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## EVALUATING THE IMPACT OF MESOPREDATORS ON OYSTER RESTORATION IN THE NEW YORK METROPOLITAN REGION

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**ABSTRACT** Predation of newly settled juvenile *Crassostrea virginica* often dominates post-settlement mortality. Resident mesopredators such as the xanthid mud crabs are abundant ( $>200/m^2$ ) on constructed subtidal oyster reefs in the New York metropolitan region and may contribute to post-settlement oyster mortality. Two study sites with differing mesopredator species, Hastings and Soundview Park, were selected to examine the role of small crustacean predators in post-settlement mortality. The white-fingered mud crab (*Rhithropanopeus harrisi*) inhabits Hastings, whereas the flat mud crab (*Eurypanopeus depressus*) and Sayi mud crab (*Dyspanopeus sayi*) inhabit Soundview Park. Using size-selective mesh cages to exclude predators, the effects of predator size on oyster predation and recruitment at Hastings and Soundview Park were examined. Overall, Soundview Park had higher consumption rates than Hastings. The highest consumption at Soundview Park occurred when predators of all sizes had access to the oyster prey. Larger-sized predators were likely responsible for oyster mortality, as oyster mortality was not different between the mesopredator and no-predator treatment at Soundview Park. Few oysters recruited at Soundview Park; thus predator size effects on oyster recruitment could not be effectively evaluated between sites. Recruitment at Hastings was not affected by predator-exclusion treatments, in agreement with the oyster predation experiments. Though abundant, no mud crab mesopredator recovered at either site was greater than 22 mm in carapace width. Mesopredators were likely not of sufficient size to be dominant predators of newly settled juvenile oysters at Hastings and Soundview Park. Instead, predation pressure at Soundview Park was likely due to larger mobile predators such as blue (*Callinectes sapidus*) and spider crabs (*Libinia* spp.). Mesopredator size is an important factor to consider when evaluating mesopredator roles on oyster reefs.

**KEY WORDS:** *Eurypanopeus depressus*, *Rhithropanopeus harrisi*, *Dyspanopeus sayi*, *Crassostrea virginica*, predation, oyster restoration

### INTRODUCTION

Predator size and habitat structure greatly influence foraging success and energy transfer in benthic communities. Species abundance, growth, and diversity tend to be higher in structured habitats than that in unstructured habitats (Edgar 1990, Lee et al. 2001, Heck et al. 2003, Tolley & Volety 2005). This is likely because structured habitats provide increased prey refuge from predation (Lee & Kneib 1994, Beukers & Jones 1997, Hill & Weissburg 2013a, Bishop & Byers 2015) by increasing searching and handling time (Stoner 2009, Alexander et al. 2012), decreasing the accessibility of prey located in crevices (Toscano & Griffen 2013), and altering olfactory cue detection (Smee et al. 2008, Ferner et al. 2009). Decapod predators, which are important in regulating bivalve populations (Hines et al. 1990, Seitz et al. 2001, Lohrer & Whitlatch 2002), tend to be mobile, actively scavenging and foraging within a structured habitat. Small decapod predators may have an advantage over larger decapod predators in their ability to access prey in hard to reach crevices (Toscano & Griffen 2013). Small decapod predators may also travel less than transient predators such as adult blue crabs [*Callinectes sapidus* (Rathbun, 1896)], which have the potential to move large distances daily (Hines et al. 1995, Carr et al. 2004). Thus, unlike transient predators, smaller resident predators may apply consistent predation pressure in a given structured habitat. Additionally, numerous studies have shown that larger decapod predators, such as *C. sapidus* and green crabs [*Carcinus maenas* (Linnaeus, 1758)], consume shellfish of the same size as smaller decapod predators, but at

higher per capita rates (Bisker & Castagna 1987, Juanes 1992, O'Connor et al. 2008). Although individual decapod mesopredators' consumption rates do not rival those of larger transient decapods, their collective consumption rates may be equivalent to or greater than those of larger transient predators due to their high abundances (Kulp et al. 2011, Rindone & Eggleston 2011, Carroll et al. 2015).

One group of potentially important decapod mesopredators includes the xanthid mud crabs, ubiquitously found in high densities in salt marsh (Silliman et al. 2004), seagrass beds (Strieb et al. 1995), and oyster reefs (Meyer 1994) along the eastern coast of the United States. Xanthid mud crabs have been suggested to be important predators of juvenile *Crassostrea virginica* (Gmelin, 1791) on oyster reefs (Bisker & Castagna 1987, Kulp et al. 2011, Rindone & Eggleston 2011). One of these, the Atlantic mud crab [*Panopeus herbstii* (Edwards, 1834)], has the largest carapace width (CW) of the xanthid mud crabs (Ryan 1956), the highest per capita juvenile oyster predation rate (Bisker & Castagna 1987), and is abundant in high-salinity sites ( $>20$ ) (McDonald 1982, Meyer 1994) coincident with the highest oyster growth rates (Paynter & Burreson 1991). Due to these listed traits, most mud crab mesopredator studies have focused on the influence of *P. herbstii* on juvenile oysters (Grabowski 2004, Toscano & Griffen 2012, Hill & Weissburg 2013a). Yet, in the locations of some oyster reef restoration projects, such as those in the New York metropolitan region, *P. herbstii* is not abundant (Kulp, personal observation). Instead, xanthid mesopredators such as the flat mud crab [*Eurypanopeus depressus* (Smith, 1834)], Sayi mud crab [*Dyspanopeus sayi* (Smith, 1869)], and white-fingered mud crab [*Rhithropanopeus harrisi* (Gould, 1841)] dominate.

Efforts to restore oyster reefs have increased in recent years, with a goal of enhancing oyster fisheries and the ecosystem

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benefits provided by oyster reefs (Wells 1961, Tolley & Volety 2005, Grizzle et al. 2008). The Hudson River Foundation constructed preliminary oyster reefs throughout the New York metropolitan region in 2010 with the goal of expanding reef sites in the future. Two of the five oyster restoration sites, Soundview Park and Hastings, were selected to examine the collective contribution of mesopredators to post-settlement oyster mortality. These sites were selected because they have different mud crab species present. At Soundview Park, *Eurypanopeus depressus* and *Dyspanopeus sayi* have been found, whereas only *Rhithropanopeus harrisi* has been observed at Hastings (Peterson & Kulp 2015). Although mud crabs can be found in high abundances at both sites ( $>200/m^2$ ), the two sites may have different predation pressures due to the different mud crab species present. Kulp et al. (2011) found that *E. depressus* consumed four times more juvenile oysters than *R. harrisi* in a laboratory environment. Thereby, *R. harrisi* may not consume oyster prey in the field as readily as other mesopredators such as *E. depressus* and *D. sayi*, which could result in lower predation pressure at Hastings than Soundview Park. As such, there may be important site-specific differences in the impact of mud crabs on juvenile oyster survival rates.

The main goal of this study was to clarify species-specific roles of mud crabs on restored oyster reefs by using predator-exclusion cages. Although Soundview Park and Hastings reefs were expected to have similar mud crab abundances, their differential mud crab species compositions were expected to lead to higher predation at Soundview Park than Hastings. Understanding these site-specific differences could help with future restoration site selection not only in New York, but also at locations that have a similar composition of mesopredator species present.

## MATERIALS AND METHODS

### Site Selection

Experiments were conducted at two constructed preliminary oyster reefs in the New York metropolitan region: Hastings (41° 0.032' N, 73° 53.068' W) and Soundview Park (40° 48.576' N, 73° 51.860' W). In 2010, the Hudson River Foundation and partners built the two continuous oyster reefs by laying shell veneer on top of a transplanted bedrock base. The footprints of the Hastings and Soundview Park oyster reefs are approximately 69 and 40 m<sup>2</sup>, respectively. Hatchery-reared juvenile oysters that settled on shell were planted at both sites in three installments: October 2010, November 2010, and June 2011. The sediment at Soundview Park was a mixture of gravel and sand, whereas the sediment at Hastings was unconsolidated mud. The two sites have different salinity regimes (Soundview Park: salinity of ca. 20–25; Hastings: salinity of ca. 5–10) and different resident mud crab species (Soundview Park: *Dyspanopeus sayi* and *Eurypanopeus depressus*; Hastings: *Rhithropanopeus harrisi*). Additionally, at the higher salinity site, Soundview Park, adult *Callinectes sapidus* and spider crabs have been regularly observed (*Libinia* spp.; Peterson & Kulp 2015). Conversely, although not regularly caught or observed, oyster toadfish [*Opsanus tau* (Linnaeus, 1766)] and adult *C. sapidus* have been observed at the Hastings site (Peterson & Kulp 2015). Overall, fewer large juvenile oyster predators are present at Hastings than Soundview Park.

### Predator Abundances

To estimate resident mesopredator abundances, four replicate trays (44 × 30 × 12 cm) lined with fiberglass window screen were placed across the longest axis of the Hastings and Soundview Park reefs for 5 and 6 wks in July and September 2012, respectively. Trays were filled with Atlantic surf clam [*Spisula solidissima* (Dillwyn, 1817)] shell veneer prior to being inserted into the reef. After retrieval, mesopredators in each tray were identified, measured, and counted. Not all trays were recoverable in July and September. One tray was missing from Hastings in July and one tray was missing from both sites in September.

To determine the presence of large mobile predators, one baited fish trap (ca. 120 × 50 × 40 cm with 20-cm-diameter doors) was deployed at Hastings and Soundview Park for 48 h in August 2012.

### Predator-Exclusion Experiments

A randomized two-factorial design comparing predator exclusion [three levels: all predators (AP), mesopredators (MP), and no predators (NP)] and oyster reef site (Hastings and Soundview Park) was used to test the effects of mud crab species identity and predator size on post-settlement juvenile oyster (spat) mortality. Spat mortality was measured using two different experiments: a short-term predation experiment and a long-term recruitment experiment.

There are multiple limitations to using naturally settled oyster spat for consumption studies, including different settling densities, variable growth rates, and orientation (Hidu 1969, Newell et al. 2007, Kulp et al. 2011). Therefore, the number, size, and arrangement of oysters were standardized by artificially attaching individual oyster spat onto 12 × 12 cm unglazed terracotta tiles using ethyl cyanoacrylate glue in the short-term predation experiment. Hatchery-reared oyster singles [5–8 mm shell height (SH)] used for the artificially adhered oyster tiles were provided by the East Hampton Town Shellfish Hatchery in East Hampton, NY. Artificially adhered oysters were given at least 1 wk to grow in a flow-through indoor seawater system at Stony Brook University's Marine Station, Southampton, NY. Individuals that died after the gluing process were replaced at least 1 day prior to deployment. Oysters less than 5 mm SH were not used due to increased mortality post-gluing. At the time of deployment, oysters had grown to between 10 and 20 mm SH, a range that mud crabs are capable of consuming (Newell et al. 2007, Kulp et al. 2011).

While using artificially adhered oysters has become a regular practice in predation studies (Kimbrow et al. 2014, Carroll et al. 2015), the artifacts on predation remains unknown. Therefore, a mesocosm experiment was conducted to quantify the difference between artificially adhering oysters versus naturally recruited oysters. Oysters were either artificially adhered to unglazed terracotta tiles ( $n = 13$ ) or naturally settled on oyster cultch ( $n = 12$ ). The oyster treatments were then offered to male *Dyspanopeus sayi* (15–23 mm CW) in mesocosms for 72 hrs. Results from this experiment suggest that artificially adhering oysters to tiles inflates predation rates (two-sample *t*-test:  $t = 2.67$ ,  $df = 23$ ,  $P = 0.014$ ), so caution should be used when interpreting consumption rates from the short-term experiment.

Because mud crabs may prefer smaller-sized oyster spat ( $<10$  mm SH; Newell et al. 2007, Kulp et al. 2011), there is the potential that fewer oysters were consumed by mesopredators

during the field experiment than would be expected with smaller spat. In an effort to address this concern, a long-term recruitment study was conducted to evaluate predation during early settlement and at oyster sizes that were not represented in the short-term experiment. The long-term recruitment experiment measured oyster recruitment onto the top and side of  $12 \times 12$  cm unglazed terracotta tiles in August 2012. Recruitment was defined as the number of settled spat present after 6 wks. The number and size of live oysters (with tissue), oyster scars (valve imprint), and oyster boxes (articulated valves with no tissue) on the top and side of each tile were recorded after retrieval. The oyster scars and boxes were used as a proxy for post-settlement oyster mortality.

In the short- and long-term experiments, each terracotta tile was haphazardly assigned to one of three predator-exclusion treatments—AP, MP, NP—that offered varying levels of protection from predation. The AP treatments offered no protection from predation; tiles were attached to a 25-mm aperture vinyl-coated lobster wire panel ( $20 \times 35$  cm). The MP treatments consisted of  $20 \times 10 \times 35$  cm cages made from 25-mm aperture vinyl-coated lobster wire so that predators larger than 25 mm could not access the prey. The NP treatments were also made from 25-mm aperture vinyl-coated lobster wire, but with Vexar polyethylene netting lining the cage interior to prevent entry of predators larger than 5 mm. To test for potential cage artifacts (Steele 1996), a cage control (CC) was used. The CC had two of the six sides missing and was lined with 5-mm Vexar polyethylene netting. In all treatments, tiles were zip-tied to the wire frame and a brick was attached on the bottom for cage stability. Four replicates of each treatment were randomized across two rows on the reef; each row had two replicates of each treatment.

In the short-term predation experiment, terracotta tiles were deployed for 1 wk during one of two consecutive experimental runs in July 2012. The second deployment at Hastings was removed after 5 days instead of 7 days due to logistical constraints. For this experimental trial, consumption was scaled to a 7-day predation rate to account for differing experimental length between sites. Any oysters missing at retrieval were assumed to have been consumed.

#### Data Analysis

All statistical analyses were performed using R software (R Core Team 2015). A two-way factorial general linear model (GLM) with quasipoisson residual errors was used to determine whether site and retrieval month affected mud crab abundance (Logan 2010).

For the short-term predation study, a two-way GLM with quasibinomial residual errors was used to determine site and predator exclusion effects (AP, MP, and NP) on oyster mortality. The 7-day scaled predation rate for the 5-day Hastings experimental run was rounded to the nearest integer prior to being analyzed. Tukey's honestly significant difference (HSD) post-hoc tests were performed comparing within-site cage treatment effects using the package "multcomp."

For the long-term recruitment experiment, only the Hastings site was analyzed due to the low recruitment at Soundview Park (<2 oysters per tile). To examine the effects of predator treatment (AP, MP, and NP) on oyster recruitment, a one-way factorial GLM with quasipoisson residual errors was used. As above, Tukey's HSD post-hoc tests were used to distinguish

between-treatment effects. Appropriate model diagnostics were run on each analysis to assess models; statistical significance  $\alpha$  was set at 0.05.

## RESULTS

### Predator Abundances

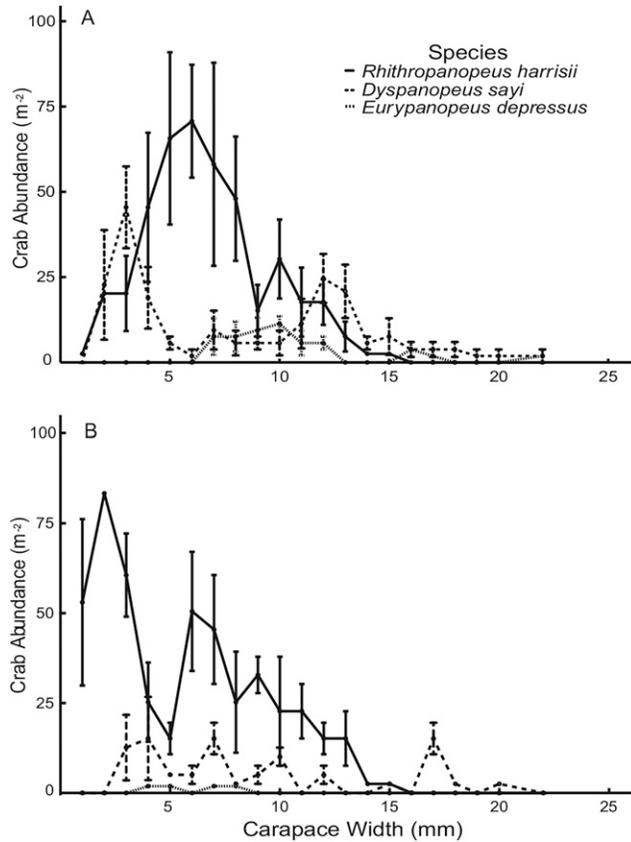
Mud crab abundance of individuals depended on both site location and retrieval month [interaction term:  $F_{(1,12)} = 7.08$ ,  $P = 0.026$ ]. Although there was no main retrieval month effect [ $F_{(1,12)} = 0.99$ ,  $P = 0.35$ ], there was a main site location effect [ $F_{(1,12)} = 24.6$ ,  $P = 0.0008$ ]. In both July and September, the Hastings site contained twice as many mud crabs as Soundview Park. The abundance of Hastings' resident species, *Rhithropanopeus harrisi*, was similar in July and August. At Soundview Park, however, the abundances of *Dyspanopeus sayi* and *Eurypanopeus depressus* decreased by 50% in August. Abundances at Soundview Park were dominated by *D. sayi* with densities 4 and 10 times greater than *E. depressus* in July and August, respectively. Thus, *D. sayi* could be a more important mesopredator than *E. depressus* at Soundview Park.

The mud crab size-distribution patterns were different at Hastings and Soundview Park (Fig. 1). Not only were *Rhithropanopeus harrisi* smaller in size than *Dyspanopeus sayi* and *Eurypanopeus depressus*, reaching no larger than 15 mm CW, but also had a greater proportion of individuals smaller than 10 mm CW. Thus, the difference in the mud crab density between sites was likely driven by high abundance of *R. harrisi* individuals less than 10 mm CW at Hastings. Although more than half of mud crabs at both sites were smaller than 10 mm CW, there was still a formidable density of mud crabs greater than 10 mm CW:  $78 \pm 14$  *R. harrisi* per  $m^2$  (mean  $\pm$  SE),  $93 \pm 9$  *D. sayi* per  $m^2$ , and  $30 \pm 3$  *E. depressus* per  $m^2$  in the July recruitment trays. The 15–22 mm CW size range also showed a difference in abundance between sites:  $33 \pm 2$  *D. sayi* per  $m^2$  and  $15 \pm 4$  *E. depressus* per  $m^2$  at Soundview Park opposed to two *R. harrisi* (both 15 mm CW) collected out of all the recruitment trays at Hastings. Because predator size strongly influences consumption rates, the mud crab abundance data suggest that there was a greater potential for mud crab oyster predation at Soundview Park than at Hastings.

In addition to differential mud crab abundance patterns, there were also different large oyster predator abundances between sites. Four adult *Callinectes sapidus* (between 80 and 180 mm CW) were collected from a fish trap at Soundview Park in September, whereas no predators were collected from the fish trap in July. Even though few were recorded in the fish traps, adult *Libinia* spp. and *C. sapidus* were both regularly observed on the Soundview Park reef during the experimental period. Conversely, no large oyster predators were collected in the fish trap or observed at Hastings. Together, these observations indicate a greater density of large, mobile predators at Soundview Park compared with Hastings.

### Short-Term Predation Experiment

Consumption rate of oyster spat depended on both site and cage treatment [interaction term:  $F_{(3,63)} = 5.32$ ,  $P = 0.003$ , Fig. 2]. Consumption was higher at Soundview Park than Hastings [ $F_{(1,63)} = 62.5$ ,  $P < 0.001$ ], with  $65.0\% \pm 14.9\%$  of oysters consumed on tiles accessible to AP compared with  $3.42\% \pm 1.60\%$  in

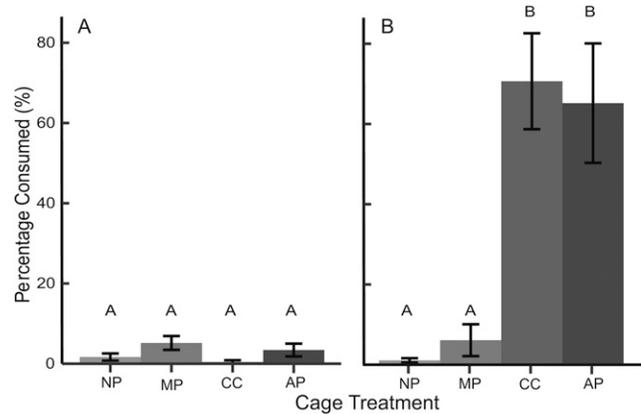


**Figure 1.** Average size–frequency distribution of mud crabs at Soundview Park and Hastings in (A) July and (B) September 2012. Four replicate colonization trays ( $0.13 \text{ m}^2$ ) filled with cultch were inserted into each reef. After 6 wks, the number of mud crabs was quantified. At Hastings, *Rhithropanopeus harrisi* were present in trays; at Soundview Park, *Dyspanopeus sayi* and *Eurypanopeus depressus* were present in trays. The mean abundance of mud crabs per  $\text{m}^2$  is shown with  $\pm 1$  SE.

Hastings. Consumption differed significantly between predator-exclusion treatments [ $F_{(3,63)} = 20.8$ ,  $P < 0.001$ ]. Specifically, consumption was more than an order of magnitude higher in the AP treatment than the MP treatment at Soundview Park ( $P < 0.001$ ), suggesting that large predators were important oyster consumers. Additionally, consumption in the MP treatment ( $5.86\% \pm 4.0\%$ ) was not significantly different from the NP treatment ( $0.833\% \pm 0.546\%$ ;  $P = 0.922$ ), further supporting the importance of large oyster predators at Soundview Park. No significant differences were observed between AP and CC treatments at Soundview Park site ( $P = 1.00$ ), indicating there were no cage artifacts affecting consumption. Unlike at Soundview Park, oyster mortality was not significantly different among cage treatments at Hastings ( $P > 0.9$ ). Overall, these results imply that mesopredators have a minimal impact on oyster spat that have reached at least 10 mm SH.

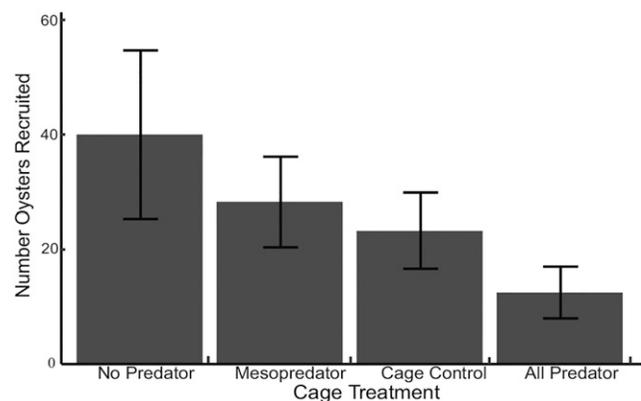
#### Long-Term Recruitment Experiment

Oysters recruited at an average density of 13–40 oysters per tile at Hastings and 0–1 oysters per tile at Soundview Park in each cage treatment. In addition to being more numerous, the recruited oysters at Hastings were also larger, ranging from 1 to 20 mm SH, whereas those at Soundview Park were all less than



**Figure 2.** Proportion of oysters consumed in short-term predation experiment conducted at (A) Hastings and (B) Soundview Park. Tiles with artificially adhered oysters were placed within three predator-exclusion treatments (NP, MP, and AP) and a CC to test for cage artifacts ( $n = 8$  for all treatments). The mean percentage of oysters consumed is shown  $\pm 1$  SE. Tukey's HSD post-hoc tests comparing within-site cage treatment are shown above each bar.

5 mm SH. No significant cage-treatment effects [ $F_{(3,15)} = 1.88$ ,  $P = 0.187$ , Fig. 3] were found at Hastings even though there was a progressive decrease in mean oyster recruitment with decreasing cage protection. Although there was a 56% reduction in oysters recruited to the AP than NP treatment, the high variability in oyster recruitment between tiles likely made detecting statistical differences difficult. For instance, in the NP cage treatments, oyster settlement ranged from 17 to 80 oysters per tile. Even if there were biologically significant cage treatment effects, the dearth of oyster scars or boxes found on any of the tiles indicates predation was not contributing to the oyster recruitment cage treatment differences exhibited. An alternative explanation for the decrease in oyster settlement with decreasing protection could be from cage artifact effects on oyster settlement. There were 50% fewer oysters recruited in the



**Figure 3.** Number of oysters recruited onto the top and side of each tile in long-term recruitment experiment at the Hastings site. Bare tiles were placed within three predator-exclusion treatment cages (NP, MP, and AP) and a CC to test for cage artifacts ( $n = 4$  for all treatments). The mean number of recruited oysters over 6 wks in August 2012 is shown with  $\pm 1$  SE. There was no significant difference found between cage treatments [ $F_{(3,15)} = 1.88$ ,  $P = 0.187$ ].

AP treatment than the CC, suggesting the cage structure artificially increased recruitment in the MP and NP treatments. Evaluating the role of oyster predators at Hastings becomes difficult due to the high variability in oyster recruitment and potential cage artifact effects. Regardless, the recruitment results indicate a limited role for oyster predators in oyster settlement and survival at Hastings.

## DISCUSSION

Decapod mesopredators have consistently been shown to be important consumers of juvenile oysters (O'Connor et al. 2008, Hill & Weissburg 2013a, Johnson et al. 2014, Carroll et al. 2015). Yet, few studies have examined the role of mud crabs on oyster reefs north of New Jersey. These northern oyster reefs, unlike those in the Carolinas (Toscano & Griffen 2012, Carroll et al. 2015), Georgia (Hill & Weissburg 2013a, 2013b), and Texas (Johnson & Smee 2012, Johnson et al. 2014), are often recruitment limited, entirely subtidal, and do not have abundant *Panopeus herbstii* populations. Therefore, this study sought to understand the mesopredator-imposed top-down control on post-settlement oyster mortality in an understudied system. Two New York metropolitan restored oyster reef sites, Hastings and Soundview Park, were studied because they had different mud crab species present. Different mesopredator roles were expected at Hastings (*Rhithropanopeus harrisi* dominant) and Soundview Park (*Dyspanopeus sayi* and *Eurypanopeus depressus* dominant), as *R. harrisi* has been shown to not consume large quantities of oyster spat (Newell et al. 2007, Kulp et al. 2011). Similar to other mud crab mesopredator studies, *D. sayi* and *E. depressus* were expected to play a critical role in structuring oyster populations on the restored oyster reefs in the New York metropolitan region in areas they inhabit. Conversely, *R. harrisi* was expected to have a minimal mesopredator role in areas they inhabit.

Contrary to expectations, there was a minimal mesopredator effect on juvenile oysters in the predation or recruitment experiments. Two studies (Johnson et al. 2014, Carroll et al. 2015) examined the roles of mesopredators using similar predator-exclusion cages on intertidal oyster reefs in North Carolina and Texas. Unlike results from this study, both studies found a MP treatment effect. Although Carroll et al. (2015) suggested that mesopredators were likely driving consumption across all treatments, Johnson et al. (2014) suggested that mesopredators were only major contributors in MP treatments. Two major differences existed between this study and previous studies conducted on southern intertidal reefs. First, some mesopredator species present in North Carolina and Texas reach sizes larger than 22 mm, including *Panopeus herbstii*. The highly abundant *P. herbstii* on southern oyster reefs can reach almost 50 mm CW (McDonald 1982). Second, both studies used larger mesh in MP cages than this study, allowing larger mud crab mesopredators to access oyster prey: 37 mm in Carroll et al. (2015) and 50 mm in Johnson et al. (2014). Although mud crab abundances on the studied New York reefs had high densities of crabs larger than 10 mm CW (approximately 100 individuals/m<sup>2</sup>), there were no mud crab individuals above 15 mm CW at Hastings or 22 mm CW at Soundview Park. Perhaps smaller mesopredators inhabiting northern subtidal oyster reefs do not have the same top-down control on oyster populations as larger mesopredators in southern intertidal oyster reefs.

Predator size affects multiple aspects of predator-prey interactions including prey selection (Toscano & Griffen 2012), foraging rate (Bisker & Castagna 1987), and movement through structure (Bartholomew 2002, 2012). For example, McDonald (1982) suggested that smaller *Eurypanopeus depressus* are able to coexist with larger *Panopeus herbstii* by foraging within smaller interstitial spaces that are inaccessible to *P. herbstii*. Small predators like mud crabs are also prey for intra-guild predators, such as *Callinectes sapidus* and *Opsanus tau* (Grabowski 2004, Hill & Weissburg 2013a). These intra-guild predators not only consume mesopredators, but have non-consumptive effects on mesopredators that decrease mesopredators foraging behavior and positively affect oyster spat survival (Grabowski 2004, Griffen et al. 2012). Toscano and Griffen (2012) further demonstrated that *O. tau* reduces foraging behavior of smaller *P. herbstii* more strongly than larger individuals. Perhaps mud crabs smaller than a certain size were less likely to venture onto experimental tiles, which rested on top of the oyster reef structure, due to habitat partitioning or the fear of being consumed. If smaller predators are less likely to venture on top of the oyster reef due to the presence of larger predators, the role of mud crabs on oyster reefs may have been underestimated using the design in this study. This could be especially important at Soundview Park, which has a more consistent intraguild predator presence than Hastings. Alternatively, as suggested by McDonald (1982), smaller-sized mud crabs may forage primarily in interstitial spaces due to intra-guild competition. Although they can readily consume juvenile *Crassostrea virginica* under laboratory studies (Kulp et al. 2011), mud crabs are scavengers, consuming multiple bivalve species and other invertebrates and detritus (Lindsey et al. 2006, Griffen 2014). Thus, mud crabs may consume alternative interstitial prey when these are available. There were nine and five alternative prey taxa for mud crabs in recruitment trays at Soundview Park and Hastings, respectively, including amphipods, polychaetes and bivalve prey such as *Mytilus edulis* (Linnaeus, 1758). Future field experiments would benefit by including interstitial oyster treatments and examining whether mud crabs shift from interstitial to reef surface predators once they reach a threshold size.

In contrast to Soundview Park, large predators may not contribute to post-settlement mortality at Hastings. First, there was low consumption of oysters greater than 10 mm exposed to all predators (<5% consumed), which should be readily consumed by larger-sized predators. Second, there were few oyster scars or boxes on the tiles, suggesting the lower recruitment on the AP treatment oyster tiles was not due to post-settlement mortality. Additionally, few large *Callinectes sapidus* and *Opsanus tau* have been detected at Hastings (Peterson & Kulp 2015), and none were caught or observed during the experimental period. Due to a reduced predator presence at Hastings, other factors could have influenced initial settlement. Most likely, cage artifact effects artificially increased oyster settlement (Hall et al. 1990, Miller & Gaylord 2007), because the CC treatment appeared to have slightly higher recruitment than tiles with AP access. Reduced flow induced by the cages could have increased larval supply, as well as alleviated the energy associated with waves (Miller & Gaylord 2007), improving settlement rate. Again, because there were limited oyster scars on tiles after 6 wks, initial settlement and not post-settlement mortality may have

driven the recruitment. Even when oyster larvae settle in controlled environments like hatcheries, they are aggregate settlers (Hidu 1969, Newell et al. 2007, Kulp et al. 2011) with high variability in settlement densities that can range from zero to a hundred per oyster shell (Kulp, personal observation). Thus, the high oyster recruitment variability might also be a result of natural variability in oyster settlement and not due to cage artifact effects. Higher replication in the future would help improve detecting natural settlement variability and potential cage artifact effects.

Results from this study suggest large mobile predators dominate juvenile oyster consumption at the Soundview Park site. Oysters (>10 mm) experienced more than an order of magnitude higher mortality at Soundview Park than at Hastings. Thereby, mortality of newly settled or seeded *Crassostrea virginica* by *Callinectes sapidus* and *Libinia* spp. is an important concern for restoration efforts being conducted at sites similar to Soundview Park. The low consumption rate observed at Hastings could be due to a lack of large predatory crabs such as *C. sapidus* and *Libinia* spp. For Hastings, initial settlement density and environmental conditions may be more important factors than predation for the establishment of oyster populations at this site. This study demonstrates that juvenile oysters experience different predation pressures at Hastings and Soundview Park that can be attributed to the presence or absence of large mobile crustacean predators.

## CONCLUSION

This study found that large mobile predators are the dominant consumers of oysters in the New York metropolitan restored oyster reefs. These results are in contrast to the prior expectations that mesopredators play a dominant role in oyster mortality, as recently suggested by a number of studies (Rindone & Eggleston 2011, Johnson et al. 2014, Carroll et al. 2015). A fundamental difference may exist between northern and southern oyster reefs due to the different sizes of dominant mud crab species in each region. Mud crab mesopredators of different size classes may use different regions of the oyster reef and contribute differently to oyster growth and mortality.

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