may be unlikely. In addition, predatory crabs utilize oysters for both food and shelter. This close spatial association may also erode the value of a strong anti-predator response if habituation is occurring (Fernández-Juricic et al. 2002). In contrast, as a slow-moving predator that relies heavily on olfaction to locate prey, *Asterias rubens* (common starfish) may be more likely to illicit the fear response observed in blue mussels (Kulakovskii and Lezin 2002).

The juvenile oysters used in this study were hatchery-raised; therefore, unlike oysters in the wild, they had not previously been exposed to oyster predators. Therefore, it is possible that the response of hatchery-reared oysters to predators is weaker than that of wild oysters. Counteracting this potential issue, the crabs were kept in close proximity to the oysters during the experiment and were fed oyster tissue prior to the experiment to maximize their olfactory presence during the trial (Weissburg et al. 2014).

Reduction of filtration rates by oysters smaller than those used in this study is unlikely to greatly reduce total reef filtration. The relative contributions to total reef filtration by oyster size can be estimated using local intertidal reef survey data (supplemental data), an intertidal oyster length to dry weight relationship (Copeland and Hoese 1966; White et al. 1988; Powell et al. 1995), and a dry weight to filtration rate relationship (Riisgård 1988). From these measurements, estimated filtration by oysters smaller than 20 mm accounted for only 5% of total reef filtration despite representing 56% of oysters by count. If oysters of this size class were to decrease filtration rates in response to the presence of a predator similar to that

exhibited by zebra mussels (25% reduction), total reef filtration would decrease by only ~1% (Naddafi et al. 2007). Given the high degree of predator residency on these reefs, as opposed to the predators used in any comparable study (Kulakovskii and Lezin 2002; Griffiths and Richardson 2006; Smee and Weissburg 2006; Naddafi et al. 2007) and the ubiquity of conspecific settlement in oysters leading to a chemical cue-saturated and conspicuous environment, even this small reduction seems unlikely.

C. virginica grow quickly, thereby reducing predation risk by achieving greater size (Menzel and Nichy 1958; Krantz and Chamberlin 1978). They may exhibit defensive behaviors in the presence of other predators, but no evidence was found that they respond to either tactile or chemosensory cues of two common predatory crabs. While individual oysters may yet display a change in filtration rates in the presence of predators, our results suggest that predators do not appear to directly impact oyster filter-feeding behavior at larger scales (i.e., oyster reef patches).

In restoration and ecosystem service contexts, average filtration is often assumed to be a constant based on a number of environmental and demographic variables (Riisgård 1988; Dame 1993; Newell and Langdon 1996). If the finding that oysters do not reduce filtration to avoid predation holds for other oyster predators, that assumption would be validated as the direct effects of predators on oyster filter-feeding behavior do not need to be accounted for in reef filtration estimates. Oyster reefs are also credited for performing a wide diversity of services that may be dependent on each other, such as serving as nursery habitat for juvenile fishes and crustaceans, stabilizing shorelines, and removing excess nitrogen. Our results suggest that oyster predators and filter-feeding behavior are decoupled. Moreover, this finding implies that the nursery function of *C. virginica* reefs does not impair their potential to provide other key ecosystem services such as excess nitrogen removal and enhanced water quality. However, any predator behaviors that have a direct or indirect effect on oyster demographics, including changes in predation when crabs avoid predators by foraging less (Grabowski 2004; Grabowski and Kimbro 2005), growth (Johnson and Smee 2012), fecundity (Johnson and Smee 2012), or recruitment, will affect reef filtration and, therefore, delivery of ecosystem functions and services. Our study highlights the primacy of the direct consumptive effects of predators in mediating oyster filtration rates rather than their influence on oyster filtering behavior. Specifically, oyster predators did not directly influence oyster behavior or affect their filtrations of chlorophyll *a*, a proxy for delivery of many ecosystem functions and services.

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References

- Breitburg, D.L., L.D. Coen, M.W. Luckenbach, R. Mann, M. Posey, and J.A. Wesson. 2000. Oyster reef restoration: convergence of harvest and conservation strategies. *Journal of Shellfish Research* 19: 371–377.
- Chapin, F.S., III, B.H. Walker, R.J. Hobbs, D.U. Hooper, J.H. Lawton, O.E. Sala, and D. Tilman. 1997. Biotic control over the functioning of ecosystems. *Science* 277: 500–504.
- Coen, L.D., and M.W. Luckenbach. 2000. Developing success criteria and goals for evaluating oyster reef restoration: ecological function or resource exploitation? *Ecological Engineering* 15: 323–343.
- Copeland, B.J., and H.D. Hoese. 1966. Growth and mortality of the American oyster, *Crassostrea virginica*, in high salinity shallow bays in Central Texas. *Publications of the Institute of Marine Science* 11: 149–158.
- Côté, I.M. 1995. Effects of predatory crab effluent on byssus production in mussels. *Journal of Experimental Marine Biology and Ecology* 188: 233–241.
- Côté, I.M., and E. Jelnikar. 1999. Predator-induced clumping behaviour in mussels (*Mytilus edulis* Linnaeus). *Journal of Experimental Marine Biology and Ecology* 235: 201–211.
- Dame, R.F. 1993. The role of bivalve filter feeder material fluxes in estuarine ecosystems. In *Bivalve Filter Feeder in Estuarine and Coastal Ecosystem Processes*, ed. R.F. Dame, 254–269. Berlin, Heidelberg: Springer-Verlag.
- Dame, R.F., R.G. Zingmark, and E. Haskin. 1984. Oyster reefs as processors of estuarine materials. *Journal of Experimental Marine Biology and Ecology* 83: 239–247.
- Elner, R.W., and R.N. Hughes. 1978. Energy maximization in the diet of the shore crab, *Carcinus maenas*. *Journal of Animal Ecology* 47: 103–116.
- Fernández-Juricic, E., M.D. Jimenez, and E. Lucas. 2002. Factors affecting intra- and inter-specific variations in the difference between alert distances and flight distances for birds in forested habitats. *Canadian Journal of Zoology* 80: 1212–1220.
- Gerdes, D. 1983. The Pacific oyster *Crassostrea gigas*: part I. Feeding behaviour of larvae and adults. *Aquaculture* 31: 195–219.
- Grabowski, J.H. 2004. Habitat complexity disrupts predator-prey interactions but not the trophic cascade on oyster reefs. *Ecology* 85: 995–1004.
- Grabowski, J.H., and D.L. Kimbro. 2005. Predator-avoidance behavior extends trophic cascades to refuge habitats. *Ecology* 86: 1312–1319.
- Grabowski J., and C. Peterson. 2007. Restoring oyster reefs to recover ecosystem services. *Theoretical Ecology Series*, 4(C): 281–298.
- Grabowski, J.H., R.D. Brumbaugh, R.F. Conrad, A.G. Keeler, J.J. Opaluch, C.H. Peterson, M.F. Piehler, S.P. Powers, and A.R. Smyth. 2012. Economic valuation of ecosystem services provided by oyster reefs. *Bioscience* 62: 900–909.
- Griffiths, R.J. 1980. Filtration, respiration and assimilation in the black mussel *Choromytilus meridionalis*. *Marine Ecology Progress Series* 3: 63–70.
- Griffiths, C.L., and C.A. Richardson. 2006. Chemically induced predator avoidance behaviour in the burrowing bivalve *Macoma balthica*. *Journal of Experimental Marine Biology and Ecology* 331: 91–98.
- Hairton, N.G., F.E. Smith, and L.B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* 94: 421–425.
- Hughes, R.N., and R. Seed. 1995. Behavioural mechanisms of prey selection in crabs. *Journal of Experimental Marine Biology and Ecology* 193: 225–238.

- Johnson, K.D., and D.L. Smee. 2012. Size matters for risk assessment and resource allocation in bivalves. *Marine Ecology Progress Series* 462: 103–110.
- Jones, C.G., J.H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* 69: 373–386.
- Krantz, G.E., and J.V. Chamberlin. 1978. Blue crab predation on cultchless oyster spat. *Proceedings of the National Shellfisheries Association* 68: 38–41.
- Kremen, C. 2005. Managing ecosystem services: what do we need to know about their ecology? *Ecology Letters* 8: 468–479.
- Kulakovskii, E.E., and P.A. Lezin. 2002. Filtration activity of the blue mussel, *Mytilus edulis* (Mytilida, Mytilidae), under influence of the starfish, *Asterias rubens* (Forcipulata, Asteroidea). *Zoologicheskii Zhurnal* 81: 292–297.
- Levin, S.A. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur Award Lecture. *Ecology* 73: 1943–1967.
- Mann, R. 2000. Restoring the oyster reef communities in the Chesapeake Bay: a commentary. *Journal of Shellfish Research* 19: 335–339.
- McDonald, J. 1982. Divergent life history patterns in the co-occurring intertidal crabs *Panopeus herbstii* and *Eurypanopeus depressus* (Crustacea: Brachyura: Xanthidae). *Marine Ecology Progress Series* 8: 173–180.
- Menge, B.A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecological Monographs* 65: 21–74.
- Menzel, R.W., and F.E. Nichy. 1958. Studies of the distribution and feeding habits of some oyster predators in Alligator Harbor, Florida. *Bulletin of Marine Science* 8: 125–145.
- Naddafi, R., P. Eklöv, and K. Pettersson. 2007. Non-lethal predator effects on the feeding rate and prey selection of the exotic zebra mussel *Dreissena polymorpha*. *Oikos* 116: 1289–1298.
- Neo, M.L., and P.A. Todd. 2011. Predator-induced changes in fluted giant clam (*Tridacna squamosa*) shell morphology. *Journal of Experimental Marine Biology and Ecology* 397: 21–26.
- Newell, R.I.E., and C. Langdon. 1996. Mechanisms and physiology of larval and adult feeding. In *The eastern oyster Crassostrea virginica*, ed. V. Kennedy and R. Newell, 185–230. College Park: Maryland Sea Grant College, University of Maryland System.
- Newell, R.I.E., J.C. Cornwell, and M.S. Owens. 2002. Influence of simulated bivalve biodeposition and microphytobenthos on sediment nitrogen dynamics: a laboratory study. *Limnology and Oceanography* 47: 1367–1379.
- Newell, R.I.E., W.M. Kemp, J.D. Hagy III, C.F. Cerco, J.M. Testa, and W.R. Boynton. 2007a. Top-down control of phytoplankton by oysters in Chesapeake Bay, USA: comment on Pomeroy et al. (2006). *Marine Ecology Progress Series* 341: 293–298.
- Newell, R.I.E., V.S. Kennedy, and K.S. Shaw. 2007b. Comparative vulnerability to predators, and induced defense responses, of eastern oysters *Crassostrea virginica* and non-native *Crassostrea ariakensis* oysters in Chesapeake Bay. *Marine Biology* 152: 449–460.
- O'Connor, N.E., J.H. Grabowski, L.M. Ladwig, and J.F. Bruno. 2008. Simulated predator extinctions: predator identity affects survival and recruitment of oysters. *Ecology* 89: 428–438.
- Paine, R.T. 1966. Food web complexity and species diversity. *The American Naturalist* 100: 65–75.
- Palmer, R.E. 1980. Behavioral and rhythmic aspects of filtration in the bay scallop, *Argopecten irradians concentricus* (Say), and the oyster, *Crassostrea virginica* (Gmelin). *Journal of Experimental Marine Biology and Ecology* 45: 273–295.
- Peterson, C.H., J.H. Grabowski, and S.P. Powers. 2003. Estimated enhancement of fish production resulting from restoring oyster reef habitat: quantitative valuation. *Marine Ecology Progress Series* 264: 249–264.
- Piehl, M.F., and A.R. Smyth. 2011. Habitat-specific distinctions in estuarine denitrification affect both ecosystem function and services. *Ecosphere* 2: art12.
- Powell, E.N., J.M. Klinck, E.E. Hofmann, E.A. Wilson-Ormond, and M.S. Ellis. 1995. Modeling oyster populations. V. Declining phytoplankton stocks and the population dynamics of American oyster (*Crassostrea virginica*) populations. *Fisheries Research* 24: 199–222.
- Reimer, O., and S. Harms-Ringdahl. 2001. Predator-inducible changes in blue mussels from the predator-free Baltic Sea. *Marine Biology* 139: 959–965.
- Riisgård, H.U. 1988. Efficiency of particle retention and filtration rate in 6 species of Northeast American bivalves. *Marine Ecology Progress Series* 45: 217–223.
- Rindone, R.R., and D.B. Eggleston. 2011. Predator-prey dynamics between recently established stone crabs (*Menippe* spp.) and oyster prey (*Crassostrea virginica*). *Journal of Experimental Marine Biology and Ecology* 407: 216–225.
- Schmitz, O.J. 2008. Effects of predator hunting mode on grassland ecosystem function. *Science* 319: 952–954.
- Schmitz, O.J., J.H. Grabowski, B.L. Peckarsky, E.L. Preisser, G.C. Trussell, and J.R. Vonesh. 2008. From individuals to ecosystem function: toward an integration of evolutionary and ecosystem ecology. *Ecology* 89: 2436–2445.
- Shin, P.K.S., C.C. Liu, Z.X. Liu, and S.G. Cheung. 2008. Marine mussels *Brachidontes variabilis* selected smaller places of refuge and enhanced byssus production upon exposure to conspecific and heterospecific cues. *Journal of Experimental Marine Biology and Ecology* 361: 16–20.
- Smee, D.L., and M.J. Weissburg. 2006. Hard clams (*Mercenaria mercenaria*) evaluate predation risk using chemical signals from predators and injured conspecifics. *Journal of Chemical Ecology* 32: 605–619.
- Sokal R.R., and F.J. Rohlf. 2012. Biometry: the principles and practice of statistics in biological research. San Francisco, W. H. Freeman and Company.
- Trussell, G.C., P.J. Ewanchuk, and C.M. Matassa. 2006. The fear of being eaten reduces energy transfer in a simple food chain. *Ecology* 87: 2979–2984.
- Uryu, Y., K. Iwasaki, and M. Hinoue. 1996. Laboratory experiments on behavior and movement of a freshwater mussel, *Limnoperna fortunei* (Dunker). *Journal of Molluscan Studies* 62: 327–341.
- Weissburg, M., D.L. Smee, and M.C. Ferner. 2014. The sensory ecology of nonconsumptive predator effects. *The American Naturalist* 184: 141–157.
- Welschmeyer, N.A. 1994. Fluorometric analysis of chlorophyll *a* in the presence of chlorophyll *b* and pheopigments. *Limnology and Oceanography* 39: 1985–1992.
- White, M.E., E.N. Powell, and S.M. Ray. 1988. Effect of parasitism by the pyramidellid gastropod *Boonea impressa* on the net productivity of oysters (*Crassostrea virginica*). *Estuarine, Coastal and Shelf Science* 26: 359–377.