

NOTE

Context-dependent effects of a marine ecosystem engineer on predator–prey interactions

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ABSTRACT: The presence of 'ecosystem engineers' alters the biophysical landscape and can shape associated animal and plant communities within terrestrial, marine and aquatic ecosystems. For instance, in shallow marine ecosystems, reefs formed by filter-feeding bivalves such as oysters provide complex structure, while simultaneously influencing water column properties (e.g. light availability) through suspension feeding. Although it is well supported that both complex structure and light level can influence trophic interactions individually, both factors are highly variable in shallow marine ecosystems and potentially interact to produce non-additive effects. To explore how the multiple influences of an ecosystem engineer affect trophic interactions, we conducted mesocosm experiments with common estuarine species (i.e. Atlantic croaker and grass shrimp, and blue crab and brown shrimp) to test the effects of habitat context (high complexity oyster reefs vs. structureless bottom) and light level on prey survival. Atlantic croaker *Micropogonias undulatus* predation on grass shrimp *Palaemonetes pugio* was significantly reduced by the presence of oyster reef structure and was not affected by light level. In contrast, blue crab *Callinectes sapidus* predation on brown shrimp *Farfantepenaeus aztecus* was influenced by the interaction of habitat context and light level: the presence of oyster reefs reduced brown shrimp survival rates at high light levels, but increased survival in low light. Therefore, predicting how habitat context influences species interactions requires an understanding of both species composition and light level. The setting and the physical factors altered by ecosystem engineers can influence community structure both individually and collectively, and consequently should be incorporated in predictive models aimed at understanding and enhancing our management of coastal ecosystems.

KEY WORDS: *Crassostrea virginica* · Predation · Refuge habitat · Indirect effects · Trophic interactions

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INTRODUCTION

Species capable of building biogenic habitats are considered 'ecosystem engineers' and often play a prominent role in structuring ecological communities (Jones et al. 1994, 1997). Kelp forests and seagrass meadows provide excellent examples of marine ecosystem engineers as they reduce water flows, stabilize sediments, and provide food directly for herbi-

vores and indirectly for many other species by aggregating their prey (Jones et al. 1994, Steneck et al. 2002, Waycott et al. 2009). Dense aggregations of suspension-feeding bivalves perform similar ecological functions, but also provide water filtration services that can modify water column properties such as clarity or light availability (e.g. Dame 1996, Coen et al. 2007). Biogenic habitats are often also characterized by elevated richness, biomass and abundance

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of many associated animals (e.g. Zimmerman et al. 1989, Heck & Crowder 1991, Heck et al. 2003).

Understanding the mechanisms by which biogenic habitats modify species interactions and shape community-level food web dynamics requires disentangling various physical and biological properties (e.g. Pace et al. 1999, Grabowski 2004, Hughes & Grabowski 2006, Scheinin et al. 2012). The 3-dimensional structure of biogenic habitats offers refuge to prey and reduces predator foraging efficiency by disrupting visualization, pursuit, or capture of prey (e.g. Crowder & Cooper 1982, Littler et al. 1989, Diehl 1992, Beukers & Jones 1998). Additionally, many biogenic habitats directly or indirectly modify water column properties that affect visualization and predator–prey interactions. For instance, water clarity and light level can affect predator foraging success, prey detection and the reactive distances of predators, although the direction and magnitude of these effects may be highly variable depending on the prey-capture and predator-avoidance behaviors of the species involved (Abrahams & Kattenfeld 1997, Meager et al. 2005). Collectively, light level and habitat context may interact to influence species interactions and community structure indirectly in a non-additive matter (Minello et al. 1987, Snickars et al. 2004).

Subtidal and intertidal oyster reefs are an excellent example of marine ecosystem engineers as they modify the local environment through the creation of 3-dimensional structure (i.e. autogenic engineering) (e.g. Lenihan 1999, Luckenbach et al. 1999, Coen et al. 2007) and by increasing available light through filter-feeding (i.e. allogenic engineering) (e.g. Dame 1996, Newell 2004, Newell et al. 2005). The complex 3-dimensional structure of oyster reefs provides refuge for many prey species, while also attracting higher trophic level organisms due to the abundant food resources (e.g. Zimmerman et al. 1989, Coen et al. 1999, Peterson et al. 2003). The filter-feeding of oyster reefs can increase light levels by removing phytoplankton and inorganic particles from the water column (e.g. Dame 1996, Grizzle et al. 2006, Newell et al. 2007). In addition to their ability to modify water column properties, oyster reefs typically occur in estuarine waters of highly variable water clarity and along a natural gradient of decreasing light availability at depths from intertidal to greater than 6 m. Given the spatial and temporal variability of light and habitat context in shallow coastal ecosystems, their potential individual effects and interactions deserve further attention to increase our understanding of the factors that structure benthic marine communities.

We conducted a series of laboratory experiments to investigate the effects of habitat context (i.e. oyster reef, structureless bottom) and light level (high, intermediate, low) on prey survival. Estuarine and coastal settings host diverse assemblages of demersal fishes and other reef-associated predators, and we chose to investigate interactions between particularly common estuarine species: Atlantic croakers *Micropogonias undulatus* preying upon daggerblade grass shrimp *Palaemonetes pugio* and blue crabs *Callinectes sapidus* preying upon brown shrimp *Farfantepenaeus aztecus*. The 2 predators exhibit drastically different foraging strategies, and have broad diets that include crustacean prey (Overstreet & Heard 1978, Alexander 1986). Atlantic croakers rely heavily on vision for prey pursuit and capture (Poling & Fuiman 1999), and blue crabs adaptively forage using both sight and chemolocation (Hughes & Seed 1995). We predicted that the complex structure of oyster reefs would reduce predator foraging success, whereas changes in light level could affect both predator and prey response, especially those that rely heavily on visual cues.

MATERIALS AND METHODS

Experimental design

All experimental trials were conducted during October 2011 under natural light conditions on the unshaded vessel dock at the Dauphin Island Sea Lab (DISL). For each experiment, the design was orthogonal with 2 levels of habitat (oyster reef or structureless bottom) and 3 light levels (high, intermediate, low). The experimental trials were conducted in aerated, round 38 l opaque mesocosms filled with 32 l of clear, salinity 25 seawater that had been passed through sand filters and treated with ultraviolet light. Oyster reef treatments received 7.5 kg of cleaned oyster shell configured into a mounded, high-relief reef (0.25 m tall) that covered the entire mesocosm bottom (0.55 m² area), but no other substrate or structure (aside from an air stone) was added.

Water clarity is influenced by the amount and composition of particles suspended in the water column and directly affects light level (Davies-Colley & Smith 2001). Light levels of high, intermediate and low were achieved by covering the experimental mesocosms with 0.6 × 0.6 m (0.32 cm thickness) Plexiglas[®] acrylic sheets (ePlastics[®]) of differing light transmission values. The utilization of acrylic lids to filter or reduce ambient light availability has

been used in coral reef physiological studies (Grottoli & Wellington 1999) and to mimic turbidity in fish behavioral studies (Sundin et al. 2010). According to the manufacturer's specifications, the clear (High), smoke (Intermediate) and mirror (Low) mesocosm lids allowed 92, 27 and 0% light transmittance, respectively. The lids were secured on the mesocosms with braided twine to assure they were not accidentally uncovered during the trials. Prior to conducting the experiments, light levels were examined within the different mesocosm treatments using a LI-COR LI-1400 Datalogger (LI-COR®) equipped with quantum sensors. The LI-1400 recorded photosynthetically active radiation (PAR) at the mesocosm bottom and in the open air. PAR values at the bottom of each mesocosm were divided by air values to determine the percentage of available light passing through each mesocosm cover. Incremental 1 min averages of these values over a 25 min period were calculated.

The predators and prey examined in these experiments are among the most numerically abundant fauna in estuarine and coastal waters of the US Gulf and Atlantic coasts. The first experiment involved 1 sub-adult Atlantic croaker (~12 cm total length) predator and 20 grass shrimp (~2 cm total length) as prey in each tank. Live croakers were collected by trawling in Mobile Bay, USA, and grass shrimp were collected with hand nets along shallow *Spartina alterniflora* marshes on Dauphin Island, Alabama, USA. The second experiment involved 1 blue crab (~10 cm carapace width) predator and 6 brown shrimp (~8 cm total length) as prey. Live blue crabs were captured with baited crab traps near Dauphin Island, and brown shrimp were locally collected and purchased from Jemison's Bait and Tackle in Coden, Alabama, USA. All predators were collected and held in the indoor mesocosm facilities at DISL, and all prey were acquired the morning each experimental trial began. While in holding tanks, all predators were fed a diet of squid and small fish twice weekly and were starved for 24 h prior to a trial. Prey densities (36 grass shrimp m⁻², 11 brown shrimp m⁻²) used in the experiments fell within the range of densities observed in created oyster reefs and adjacent mud-flat habitats (Scyphers et al. 2011). Individual predators and prey were only used in 1 trial each.

To begin a trial, all prey and 1 caged predator were introduced into the mesocosm and allowed to acclimate for 30 min before the predator was released at 11:00 h each day and trials lasted 22 h. The 22 h trial length was chosen to incorporate a nearly diel light cycle and allow adequate time to end and begin the

subsequent trial. After predators were released, each mesocosm was covered with its randomly assigned lid that was not removed until the trials ended. To end each trial, the predator was removed, measured and released alive. Structured habitats were removed and carefully examined to ensure that they did not contain any prey items. Remaining seawater was passed through a 500 µm sieve to recover all prey items. All recovered live prey were immediately placed on ice and returned to the laboratory to be enumerated and measured. A recapture control trial was conducted without predators to assure that all prey not consumed by predators were effectively recaptured and enumerated at the end of each trial. This trial included all light and habitat treatment pairings and was run in an identical way to the trials with predators.

Statistical analyses

To test the effects of each light treatment (i.e. mesocosm lid type) on PAR reaching the mesocosm bottom, a 1-factor ANOVA was run on the LI-COR data. The fixed main effects of habitat context and light level as well as their interaction were tested using ANOVA. Prior to ANOVA, all data were subjected to a Shapiro-Wilk test for normality and Levene's test for homogeneity of variance, and all proportional survival data were arcsine transformed. When applicable, significant ANOVA results were followed by Tukey's HSD post hoc tests to determine differences between factor levels. All analyses were conducted using SPSS, and results for all tests were considered significant at $p < 0.05$.

RESULTS

Light level treatment (i.e. mesocosm lid type) had a measureable effect on the proportion of PAR reaching the mesocosm bottom (Fig. 1) ($n = 25$, $F_{2,72} = 1274.6$, $p < 0.001$). In mesocosms with clear lids (high), 40.6% (± 1.2 SE) of PAR penetrated the 0.3 m water column and reached the mesocosm bottom. In mesocosms with smoke lids (intermediate) and mirror lids (low), 12.8 (± 0.1) and 0.6 (± 0.01)% reached the mesocosm bottoms, respectively. Measured PAR values were 2133.9 ± 85.8 µmol m⁻² s⁻¹ for air, 965.4 ± 66.4 for clear, 359.82 ± 10.9 for smoke, and 6.36 ± 0.2 for mirror lid treatments. Water temperature, as measured in control tanks during the 22 h duration of a trial, was slightly higher in mesocosms with clear

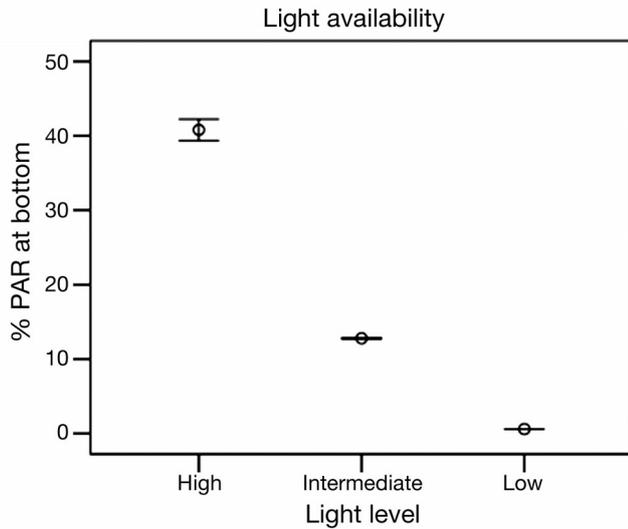


Fig. 1. Effect of each Plexiglas™ cover establishing different light levels (high: clear lid; intermediate: smoke lid; low: mirror lid) on photosynthetically active radiation (PAR) measurements at mesocosm bottom; values are \pm SE

($25.7 \pm 0.2^\circ\text{C}$) and smoke ($25.1 \pm 0.2^\circ\text{C}$) than mirror lids ($24.3 \pm 0.2^\circ\text{C}$).

The overall influence of habitat context and light level differed for both common species pairings. In the experiment using Atlantic croaker and grass shrimp, 2-factor ANOVA determined that the presence of oyster reef habitat significantly increased prey survival by $23 \pm 3\%$, and the effect of light level was non-significant ($n = 6$; Table 1, Fig. 2A). The interaction of habitat context and light was also non-significant. Brown shrimp survival in the presence of blue crab was significantly affected by light and the

Table 1. Two-factor ANOVA testing the effects of light and habitat context on prey survival for Atlantic croaker *Micropogonias undulatus* predation on grass shrimp *Palaemonetes pugio* and blue crab *Callinectes sapidus* predation on brown shrimp *Farfantepenaeus aztecus*. * $p \leq 0.05$, ** $p \leq 0.01$

	df	SS	MS	F	p
Croaker–grass shrimp					
Light	2	152.9	76.5	0.295	0.747
Habitat context	1	2552.9	2552.9	9.835	0.004 **
Light \times Habitat context	2	222.7	111.4	0.429	0.655
Error	30	7787.2	259.6		
Total	36	145 621.6			
Blue crab–brown shrimp					
Light	2	3364.3	1682.2	4.503	0.022 *
Habitat context	1	10.4	10.4	0.028	0.869
Light \times Habitat context	2	2887.8	1443.9	3.865	0.035 *
Error	24	8965.8	373.6		
Total	30	53 917.8			

interaction of light and habitat context ($n = 5$; Table 1). Under high light levels, prey survival was $33 \pm 4\%$ higher in structureless than in oyster reef treatments (Fig. 2B). Conversely, prey survival was 10 ± 2 and $23 \pm 9\%$ higher in oyster reef than in structureless treatments at intermediate and low light levels, respectively. Results from Tukey's HSD post hoc tests indicated that overall survival was lower in low light treatments than intermediate or high light, but this effect interacted with habitat context. Prey survival was 100% across all treatments in the recapture control trial.

DISCUSSION

Improving our mechanistic understanding of the linkages between biogenic habitats, physical characteristics of the environment, and ecologically and economically important predators and prey, such as the organisms examined in this study, is an essential step towards implementing ecosystem-based management for coastal ecosystems (Thrush & Dayton 2010). We found that grass shrimp survival from predation by Atlantic croakers was higher in oyster reef than in structureless treatments, which further supports the notion that complex, structured habitats can provide refuge for lower trophic level species (Crowder & Cooper 1982, Heck et al. 2003). These results were not unexpected, since grass shrimp are highly associated with complex structured habitats and have been shown to preferentially select oyster reef when threatened by predators (Posey et al. 1999).

Furthermore, Atlantic croakers are among the most abundant demersal predators in temperate to sub-tropical coastal waters and are often found in high densities near a variety of habitats, including oyster reefs (Geraldi et al. 2009, Scyphers et al. 2011), but are not considered to be directly enhanced by oyster reef structure (Peterson et al. 2003). On the other hand, the similar survival rates of grass shrimp observed across all light levels were largely unexpected, since previous studies have found the foraging efficiency of Atlantic croakers to be reduced by turbid water (Minello et al. 1987). Our results suggest that the beneficial effects of structured habitat on prey survival may outweigh the effect of light on visual predator foraging efficiency. However, as with all mesocosm experiments, some caution is necessary when interpreting behaviors and predation rates in view of the confined environment involved.

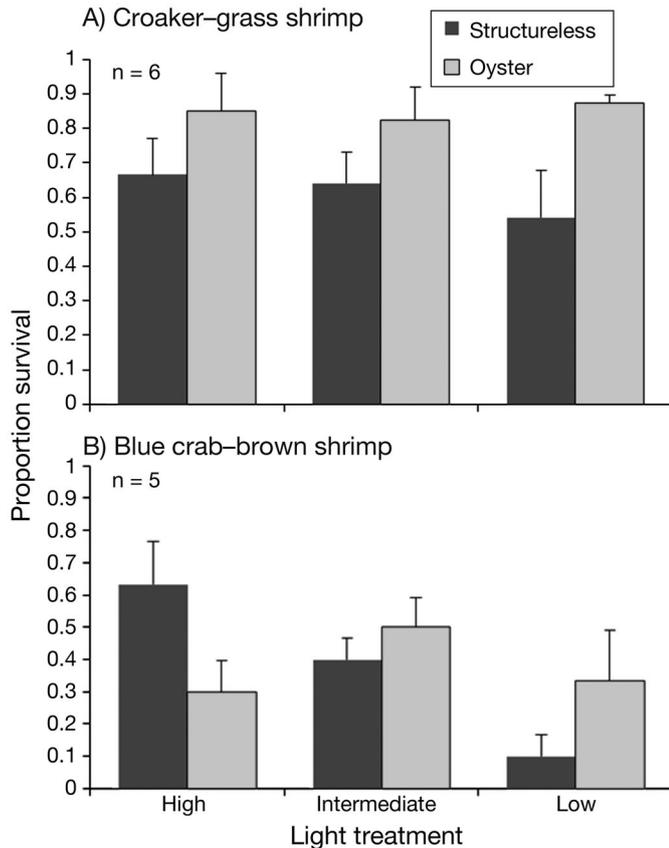


Fig. 2. Proportional survival (+1 SE) of prey in light treatment experiments at 2 habitat levels (oyster reef and structureless bottom) with (A) Atlantic croaker *Micropogonias undulatus* and grass shrimp *Palaemonetes pugio* and (B) blue crabs *Callinectes sapidus* and brown shrimp *Farfantepenaeus aztecus*

Blue crab–brown shrimp trials revealed a complex relationship between habitat context and prey survival as affected by light level. The significant interaction resulted from similar prey survival in oyster reef treatments across all light levels, while prey survival in structureless treatments decreased in concert with light level. The very low prey survival in low light and structureless treatments suggests that multi-sensory predators may be very efficient at foraging without visual cues and potentially benefit from the element of surprise in the absence of structural refuge for prey. Since previous studies have shown that blue crab may exhibit higher growth, activity and feeding rates at higher water temperatures (Eggleston 1990), it is worth noting that our temperature data indicated that high light treatments averaged 1.4°C warmer than low light treatments. In high light conditions, prey survival was higher in structureless habitats, suggesting that the prey avoidance behavior of shrimp may be more efficient than the prey capture efficacy of blue crabs under

these conditions. In other words, prey survival declined with diminishing light level in structureless treatments but was consistent across all structured treatments, which suggests that complex structure may mitigate the effects of highly variable light levels and could shelter prey from multi-sensory predators in low light conditions. Reduced water clarity and low light are generally expected to decrease the encounter rate between predators and prey (Benfield & Minello 1996), but the refuge value may be lessened for prey faced with predators that can respond to both visual and chemical cues. Nearly all previous studies have found that the refuge value of complex structure diminishes with reduced water clarity (Gregory & Levings 1996, Snickars et al. 2004, Gadomski & Parsley 2005), but the one study involving brown shrimp prey also found an interaction between water clarity and substrate type (Minello et al. 1987). Furthermore, the preferential use of structured habitats by some small prey species has been shown to decline in turbid water conditions (Snickars et al. 2004).

The interaction between light and habitat context in the blue crab and brown shrimp trials suggests that predator–prey dynamics may be affected on larger scales if oyster filtration results in increased light availability beyond the reef setting. Specifically, these results suggest that brown shrimp survival from blue crab predation may be increased in structureless habitats if light level is increased. Some evidence supports the notion that ecosystem engineering bivalves can measurably reduce water column seston at localized (Cloern 1982, Grizzle et al. 2008) and potentially larger scales (Newell 2004, Newell et al. 2007, but see Pomeroy et al. 2006, 2007). Recent studies have estimated that oysters could remove up to 37% of total seston in the water column (Grizzle et al. 2006, 2008). Turbidity affects species interactions through the scattering of available light and disrupting the visual capabilities of aquatic species (Abrahams & Kattenfeld 1997). We investigated this single component of water clarity by directly manipulating light level instead of altering turbidity, and our approach yielded light levels very similar to field measurements of irradiance near shallow (<1 m) oyster reefs and unstructured bottoms ($\sim 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$; Plutchak et al. 2010). However, in addition to improving water clarity, the filter-feeding of oysters could also influence species interactions through the removal of phytoplankton, algae and other biotic components of turbidity (Cobcroft et al. 2001). Considering the broad distribution and ecological functions of oyster reefs and the fact that only habitat context and light were manipulated in these experi-

ments, it is conservative to assert that the setting and physical–biological coupling of ecosystem engineers may result in diverse and unexpected species interactions.

Our study, coupled with the vast literature on other physical factors such as water flow and wave energy that affect species interactions in shallow benthic communities (e.g. Wootton 1994, Powers & Kittinger 2002, Smee et al. 2010, Large et al. 2011), demonstrates that physical and biological factors are inextricably coupled in coastal marine ecosystems. As destructive anthropogenic practices have targeted and widely reduced both complex biogenic habitats and filter-feeding bivalves in coastal ecosystems, habitat restoration and enhancement activities have been increasingly utilized to mitigate ecosystem service losses and sustain fishery harvests (e.g. Peterson & Lipcius 2003, Powers et al. 2009, Beck et al. 2011). Developing a predictive understanding of how multiple physical and ecological factors collectively influence community structure will be integral for implementing ecosystem-based management in coastal marine ecosystems, and clearly this will require understanding much more complex trophic and species–environment interactions.

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