WHO CONTROLS WHOM? LINKING PREDATOR-PREY DYNAMICS BETWEEN MUD CRABS AND JUVENILE EASTERN OYSTERS TO RESTORATION EFFORTS IN THE NEW YORK METROPOLITAN REGION

A Final Report of the Tibor T. Polgar Fellowship Program

Rebecca E. Kulp

Polgar Fellow

Marine Sciences Program
Stony Brook University
Stony Brook, NY 11794

Project Advisor:

Bradley J. Peterson
Marine Sciences Program
Stony Brook University
Stony Brook, NY 11794

Kulp, R.E. and B.J. Peterson. 2013. Who controls whom? Linking the predator-prey dynamics between mud crabs and juvenile Eastern oysters to restoration efforts in the New York Metropolitan Region. Section IV: 1-32 pp. *In* S.H. Fernald, D.J. Yozzo and H. Andreyko (eds.), Final Reports of the Tibor T. Polgar Fellowship Program, 2012. Hudson River Foundation.

ABSTRACT

Predation of newly settled juvenile Eastern oysters (*Crassostrea virginica*; spat) often dominates post-settlement mortality. Mesopredators such as the flat mud crab (*Eurypanopeus depressus*), Say mud crab (*Dyspanopeus sayi*) and white-fingered mud crab (*Rhithropanopeus harrisii*) are abundant on the newly constructed oyster reefs in the New York Metropolitan Region at both Hastings and Soundview Park, and potentially control spat post-settlement mortality. Predator-exclusion studies were conducted at both sites over the summer using glued hatchery-reared oyster singles and naturally recruited oysters. The study not only separated the effect of spat predators by size classes (all sizes, <25 mm, and <5 mm), but also examined the role oyster reefs have in enhancing or decreasing predation pressure. While there was a site and cage treatment interaction ($P<0.001$), there was not a reef structure effect. The naturally recruited tiles showed no difference between 25 mm and exposed cage treatments, regardless of settlement time period and site ($P<0.05$). Results indicate that mesopredators are not important in spat post-settlement mortality at Hastings or Soundview Park.

Since the cage field study could not measure mud crab predation directly, an additional pilot study was performed to test the plausibility of using stable isotope signatures for species-specific interactions. $\delta^{13}C$ and $\delta^{15}N$ signatures were compared between oyster spat, *D. sayi* fed an all-spat diet, and control *D. sayi* not fed oyster spat. While control *D. sayi* had significantly enriched $\delta^{13}C$ signatures compared to laboratory *D. sayi* ($P<0.001$), the $\delta^{15}N$ values did not differ ($P>0.05$). Further research is needed to evaluate whether filter feeders are an important food resource for *D. sayi*, as results suggest *D. sayi* may depend on benthic and not pelagic carbon fixation.

TABLE OF CONTENTS

LIST OF FIGURES AND TABLES

INTRODUCTION

Oyster reef restoration efforts have been increasing in recent years with the goal of enhancing both oyster fisheries and the ecosystem benefits provided by oyster reefs. The Hudson River Foundation (HRF) has been developing oyster reefs throughout the New York Metropolitan Region. Constructing oyster reefs in the New York Metropolitan Region has the potential to restore ecosystem services, ranging from improving water quality (Nelson et al. 2004; Grizzle et al. 2008) to habitat provision (Wells 1961; Tolley and Volety 2005).

Understanding the community's response to the restoration process is not only important in evaluating restoration success, but also in understanding food-web dynamics. Juvenile Eastern oysters (spat) are an important food resource for a multitude of predators, including the Xanthid mud crab mesopredators. Xanthid mud crabs are abundantly found throughout the Western Atlantic in a wide variety of structured intertidal and subtidal habitats ranging from seagrass meadows to oyster reefs. The four most common species in the mid-Western Atlantic (common mud crab, *Panopeus herbstii*; flat mud crab, *Eurypanopeus depressus*; Say mud crab, *Dyspanopeus sayi*; and white-fingered mud crab, *Rhithropanopeus harrisii*) are found in different salinity regimes and are thus restricted to specific portions of estuaries (Ryan 1956).

There are important species-specific ecological differences between these mud crab species. For example, Kulp et al. (2011) found that *E. depressus* consumed four times more oyster spat than *R. harrisii* in a laboratory experiment. There may be important site-specific differences in the ecological roles for mud crabs, as each species prefers different environmental conditions. Most laboratory studies have examined *P.*

herbstii, which has the largest carapace width of the mud crabs (Ryan 1956), the highest per capita juvenile oyster predation rate (Bisker and Castagna 1987; Kulp et al. 2011) and a salinity preference (35 psu) coincident with the highest oyster growth rates (e.g. Paynter and Burreson 1991). Yet, many oyster reefs and restoration efforts are being conducted in estuaries where *P. herbstii* are not the most abundant mesopredator. Preliminary data suggest that there are low to non-existent abundances of *P. herbstii* on the newly constructed Hudson River oyster reefs (Peterson, *unpublished results*). Additionally, *E. depressus*, *D. sayi* and *R. harrisii* abundances have been estimated to lie between 50 and 150 m^{-2}. Therefore, further research is needed to understand whether *E. depressus*, *D. sayi* and *R. harrisii* play roles similar to *P. herbstii* in the Hudson River.

Examining *E. depressus*, *D. sayi*, and *R. harrisii* are not only important for conservation efforts, but also for evaluating their ecological roles in benthic food webs. Mesopredators transfer energy to higher trophic levels (e.g. Harley and Lopez 2005), thereby serving as an important food source for commercially important organisms such as blue crabs (*Callinectes sapidus*). With the current decline in apex predators worldwide (Heithaus et al. 2008), mesopredators may serve a more critical role in developing food web communities. O'Connor et al. (2008) found that *P. herbstii* could fulfill the functional roles served by blue crabs and stone crabs (*Menippe mercenaria*) if they were of equivalent biomass. The understudied *E. depressus*, *D. sayi*, and *R. harrisii* species may similarly play important roles as adult blue crabs and spider crabs (*Libinia* spp.).

Studying species-specific predation on a resource, such as oyster spat, becomes challenging in the field when there is high predator species diversity (e.g. Eggleston 1990; Newell et al. 2000; O'Connor et al. 2008). Underwater photography/videography

can be costly and challenging to deploy in turbid, urban settings. Therefore, molecular approaches such as stable isotope analysis could be useful in evaluating predator-prey interactions. Stable isotope techniques evaluate long-term trends in diet composition, help determine major nitrogen and carbon sources fueling a food web, and provide a more precise method of examining energy transfers between trophic levels. As such, stable isotopes have been used widely in the study of food web structure and function (e.g. Darnaude 2005; Parker et al. 2008). Yet, a major limitation of this technique is that each prey resource needs to have distinctive $\delta^{13}C$ and $\delta^{15}N$ signatures. Organisms from the same functional feeding group, such as the Eastern oyster and barnacles (*Balanus* spp.), have the potential to consume the same food source and thus could have similar $\delta^{13}C$ and $\delta^{15}N$ values. Since mud crabs are omnivores, capable of consuming multiple filter-feeder species, the $\delta^{13}C$ and $\delta^{15}N$ signatures fractionated from oyster spat may be masked. Additionally, since stable isotope analysis can be costly, pilot studies need to be conducted before performing a large-scale food-web study.

The goals of this study were to determine the role oyster spat and reef structures have in enhancing mud crab populations, and to quantify how these mud crab populations influence spat abundance. The reef structure was expected to increase mesopredator abundances and coincide with increased predation rates. To partition the spat mortality from mesopredators, two predator-exclusion cages were used. The largest sized cage (25 mm lobster wire) was used to determine mesopredators contribution to overall spat mortality at the population level. Conversely, the smallest size cage (5 mm plastic mesh) was used to prevent all oyster spat predators from accessing the oyster spat and measure the natural mortality of oyster spat due to other environmental factors. The

mesopredators were expected to contribute at least 25% of the total spat mortality. Additionally, a laboratory stable isotope study was conducted to determine whether $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures in mud crab cheliped tissues could be distinguished between individuals on an all-oyster diet or no-oyster diet. The stable isotope approach was expected to show significantly different isotopic signatures between treatments, providing evidence for conducting a larger-scale stable isotope experiment.

Mud crabs are abundant mesopredators, whose populations have the potential to regulate oyster post-settlement mortality and impact the trophic transfer and community development of oyster reefs. The completed research worked to clarify the roles of mud crabs on restored oyster reefs, examine the biotic control of post-settlement mortality of oyster spat, and predict the effect of predation by mud crabs on restoration efforts currently underway in the Hudson River.

METHODS

Site selection. Experiments were conducted at two newly constructed preliminary oyster reefs in the New York Metropolitan Region: Hastings and Soundview Park (Figure 1). In 2010, the HRF and partners built the oyster reefs by laying shell veneer on top of a transplanted bedrock base. The footprints of the Hastings and Soundview Park sites are approximately 69 m^2 and 40 m^2, respectively. The two sites have different salinity regimes (Soundview Park: *ca.* 20-25 psu; Hastings: *ca.* 5-10 psu), which influenced the dominant mesopredator mud crab species. *E. depressus* and *D. sayi* both were found only at Soundview Park, whereas *R. harrisii* was found only at Hastings. While oysters naturally settle at both sites, hatchery-reared juvenile oysters settled on shell (spat-on-

shell) were planted at both sites in two installments, October/November 2010 and June 2011.

After visiting the sites in May, there was evidence of tidal erosion, as a large proportion of the spat-on-shell and veneer shell layer were gone. The Hastings site additionally had high turbidity, such that the west side of the reef was often covered in mud after a heavy storm. Regardless, both sites allow for the effects of a reef structure and presence of different mesopredator species to be tested.

In each site, there was an on and off-reef experimental location. The off-reef site had the same footprint as the reef site, approximately 25 m east and north of the reef sites at Soundview Park and Hastings, respectively. While the off-reef site was characterized by no structure, there was mixture of gravel and sandy substrate at Soundview Park. Conversely, the substrate at Hastings consisted of unconsolidated mud with no additional structure.

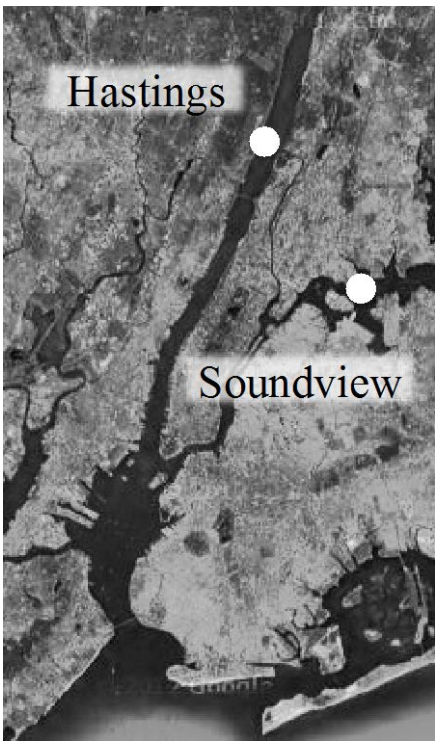

Figure 1. **Study site locations within the New York Metropolitan Region. Hastings was at a lower salinity site than Soundview Park (Soundview Park: *ca.* 20-25 psu; Hastings: *ca.* 5-10 psu). The footprint of Hastings and Soundview Park were 69 m^2 and 40 m^2, respectively. Each site had an off-reef study location with an equal footprint. Map was generated from Google Maps, ©2012Google.**

Predator-exclusion experiment. A randomized 2-factorial design comparing cage treatment by within site location was conducted at both Hastings and Soundview Park to test the effect different size classed predators have on post-settlement spat mortality, as well as how the reef structure influences predation patterns. The same design was conducted using two alternative strategies for exposing spat (<20 mm shell height [SH]) to predation. The first strategy was to standardize the number, size and arrangement of oysters by gluing oyster singles onto 10 x 10 cm ceramic tiles. The second strategy was to measure natural oyster recruitment onto the top and bottom of 10 x 10 cm ceramic tiles. Recruitment was defined as the number of settled spat present at the time of retrieval.

For the glued tiles, hatchery-reared oyster singles (5-8 mm SH) were provided by the Cornell Cooperative Extension's hatchery in Southold, NY and the East Hampton Town Shellfish hatchery in East Hampton, NY. Artificially adhered oysters were given at least one week to grow in the sea tables at Stony Brook University's Marine Station, Southampton, NY. All sea tables were supplied continuously with ambient seawater. Individuals that died from the gluing process were replaced and given at least 1 day to recover before deployment. As glued oysters were exposed to ambient seawater, the growth rate in the sea table changed during the course of the experiment. At the time of deployment, oysters were all within a size range mud crabs were capable of consuming (8-20 mm; *e.g*. Kulp et al. 2011).

To measure the potential effects of artificially attaching oysters onto tiles, a laboratory experiment was conducted to compare the number of glued oysters, naturally settled and spat-on-shell oysters consumed by *D. sayi*. Glued and naturally recruited

oysters were adhered to 10 x 10 cm ceramic tiles. Larval oysters were allowed to naturally settle on tiles and grow at the hatchery of the Urban Assembly New York Harbor School two months prior to the experiment. The spat-on-shell were similarly obtained from the New York Harbor School. Of the 30 tiles provided to the hatchery, 13 had successful settlement and could be used for the mesocosm study. Spat are known to be aggregate settlers (Tamburri et al. 2007), explaining the variable oyster densities observed on the spat-on-shell and recruited tiles. If there were more than twenty-five spat on the spat-on-shell and recruited tiles, then the extra spat were randomly removed. To standardize the glued tile treatments, 25 oysters were adhered with super glue and given 1 week to grow in the sea table. All oyster sizes were within the same range (5 to 15 mm shell height [SH]).

The experiment was conducted in 95 L flow-through mesocosms for 72 hours. *D. sayi* (15-23 mm carapace width [CW]) were collected from Shinnecock Bay and starved for 24 hours in the mesocosms before oyster treatments were added. There were four replicate controls of each oyster treatment without a mud crab present to measure natural oyster spat mortality. All treatment replicates were performed in one experimental run. Any molted or dead crabs were not included in the analysis. Since not all oyster treatments had 25 oysters initially present, percentages of oysters consumed were calculated and compared between treatments.

In the field predator-exclusion experiment, each tile was assigned to one of three predator-exclusion treatment cages (exposed, 25 mm aperture, and 5 mm aperture) that offered varying levels of protection from predation. The exposed treatment offered no protection from predation. The 25 mm cage (10 x 10 x 35 cm) was made of lobster wire

with 25 mm aperture, so that predators >25 mm could not access the prey. The 5 mm cage also had a 25 mm lobster wire frame, but with 5 mm polyvinyl plastic lining the interior to prevent predators > 5 mm entry. To test for potential cage artifact effects (Steele 1996), a cage control cage was used. The cage control was identical to the 5 mm cage treatment, except that 2 of the 6 sides were missing. Tiles were zip-tied within each cage treatment and a brick was attached onto the cage bottom for stability. The brick was then inserted into the substrate, making the cage relatively level with the substrate. There were four replicates of each treatment randomized and lined into two rows at the on and off-reef sites (Figure 2).

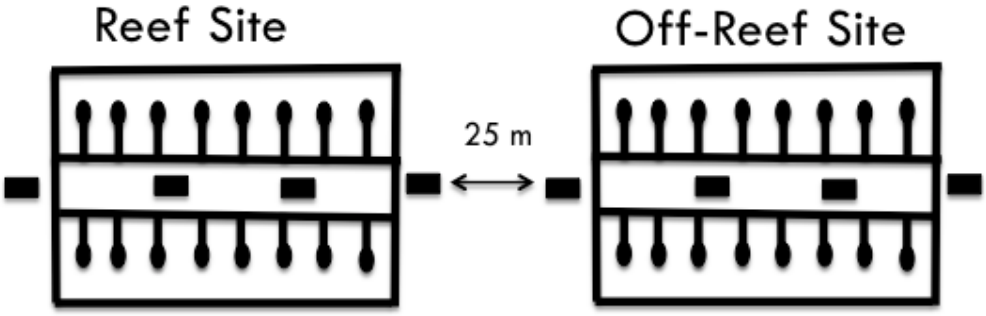

Figure 2. Diagram of on and off-reef study locations. The two study sites had the same footprint and were approximately 25 m apart. Cage treatments were distributed in two rows across the site and recruitment trays were inserted in a row in the middle of the study sites.

A picture was taken before and after deployment for the glued tiles to determine the number of oysters consumed. Any oysters missing at retrieval were assumed consumed. Four deployments were made between May and July 2012. Methods were slightly altered between deployments due to different logistical constraints. For the May deployment, 49 oysters were glued on a tile using super glue and deployed for 48 hours. Since less than 40% of oysters were consumed, 30 oysters were glued per tile for the next

three deployments to decrease gluing effort in the laboratory. Additionally, approximately half of the tiles lost at least one oyster during transport to the field. As such, an alternative adhesive, Z-Spar epoxy, was used in the June deployment. A maximum of 4 oysters $tile^{-1}$ were consumed during the June deployment. Unlike the super glue, oysters were pushed into the Z-Spar epoxy, smoothing the edges around the oyster and potentially increasing the handling time required for consumption. Therefore, super glue was used for the last two deployments in July to remove any artificial edge protection created by the Z-Spar. The deployment periods for the last two deployments in July were increased from 48 hours to one week to increase predator exposure. However, due to logistical constraints, the second July deployment at Hastings was retrieved after five days. Due to the changes in methodology throughout the summer, the June deployment was not included for trend analysis and the May and July deployments were analyzed separately.

Between glued tile deployments, 10 x 10 cm ceramic tiles were placed in the predator-exclusion cages to test predator effects on oyster recruitment. In June and July, tiles were retrieved after three weeks, and in August, the tiles were retrieved after six weeks. The number and size of oysters on the top and bottom of each tile was recorded after retrieval. Only oyster size ranges were recorded in the July retrieval at Soundview Park.

To estimate resident mesopredator abundances, four replicate trays (45 x 30 x 10 cm) lined with fiberglass window screen were inserted into the on and off-reef sites for three, five and six weeks before retrieval in June, July and August, respectively. The trays placed at the on-reef site were filled with veneer shell, whereas trays at the off-reef

site were filled with the excavated sediment. After retrieval, the number of mesopredators was quantified. Additionally, two mud crab traps were placed at the on and off-reef sites during the glued tile deployment to obtain a mesopredator catch per unit effort measurement. The mud crab traps had a 5 mm polyvinyl mesh lining a lobster wire frame. The square traps had a 25 mm door, thus targeting mesopredators capable of entering the 25 mm predator-exclusion cage treatment. One baited fish trap (*c.a.* 0.25 m diameter doors) was deployed at an on and off-reef site for 48 hours when the recruitment tiles were deployed. The off-reef site was not in the same location the cage and trays were deployed, but were at least 25 m from the reef.

Stable Isotope Analysis. A pilot stable isotope laboratory experiment was conducted to explore whether a large-scale stable isotope experiment could be performed at the oyster reefs. Thirty *D. sayi* collected from Heady Creek, Shinnecock Bay, NY were fed oyster spat (10-20 mm SH) for 28 days to allow sufficient time for tissue turnover. All spat were reared at the East Hampton hatchery and kept in the Marine Station's sea table for at least two weeks prior to consumption. A subsample of 15 oyster individuals (14-20 mm SH) were selected and frozen for determining baseline isotopic signatures prior to fractionation by crab individuals. At the conclusion of the experiment, thirty additional *D. sayi* were collected from Heady Creek. The Heady Creek site was characterized by having high densities of the common slipper shell (*Crepidula fornicata*) that lived on top of a *Crepidula* shell hash base. As such, Heady Creek offered a low relief, three-dimensional habitat that were abundantly inhabited by *D. sayi* (*ca.* 80-150 m^2). There have been no recorded oyster recruitment in Shinnecock Bay in the past two summers

(Peterson, *unpublished*), thus the control *D. sayi* samples represent individuals without an oyster spat diet. All samples were frozen before processing.

Fifteen crabs (15-22 mm CW) were randomly selected from individuals fed an all-oyster diet and those collected from Heady Creek. Cheliped muscle was extracted from the crab samples to standardize the tissue type, as tissues can have different turnover rates (Llewellyn and Peyre 2011). To have enough material for the analysis, the entire oyster body tissue was used. Samples were dried, ground, and 1 ± 0.1 mg of tissue sample was sent to the Stable Isotope Laboratory at Boston University for $\delta^{13}C$ and $\delta^{15}N$ analysis. Accuracy and precision of analysis was verified through the use of standards and duplicate samples.

Data Analysis. For the glued and naturally recruited oyster tile experiment, the data could not be normalized. As such, glued and naturally recruited oyster tile experiment data were rank-transformed and the parametric analysis of variance on ranks (ANOVA on ranks; Potvin and Roff 1993) used for statistical comparisons. For the glued oyster tile experiment, a three-way ANOVA on ranks was performed, comparing the site, treatment location and cage treatment effects. For the naturally recruited oyster tile experiment, a three-way ANOVA on ranks was performed, comparing recruitment month, treatment location and cage treatment effects between the July and September at Soundview Park. Additionally, a three-way ANOVA on ranks was performed, comparing site, treatment location and cage treatment effects in August. Due to low replication the abundances from the fish and crab traps were not statistically compared. Catch per unit effort was summarized into tables.

A one-way ANOVA was performed on the laboratory trial performed in the mesocosms between oyster treatment and percentage of oysters consumed. Data was arcsine transformed to meet necessary parametric assumptions. Student's t-test was used to compare $\delta^{13}C$ and $\delta^{15}N$ signatures from control and experimental *D. sayi*. To normalize data, $\delta^{15}N$ signatures were raised to the 10^{th} power before analysis was performed.

Tukey's HSD post-hoc test was performed when significant differences existed between treatment means. All statistical analyses were performed in R statistical software, version 2.15.1. Statistical significance α was set at 0.05.

RESULTS

Predator-exclusion experiment. The May and July glued tile deployments showed similar trends; therefore only July deployments will be summarized. Soundview Park had more than 50% oyster consumption compared to Hastings in all the cage treatments except the 5 mm cage. There was a significant interaction between oyster consumption differences in cage treatment types observed between sites ($P<0.001$; three-way ANOVA on ranks; Figure 3). At Soundview Park, significant differences were observed between the exposed and 5 mm treatment, as well as the exposed and 25 mm treatments ($P<0.05$; Tukey's HSD). The exposed treatment had 64.6% ± 40.2% oysters consumed $tile^{-1}$ (mean ± 1 SD) with a maximum of 30 and minimum of zero oysters consumed $tile^{-1}$. Conversely, there were no differences between the exposed and cage control or the 5 and 25 mm treatments. Unlike Soundview Park, no significant differences were observed between cage treatments at Hastings ($P>0.05$; Tukey's HSD). Furthermore, no

significant differences were observed between on and off-reef oyster consumption (P >0.05; three-way ANOVA on ranks).

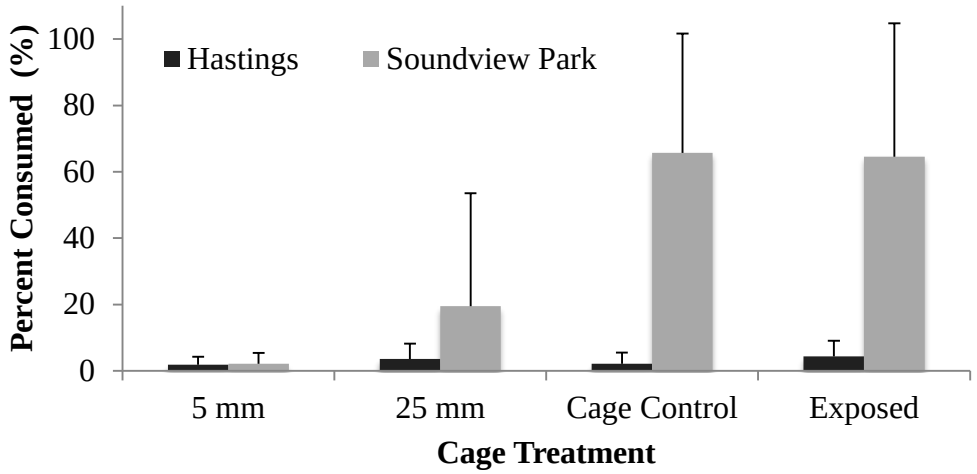

Figure 3. **Percent oyster consumed by site and cage treatment in July from the on-reef location. At Hastings and Soundview Park, there were three different cage exclusion treatments: a cage with 5 mm mesh, 25 mm lobster wire and an exposed treatment. There was also a cage control that had four 5 mm mesh sides. The average percent consumed was calculated for two deployments in July, left out for one week each. The error bars are +1 SD. A significant interaction was observed between site and cage treatment (P<0.001; three-way ANOVA on ranks).**

Oysters naturally recruited to bare tiles at Soundview Park in July and August and at Hastings in August. At Soundview Park, recruitment in July and August was low with 4.6 ± 3.3 oysters tile^{-1} and 1.5 ± 1.3 oysters tile^{-1} averages, respectively. Even though oyster densities decreased in August, the oyster sizes were greater, ranging from 3-15 mm SH in comparison to 1-5 mm in July. There was an interaction between recruitment month and cage treatment ($p<0.05$; three-way ANOVA on ranks; Figure 4). There was additionally a significant treatment location effect ($p<0.01$; three-way ANOVA on ranks), where the off-reef location had twice as many oysters recruited than the reef location.

When comparing the August oyster recruitment period between Hastings and Soundview Park, there was a significant site and treatment location interaction ($P<0.001$; three-way ANOVA on ranks; Figure 5). Hastings had a higher number of oysters recruited than Soundview Park, averaging between 25 and 36 oyster tile^{-1} in each cage treatment type, and a larger size range, ranging between 2-21 mm SH. Furthermore, the on and off-reef site location significantly influenced predation at Soundview Park, but not at Hastings ($P<0.05$; Tukey's HSD). The cage treatments had a significant effect on percentage of oysters recruited ($P<0.05$; three way ANOVA on ranks), where the 5 mm cage treatment had fewer oysters recruited than the cage control ($P<0.05$; Tukey's HSD).

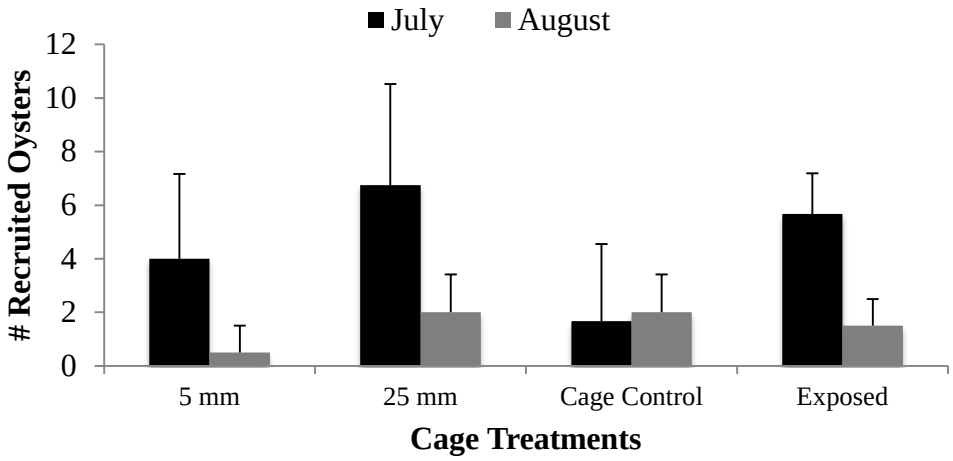

Figure 4. **Number of oysters recruited at Soundview Park in July and August at the on-reef location. Tiles were deployed for 3 weeks in July and 6 weeks in August. Averages include the number of oysters recruited on the top and bottom of tile. There were significant differences in number of oysters recruited between July and August, as well as the on and off-reef site location ($P<0.05$; three-way ANOVA on ranks). There were no cage treatment effects observed ($P>0.05$; three-way ANOVA on ranks). Error bars are +1 SD.**

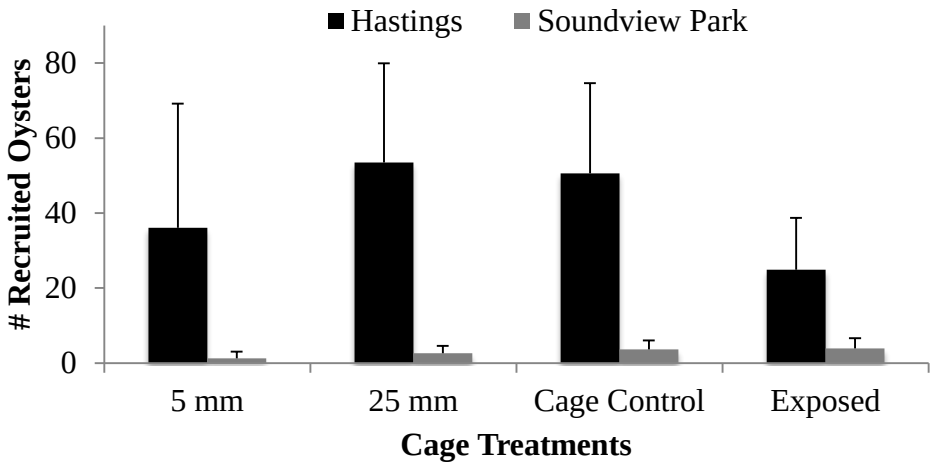

Figure 5. **Number of oysters recruited onto a tile in August at Hastings and Soundview Park. Averages include the number of oysters recruited on the top and bottom of tile retrieved from the on and off-reef site. There were significant differences between site and treatment location ($P<0.05$; three-way ANOVA on ranks). The cage treatments also had a significant effect on percentage of oysters recruited ($P<0.05$; three-way ANOVA on ranks). Error bars are +1 SD.**

A maximum of four mud crabs were collected from the mud crab traps with averages ranging from zero to one mud crab collected on and off-reef at both sites over the summer. There was one outlier of three crabs collected during the July retrieval at Hasting's off-reef location. The low crab collections may be a result of trap malfunction. To test this hypothesis, three traps were deployed in separate mesocosms with 13 mud crabs. Crab abundances in the trap reached four crabs within two hours, but then subsequently decreased, indicating that the cage design may not have effectively prevented escape. Therefore, the cage trap counts were not estimating catch per unit effort, but served to confirm the presence or absence of predators. No differences were

found between predator species caught on and off the reef. At Soundview Park, mud crab traps caught not only *D. sayi*, but also juvenile blue crabs. Conversely, *R. harrisii* were the only predator species caught at Hastings. A small number of juvenile blue crabs (2 individuals) were also collected at Hastings inside the 5 and 25 mm cage treatments during tile retrieval in September, but not within the crab traps.

Fish traps were additionally used to measure catch per unit effort over 48 hours (Table 1). Blue crabs and spider crabs were collected at Soundview Park both on and off-reef over the summer, whereas blue crabs were collected at Hastings only during the June deployment. White perch (*Morone americana*) were additionally collected at Hastings throughout the summer, while no fish were collected at Soundview Park. Unlike fish traps, the trays inserted into the on-reef location recorded higher abundances of resident crustacean predator species (Table 2). The on-reef trays at Hastings showed the highest mud crab abundances throughout the summer, reaching average densities of 61 ± 18.4 *R. harrisii* individuals in September. While Hastings had a gradual increase in mud crab abundances over the course of the summer, Soundview Park showed a peak in July with 23.5 ± 9.3 *D. sayi* individuals and 8.3 ± 2 *E. depressus* individuals. As expected, the off-reef location showed lower mud crab abundance. At both sites, averages ranged from zero to one mud crab over the summer. Hastings had the maximum number of mud crabs recorded with two mud crab individuals tray^{-1} in September.

	On-Reef		Off-Reef	
	Callinectes sapidus	*Libinia* spp.	*Callinectes sapidus*	*Libinia* spp.
May	1	1	0	2
June	8	3	3	2
July	0	0	3	0
September	4	0	1	0

Table 1. Crustacean catch per unit effort from fish traps in on and off-reef locations at Soundview Park. One baited fish trap was deployed for 48 hours in May, June, July and September at an on and off-reef location. The fish trap off-reef site was not in the same location as the off-reef tray abundance location.

	Hastings		Soundview Park			
	Rhithropanopeus harrisii		*Dyspanopeus sayi*		*Eurypanopeus depressus*	
	On-reef	Off-reef	On-reef	Off-reef	On-reef	Off-reef
June	23.3±12.9	0.3±0.5	9.5±4.2	0.3±0.5	0.5±0.6	0
July	43.3±26.4	1±1	23.5±9.3	0.3±0.5	8.3±2.2	0
Sept	61±18.1	0.3±0.6	19±10.5	0	2±2	0

Table 2. Number of mud crabs collected at on and off-reef locations. Numbers were averaged across four recruitment trays that were deployed for 3, 5 and 6 weeks before retrieval in June, July and August, respectively. Values represented as the average ± 1 SD.

In the mesocosm predator experiment, glued tiles had the highest consumption with an average of 45.8% ± 33.5% oysters consumed, while the spat-on-shell and naturally recruited oyster treatments had 18% ± 18.3% and 23% ± 24.7%, respectively. The statistical test resulted in a P value of 0.0502 (one-way ANOVA; n = 13 for glued, n = 14 for spat-on-shell, and n = 9 for naturally recruited oysters; Figure 6), indicating there were differences in the percentage of oyster spat consumed among the three forms of oyster prey: glued oysters, naturally recruited oysters, and spat settled on oyster shell. The glued tiles were the only treatment that had 100 percent consumption of the 25 oysters; however, there was high variability in oyster consumption, with values ranging from zero to 25 oysters.

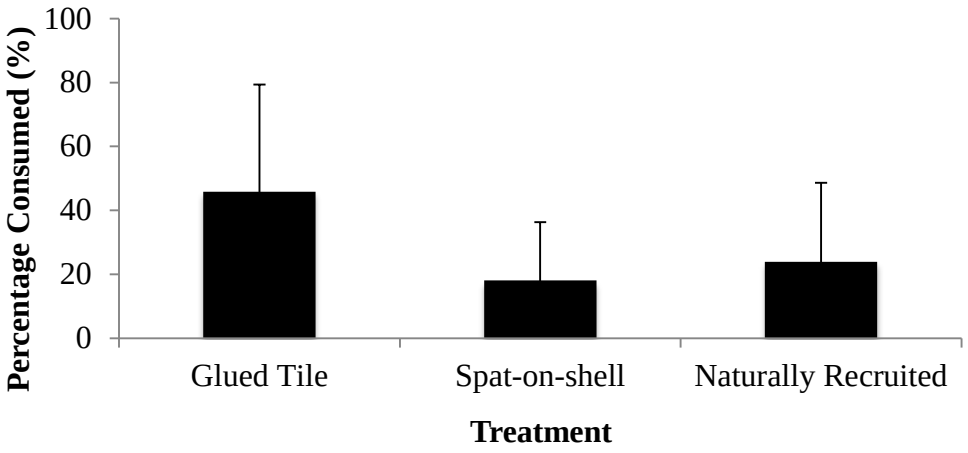

Figure 6. **Percentage of oysters consumed in the mesocosm predator experiment. The three oyster treatments were glued oyster singles (GT), spat-on-shell (SOS), and naturally recruited oysters (NRT). Experiments were conducted within flow-through mesocosms over a 72 experimental period with *Dyspanopeus sayi* individuals. The test statistic had a p value of 0.0502 (one-way ANOVA; n = 13 for GT; n = 14 for SOS; n = 9 for NRT), indicating oyster treatments were different. Error bars are + 1 SD.**

Stable isotope analysis. The $\delta^{13}C$ signatures from the oyster-fed laboratory *D. sayi* were significantly different from control non-oyster fed *D. sayi* $\delta^{13}C$ signatures collected from Shinnecock Bay, NY ($P<0.001$; Student's t-test; n = 15; Figure 7). Control *D. sayi* were enriched in $\delta^{13}C$ with values of -14.9 $^{0}/_{00}$ ± 0.6 $^{0}/_{00}$ compared to -16.6 $^{0}/_{00}$ ± 0.5 $^{0}/_{00}$ from laboratory *D. sayi* that were fed oysters exclusively. Conversely, $\delta^{15}N$ signatures were not statistically different between the laboratory and control *D. sayi* individuals ($P>0.05$; Student's t-test; n=15). Sampled oyster spat $\delta^{13}C$ signature was -19.0 $^{0}/_{00}$ ± 1.4 $^{0}/_{00}$ and $\delta^{15}N$ signature was 8.8 $^{0}/_{00}$ ± 0.2 $^{0}/_{00}$. Laboratory *D. sayi* fractionated spat $\delta^{13}C$ and $\delta^{15}N$ signatures by 2.5 $^{0}/_{00}$ and 2.3 $^{0}/_{00}$, respectively.

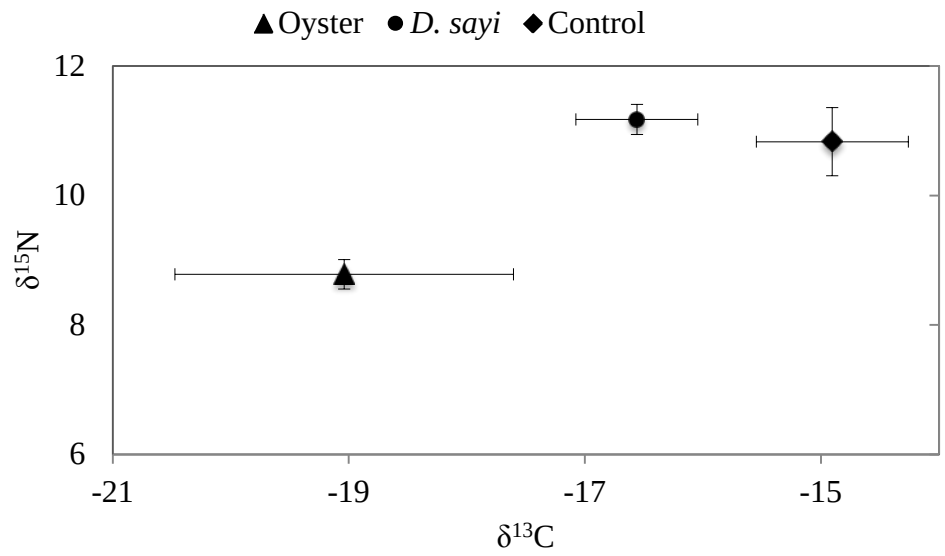

Figure 7. **Comparing $\delta^{13}C$ and $\delta^{15}N$ signatures between *Dyspanopeus sayi* with or without an all-oyster diet. Control *D. sayi* individuals were collected at Heady Creek, Shinnecock Bay, NY, where no oyster spat were present. Experimental *D. sayi* were fed an all-oyster diet in the laboratory for 28 days. The oyster spat $\delta^{13}C$ and $\delta^{15}N$ signatures represent baseline values before fractionation by *D. sayi*. There were no significant differences between laboratory and control *D. sayi* in $\delta^{15}N$ signatures ($P>0.05$; Student's t-test; n=15); however, there were significant differences in $\delta^{13}C$ signatures ($P<0.001$; Student's t-test; n=15). Error bars are ± 1 SD.**

DISCUSSION

The conducted experiments were aimed at evaluating the role of mesopredators in post-settlement mortality of juvenile Eastern oysters. The hypothesis that mud crabs contribute to 25% of overall oyster spat consumption was not supported, as the percentage of oysters consumed did not differ between the 25 mm and 5 mm cage treatments. Since mud crabs at Hastings and Soundview Park have rarely been observed to be larger than 25 mm CW (Peterson, *unpublished observations*), the 25 mm treatment was intended to record the contribution of mud crab predation. The results were

unexpected, as previous laboratory research by Kulp et al. (2011) estimated that these mud crab populations have the potential of consuming half the seeded spat planted on Maryland oyster reefs. The results provide evidence that laboratory predation rates may not be representative of population-level predation rates. Under laboratory conditions, crustacean predation studies typically starve individuals for 24 to 72 hours, separate predators into individual containers, and provide one prey resource (Eggleston 1990; Kulp et al. 2011). Even though these laboratory procedures standardize predation and decrease variability, biological and physical interactions occurring in the field may override results found in the laboratory. While recent laboratory experiments have increased design complexity by testing for prey preference (Mascaró and Seed 2001) and effects of conspecific and interspecific biological interactions (Griffen 2006; Bèlair and Miron 2009), there are still limitations to extrapolating results to field conditions. Perhaps spat are not the preferred prey resource of these mud crab species in the field, or the field consumption rates are less than those observed in the laboratory.

Prey preference may not only be related to the prey species, but also the level of risk associated with consuming a resource. Predator driven behavioral changes that do not involve direct consumption are known as trait-mediated indirect interactions (TMIIs; Werner and Peacor 2003). Such non-consumptive interactions of predators on mesoconsumers can lead to decreased control of lower trophic levels. *Panopeus herbstii,* another mud crab species dominant in southern coastal oyster reef systems, has been used as the model mesoconsumer in studying TMIIs. Grabowski (2004) found that the presence of a mud crab predator, the oyster toadfish (*Opsanus tau*), decreased mud crab foraging rates on oyster spat. Recently, Griffen et al. (2012) examined how TMIIs vary

depending on the habitat and size of *P. herbstii*. Results indicate that small individuals alter their behavior more than large individuals. Griffen et al. (2012) had used *P. herbstii* between 30 and 40 mm, which are larger than the mud crab species found at Hastings and Soundview Park. As such, predators of mud crabs, including blue crabs and oyster toadfish, that were found in the fish traps at both Hudson oyster reef sites may have a stronger effect on *D. sayi*, *E. depressus*, and *R. harrisii* individuals than *P. herbstii* due to their smaller sizes. The observed low oyster consumption in the predator-exclusion experiment may have been due to TMIIs exhibited by mud crab species. On the other hand, the experimental design may have created an artificial risk by using a flat ceramic tile opposed to the concave oyster cultch. In other mud crab predation studies (Grabowski 2004), oyster cultch was used instead of ceramic tiles, which could provide increased structural complexity and decrease risk associated with oyster consumption. Future experiments could incorporate assessments of the potential risk associated with exposing prey to predators in the field.

Another potential explanation for decreased mesopredator oyster spat consumption involves the size of oysters used in the experiment. Bivalve size has consistently been shown to impact the predation rate of crustacean predators, as predators usually will prefer smaller sized bivalves (Seed 1980; Eggleston 1990; Kulp et al. 2011). While the sizes used in the glued oyster tile experiment were within the size range consumed by mud crabs (Bisker and Castagna 1987; Kulp et al. 2011), they were not at the size that showed the highest consumption rates (Kulp et al. 2011). As predation rate declines with increasing size, the glued oysters may not have been within a desirable size range to overcome the risk associated with accessing the oyster prey.

The naturally recruited oysters, which were at smaller sizes than the glued tile experiment, also did not show a 25 mm treatment effect. The naturally recruited oysters could have been more challenging to remove from the tile than the glued oysters. While predation rates between treatments in the mesocosm study were not statistically different (P=0.0502), there could have been an important biological difference. Glued tiles were the only treatment type that had 100% consumption and had the highest mean consumption rate. As such, the glued oyster singles could have been easier to remove from the substrate than the settled oyster spat that conformed to the substrate. Additionally, perhaps the density of naturally recruited oysters was not high enough at Soundview Park to attract mud crab predators. Densities were no greater than 12 oysters on the tile bottom, which was almost completely protected from macroalgal growth and likely represents potential spat settlement on the top of the tile. Conversely, Hastings had high oyster densities, up to 72 oysters on the tile bottom and 69 oysters on the tile top. *Rhithropanopeus harrisii*, the mud crab living in high densities at Hastings, was shown to eat a minimal amount of oyster spat in previous studies (Kulp et al. 2011). As such, *R. harrisii* was not expected to be a dominant oyster predator. Low predation at Hastings may have been related to low abundances of other oyster predators; only one blue crab was collected in the fish trap during the study period.

In addition to investigating the role of mud crab predation, the experiment also examined the role oyster reef structure has on predation rates. The field experiments did not support our hypothesis that the oyster reef would enhance predation rate. One potential reason could involve predator mobility. Since the exposed treatments showed the highest oyster consumption at Soundview Park, the largest size classes of predators,

such as blue and green crabs, were the most important contributors to oyster spat mortality. These larger-sized predators are transient species and have the ability to migrate large distances. For example, male blue crabs have been recorded to travel 85 m day^{-1} (Wrona 2004); therefore, the off-reef site (25 m off the reef) could have been easily accessible by these highly mobile larger crustacean predators. There was no cage artifact effect observed in the study, as there was no difference in oyster consumption between the cage control and exposed treatment. As such, the lack of a reef effect on predation rates was most likely due to the mobility of the predators and not from a cage artifact effect. Blue crabs have been well recorded as an important oyster spat predator (e.g. Egglestone 1990; O'Connor et al. 2008), so the results from the predation study confirm their important predation role in post-settlement mortality of oyster spat.

A limitation of the field experiment was the inability to confirm the identity of the predators responsible for the consumption on the tiles. Therefore, the final component of the mud crab experiment was to determine whether stable isotopes would be useful in evaluating the species-specific interactions between mud crabs and oyster prey. While *D. sayi* fractionated oyster tissue by an expected 2.3 $^{0}/_{00}$ for $\delta^{15}N$ signature, *D. sayi* fractionated the $\delta^{13}C$ signature by an unexpected 2.5 $^{0}/_{00}$. Standardized fractionation values have been estimated to be approximately 1.0 $^{0}/_{00}$ for $\delta^{13}C$ and 2.5 $^{0}/_{00}$ (Vanderklift and Ponsard 2003; Zanden and Rasmussen 2001). As such, the $\delta^{13}C$ signature value was more enriched than expected. Llewellyn and Peyre (2011) performed a 20-day laboratory feeding study with blue crabs and found that the muscle tissue was more enriched than expected while the hepatopancreatic tissue was not. The cheliped muscle similarly may need more than 28 days to turnover tissue $\delta^{13}C$ values. Regardless of the unexpected

enriched $\delta^{13}C$ signatures in the laboratory *D. sayi*, the *D. sayi* individuals collected directly from Shinnecock Bay had significantly different $\delta^{13}C$ signatures from the laboratory *D. sayi* ($P<0.001$; Student's t-test; $n=15$). Pelagic and benthic primary production fractionate solubilized carbon differently, thus having different $\delta^{13}C$ values (France 1995). Thus, the more enriched $\delta^{13}C$ signatures found in the control *D. sayi* individuals suggests that the mud crabs at Heady Creek in Shinnecock Bay consume prey that feed on the benthos or benthic detritus directly and not those that filter-feed. Perhaps one reason why filter feeders are not consumed at Heady Creek involves increased risk associated with consuming filter-feeding prey. Therefore, stable isotope results suggest that TMIIs could also be an important biological interaction in *Crepidula* benthic environments. Additional studies need to be performed before conclusions can be drawn about whether filter feeders are an important resource for *D. sayi* in benthic habitats, as well as whether oyster tissue $\delta^{13}C$ and $\delta^{15}N$ signals differ from other filter feeders.

AKNOWLEDGEMENTS

There were multiple collaborators and individuals who assisted in the completion of the Hudson River Tibor T. Polgar Fellowship. Among the collaborators, the Cornell Cooperative Extension, East Hampton Hatchery, and Urban Assembly New York Harbor School donated hatchery-reared oyster spat and provided space for the recruitment and growth of oysters. The SUNY Maritime College provided boat mooring space in-between collection dates. Additionally, C. Garcia, G. Oh, V. D'Ambrosia, L. Jackson, A. Stubler, J. Carroll, and B. Furman assisted with the data collection, analysis, and interpretation of results. Finally, my advisor, Bradley Peterson, was instrumental is the support and completion of the project. The Hudson River Foundation funded the project and ultimately made the project possible.

LITERATURE CITIED

Bélair, M. and G. Miron. 2009. Predation behavior of *Cancer irroratus* and *Carcinus maenas* during conspecific and heterospecific challenges. Aquatic Biology 6: 41-49.

Bisker, R. and M. Castagna. 1987. Predation on single spat oysters *Crassostrea virginica* (Gmelin) by blue crabs *Callinectes sapidus* Rathbun and mud crabs *Panopeus herbstii* Milne -Edwards. Journal of Shellfish Research 6: 37-40.

Darnaude, A.M. 2005. Fish ecology and terrestrial carbon use in coastal areas: implications for marine fish production. Journal of Animal Ecology 74: 864-876.

Eggleston, D.B. 1990. Foraging behavior of the blue crab, *Callinectes sapidus*, on juvenile oysters, *Crassostrea virginica*: effects of prey density and size. Bulletin of Marine Science 46: 62-82.

France, R.L. 1995. Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. Marine Ecology Progress Series 124: 307-312.

Grabowski, J.H. 2004. Habitat complexity disrupts predator-prey interactions but not the trophic cascade on oyster reefs. Ecology 85: 995-1004.

Griffen, B.D. 2006. Detecting emergent effects of multiple predator species. Community Ecology 148: 702-709.

Griffen, B.D., Toscano, B.J., and J. Gatto. 2012. The role of individual behavior type in mediating indirect interactions. Ecology 93: 1935-1943.

Grizzle, R.E., Greene, J.K., and L.D. Coen. 2008. Seston removal by natural and constructed intertidal eastern oyster (*Crassostrea virginica*) reefs: a comparison with previous laboratory studies, and the value of in situ methods. Estuaries and Coasts. 31: 1208-1220.

Harley, C. D. G. and L.P. Lopez. 2005. The natural history, thermal physiology, and ecological impacts of intertidal mesopredators, *Oedoparen*a spp. (Diptera: Dryomyzidae). Invertebrate Biology 122: 61-73.

Heithaus, M . R., Frid, A., Wirsing, A. J., and B. Worm. 2008. Predicting ecological consequences of marine top predator declines. Trends in Ecology and Evolution 23: 202-210.

Llewellyn, C. and M.L Peyre. 2011. Evaluating ecological equivalence of created marshes: comparing structural indicators with stable isotope indicators of blue crab trophic support. Estuaries and Coasts 34:172-184.

Kulp, R., Politano, V., Lane, H. A., Lombarde, S. A., and K.T. Paynter. 2011. Predation of juvenile *Crassostrea virginica* by mud crabs in the Chesapeake Bay. Journal of Shellfish Research 30: 261-266.

Mascarò, M. and R. Seed. 2001. Foraging behavior of juvenile *Carcinus maenas* (L.) and *Cancer pagurus* (L.). Marine Biology 139: 1135-1145.

Nelson, K.A., Leonard, L.A., Posey, M.H., Alphin, T.D., and M.A.Mallin. 2004. Using transplanted oyster (Crassostrea virginica) beds to improve water quality in small tidal creeks: a pilot study. Journal of Experimental Marine Biology and Ecology 298: 347-368.

Newell, R.I.E., Alspach, G.S., Kennedy, V.S., and D. Jacobs. 2000. Mortality of a newly metamorphosed eastern oysters (*Crassostrea virginia*) in mesohaline Chesapeake Bay. Marine Biology 136: 665-676.

O'Connor, N.E., Grabowski, J.H., Ladwig, L.M., and J.F. Bruno. 2008. Simulated predator extinctions: predator identity affects survival and recruitment of oysters. Ecology 89: 428-438.

Parker, J.D., Montoya, J.P., and M.E. Hay. 2008. A specialist detritivore links *Spartina alterniflora* to salt mash food webs. Marine Ecology Progress Series 364: 87-95.

Paynter, K.T. and E.M. Burreson. 1991. Effects of *Perkinsus marinus* infection in the Eastern oyster, *Crassostrea virginica*: II. Disease development and impact on growth rate at different salinities. Journal of Shellfish Research 10: 425-431.

Potvin, C. and D.A. Roff. 1993. Distribution-free and robust statistical methods: viablealternatives to parametric statistics. Ecology 74: 1617-1628.

Ryan, E.P. 1956. Observations on the life histories and the distribution of the Xanthidae (mud crabs) of Chesapeake Bay. American Midland Naturalist 56: 138-162.

Seed, R. 1980. Predator-prey relationships between the mud crab *Panopeus herbstii*, the blue crab, *Callinectes sapidus* and the Atlantic ribbed mussel *Geukensi*a (=*Modiolus*) *demissa*. Estuarine and Coastal Marine Science 20: 445-458.

Steele, M.A. 1996. Effects of predators on reef fishes: separating cage artifacts from effects of predation. Journal of Experimental Marine Biology and Ecology 198: 249-267.

Tamburri, M.N., Zimmer, R.K., and C.A. Zimmer. 2007. Mechanisms reconciling gregarious larval settlement with adult cannibalism. Ecological Monographs 77: 255-68.

Tolley, S.G. and A.K. Volety. 2005. The role of oysters in habitat use of oyster reefs by resident fishes and decapods crustaceans. Journal of Shellfish Research 24: 100-1012.

Vanderklift, M.A. and Ponsard, S. 2003. Sources of variation in consumer-diet δ^{15} N enrichment: a meta-analysis. Oecologia 136: 169-182.

Wells, H.W. 1961. The fauna of oyster beds, with species reference to the salinity factor. Ecological Monographs 31: 239-266.

Werner, E. E. and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology 84: 1083-1100

Wrona, A.B. 2004. Determining movement patterns and habitat use of blue crabs (*Callinectes sapidus* Rathbun) in a Georgia saltmarsh estuary with the use of ultrasonic telemetry and a geographic information system (GIS). Doctoral dissertation. University of Georgia, Athens, Georgia.

Zanden, M.J. and J.B. Rasmussen. 2001. Variation in δ^{15} N and δ^{13} C trophic fractionation: Implications for aquatic food web studies. Limnology and Oceanography 46: 2061-2066.