PREDATION OF JUVENILE *CRASSOSTREA VIRGINICA* BY TWO SPECIES OF MUD CRABS FOUND IN THE CHESAPEAKE BAY

REBECCA E. KULP, VINCE POLITANO, HILLARY A. LANE, SARA A. LOMBARDI AND KENNEDY T. PAYNTER*

Department of Biology, University of Maryland, College Park, Maryland 20742

ABSTRACT Two species of mud crabs—the flat mud crab (*Eurypanopeus depressus*) and the white-fingered mud crab (*Rhithropanopeus harrisii*)—commonly inhabit subtidal oyster reefs in the Maryland portion of the Chesapeake Bay. Predation of juvenile *Crassostrea virginica* (spat) by mud crabs could be one of the major contributors to early juvenile spat mortality, hindering natural recruitment and restoration efforts in the Chesapeake Bay. The purpose of this study was to measure the number and size of spat preyed on by *E. depressus* and *R. harrisii*. Spat settled on oyster valves were placed in an experimental tank with one crab over a 96-h study period. Every 24 h, the number and size of spat scars were measured. *E. depressus* consumed nearly 40% of the spat offered whereas *R. harrisii* consumed less than 10%. *E. depressus* also consumed significantly more spat than *R. harrisii* within each spat size class (for all spat size classes, *P* < 0.0001). Although available spat sizes ranged from 1–29 mm, approximately 75% of spat preyed on by both species were less than 8 mm in size. Our data suggest *E. depressus* may have the potential to reduce spat survival significantly, with *R. harrisii* playing a minor role. Considering restoration strategies that reduce spat predation by mud crabs may increase the success of natural recruitment and restoring oyster populations.

KEY WORDS: *Crassostrea virginica*, *Eurypanopeus depressus*, *Rhithropanopeus harrisii*, spat mortality, predator–prey dynamics, oyster restoration

INTRODUCTION

The Eastern oyster, *Crassostrea virginica* (Gmelin, 1791), historically created reefs throughout the mesohaline subtidal regions of the Chesapeake Bay. The heterogeneous 3-dimensional structures formed by oyster reefs provide settlement surfaces for epifauna and habitat for benthic organisms, serving as the base for a complex ecosystem (Wells 1961, Dame 1979, Kennedy 1996, Tolley & Volety 2005). In addition, oyster reefs have supported a commercial oyster industry and have been shown to improve water quality (Nelson et al. 2004, Porter et al. 2004, Grizzle et al. 2008). Although *C. virginica* serves an important role in the Chesapeake Bay, adult population levels have declined an estimated 100-fold in the past century as a result of a combination of disease, degraded water conditions, and overharvesting (Newell 1988, Burreson & Ragone Calvo 1996, Ford & Tripp 1996, Kemp et al. 2005, Kirby & Miller 2005). In addition, for the past 10 y, natural recruitment has been low on most Maryland oyster bars (Tarnowski 2010). As a result, the historic complex reef structures have either been destroyed or dramatically reduced (Rothschild et al. 1994, Woods et al. 2005).

As a result of the extensive decline in *C. virginica* population levels in the Chesapeake Bay, efforts have been undertaken to restore oyster reefs in select areas. One organization, the Oyster Recovery Partnership, has been seeding historic oyster bars in the Chesapeake Bay with hatchery-reared juvenile oysters (spat) for the past 11 y (Paynter 1999, Paynter et al. 2010). Newly seeded spat suffer mortality rates that range from 25–100% within a few weeks after planting (Paynter 2009). Exploring the causes of spat mortality may provide valuable information for improving restoration success and understanding recent changes in natural recruitment rates.

Predation by benthic invertebrates is one source of spat mortality. Known spat predators in the Chesapeake Bay include polyclad flatworms (*Stylochus ellipticus* Girard, 1850), blue crabs (*Callinectes sapidus,* Rathbun, 1896), and the common black-fingered mud crab (*Panopeus herbstii* (Edwards, 1834)) (Bisker & Castagna 1987, Eggleston 1990, Newell et al. 2000, O'Conner et al. 2008). In addition to *P. herbstii*, four other xanthid crabs have been reported to inhabit the Chesapeake Bay (Ryan 1956). Of these species, the flat mud crab (*Eurypanopeus depressus* (Smith, 1869)) and the white-fingered mud crab (*Rhithropanopeus harrisii* (Gould, 1841)), have been found in high abundances on oyster reefs in the middle to upper Chesapeake Bay (Harwell 2010, Rodney & Paynter 2006). Although predation by *P. herbstii* has been well documented (Seed 1980, Whetstone & Eversole 1981, Bisker & Castagna 1987, Grabowski 2004, O'Conner et al. 2008), few studies have examined oyster predation by *E. depressus* and *R. harrisii*. McDermott (1960) measured *E. depressus* predation on oyster spat and found a mean predation rate of 3.8 spat per crab per day. However, crabs in that study (McDermott 1960) were not separated into individual cages, so intraspecific competition may have artificially reduced the estimated predation rates. Newell et al. (2007) compared the percentage of *C. virginica* and *Crassostrea ariakensis* (Fujita, 1913) spat consumed by a range of predators, including *E. depressus* and *R. harrisii*, over a 30-day study period. They showed that *E. depressus* preyed on a larger percentage of *C. virginica* spat than *R. harrisii,* and that both species consumed spat smaller than 7 mm, even though they had access to larger spat. Because individuals had a choice of consuming *C. ariakensis*, a food source not currently available in the Chesapeake Bay, the results observed might not reflect natural predation potential. Milke and Kennedy (2001) showed that *E. depressus* not only preyed upon a larger size range of mytiliform bivalves than *R. harrisii*, but also had a significantly greater mechanical advantage in their crusher claw. Although previous studies (McDermott 1960, Milke & Kennedy 2001, Newell et al. 2007) have examined

predation pressures exerted by *E. depressus* and *R. harrisii*, we have no estimates of the size or quantity of hatchery-reared spat consumed by these crabs on Chesapeake Bay oyster reefs. To investigate the spat predation rates by *E. depressus* and *R. harrisii*, we quantified spat predation by each of these species over a 96-h study period. Because *E. depressus* is generally larger than *R. harrisii*, we expected *E. depressus* to prey on oyster spat at a higher rate and on a larger size range than *R. harrisii*.

METHODS

Spat and Mud Crab Preparation

Spat of *C. virginica* were produced at the oyster hatchery at Horn Point Laboratory in Cambridge, Maryland. Spat settlement densities and sizes varied among oyster shells ($\mu = 28.1 \pm 20.7$ spat per shell; range, 1–29 mm). Between experimental runs, spat-on-shell were maintained in floating mesh containers in the South River. Before the spat were used, epifaunal organisms were scrubbed off the shells.

Individual crabs were collected from the Choptank (*E. depressus*) and South rivers (*R. harrisii*). Crabs were given at least 4 days to acclimate to laboratory conditions in holding tanks and were held no longer than 11 days. In each holding tank, 2–3 g of macerated scallop meat was fed to the crabs every other day. Holding tanks were at ambient room temperature, approximately 25°C, and filled with artificial seawater kept at, approximately, a salinity of 10.

Predation Experiments

Experimental runs were conducted within three 55-gal. tanks, each of which held 6 2.5-gal. plastic drum bowl tanks. The 55-gal. tanks were covered with a fitted brown tarp to simulate low-light water conditions and to reduce the possibility of human activity altering the predatory behavior of the crabs. Similar to the mud crab holding tanks, water was at ambient room temperature and filled with artificial seawater kept at a salinity of approximately 10. Water flow was distributed among the 6 2.5-gal. tanks using PVC piping, and water flowed out of each tank through holes on the side. Water changes were performed between experimental runs. In addition, each 2.5-gal. tank contained approximately 3 cm cleaned commercial river pebbles.

Within each 55-gal. tank, five or the six 2.5-gal. tanks were experimental, in which a single crab was starved for 24 h before spat-on-shell were placed in the tank. The final 2.5-gal. tank was used as a control, where spat-on-shell were placed in the tank without a crab. The number of spat placed in a tank was recorded prior to each experimental run. Across all the experimental runs, the number of spat presented to *E. depressus* ranged from 26–136, and 19–93 for *R. harrisii*; the spat were spread over 1–3 shells in any given experimental run. To expose the highest shell surface area, the convex side of each shell was leaned against the front of the 2.5-gal. tank (Fig. 1).

Crabs were arbitrarily assigned to each 2.5-gal. tank after having their carapace widths (CWs) measured to the nearest 0.01 mm using digital calipers. Forty-five crabs were tested for each species. Each experimental run lasted 96 h; shells were removed from the experimental tanks every 24 h, and the number and size (shell height) of spat scars (visual representations of recently preyed on spat) were recorded. Shell height was measured as the length from the umbo to the marginal lip; measurements were made to the nearest millimeter.

Data Analysis

For general trends, mean total and daily predation rates were calculated for each species, as well as the mean size of spat consumed. Total predation rate was calculated as the number of spat preyed on during the 4-day study period. Daily predation rates were calculated as the number of spat preyed on in each 24-h period. Daily predation rates were based on the initial spat count taken for each day. To account for the high variability in the number and size of spat provided, predation rates were also represented as the percentage of available spat consumed. The percentage of available spat consumed was categorized into three spat size classes: small (1–5 mm), medium (6–10 mm), and large (>10 mm). Mean percentage of available spat consumed within each spat size class were then also calculated for each species.

JMP 5.0.1 Statistical Discovery Software was used for statistical comparisons ($\alpha = 0.05$ for all comparisons). Because
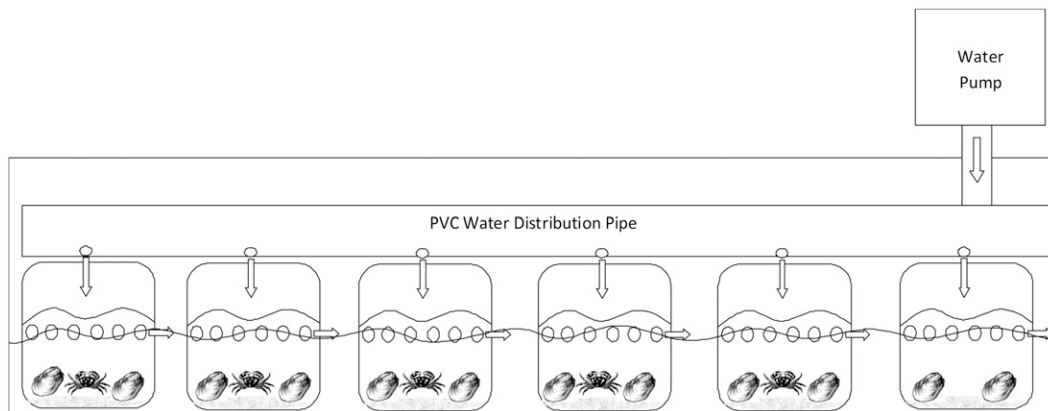

Figure 1. **Experimental tank setup. Each experimental run consisted of three identical experimental tanks. Six 2.5-gal. plastic tanks were contained in a 55-gal. glass tank. Water flow was distributed among the six 2.5-gal. tanks from a common holding tank using a water pump and PVC piping with equally spaced 3/16-in. holes. Water flowed out of each 2.5-gal. tank through six 3/8–in. holes on the tank side into the 55-gal. tank. Arrows indicate water flow. Within each 2.5–gal. tank, spat were spread over 1–3 individual shells. Five of the six 2.5-gal. tanks were experimental, in which a single crab was starved for 24 h before spat-on-shell were placed in the tank. The final 2.5–gal. tank was used as a control, where spat-on-shell were placed in the tank without a crab. In addition, each 2.5-gal. tank contained approximately 3 cm of cleaned commercial river pebbles.**

data could not be normalized with transformations, nonparametric tests were used. Spearman's rho rank correlation test was used to analyze trends in the size and number of spat consumed. Wilcoxon's rank sum test was used to determine significant differences between groups. For analyzing predation rates, only the mean percentage of available spat consumed within each spat size class was compared statistically. Crabs that had molted or died during the experiment were removed from analyses.

RESULTS

CW was significantly different between species (Wilcoxon's rank sum test, $P < 0.0001$), where *E. depressus* had a mean CW of 15.8 ± 0.5 (SEM) mm and *R. harrisii* had a mean of 9.1 ± 0.3 mm. More oyster spat were preyed on by *E. depressus* than *R. harrisii* during the 96-h study period. The mean number of spat consumed in 4 days by *E. depressus* was 22.7 ± 2.9 spat per crab, or $37.2 \pm 3.4\%$ of available spat. Conversely, the mean number of spat consumed in 4 days by *R. harrisii* was 4.5 ± 0.9 spat per crab, or $9.2 \pm 1.7\%$ of available spat. Both species preyed on the greatest amount of oyster spat within the first 24 h, where *E. depressus* and *R. harrisii* consumed $16.2 \pm 2.1\%$ T1 and $6.1 \pm 1.3\%$ of available spat, respectively (Table 1). After the first 24 h, daily predation rates continued to decline, decreasing from an initial rate of 10.4 ± 1.7 spat per crab to a final rate of 2.9 ± 0.5 spat per crab for *E. depressus,* and 2.9 ± 0.6 spat per crab to 0.4 ± 0.1 spat per crab for *R. harrisii.*

The number of spat consumed throughout the study period was positively correlated with the number of spat provided for *E. depressus* (Spearman's rho = 0.6469, $P < 0.0001$), but was not correlated for *R. harrisii* (Spearman's rho = 0.2536, $P > 0.05$). The percentage of available spat consumed was not correlated with the number of spat provided in either species (*E. depressus:* Spearman's rho = 0.1516, $P > 0.05$; *R. harrisii:* Spearman's rho = 0.0489, $P > 0.05$).

Both species exhibited a similar pattern in the spat sizes they F2 consumed (Fig. 2). Spat size was negatively correlated with the mean number of spat consumed (*E. depressus:* Spearman's rho = −0.8488, $P < 0.0001$; *R. harrisii:* Spearman's rho = −0.8767, $P < 0.0001$). Approximately 75% of spat preyed on by both species were less than 8 mm. Mean spat size preyed upon for *E. depressus* was 5.92 ± 0.25 mm, and 5.52 ± 0.29 mm for *R. harrisii*. The largest spat that *E. depressus* and *R. harrisii* preyed on were 23 mm and 12 mm, respectively.

Spat Predation by Size Class

Within each size class, *E. depressus* preyed on a significantly larger proportion of available spat than *R. harrisii* (individual

TABLE 1.

Percentage of *Crassostrea virginica* spat preyed on by *Eurypanopeus depressus* and *Rhithropanopeus harrisii* during each 24-h time period of the study.

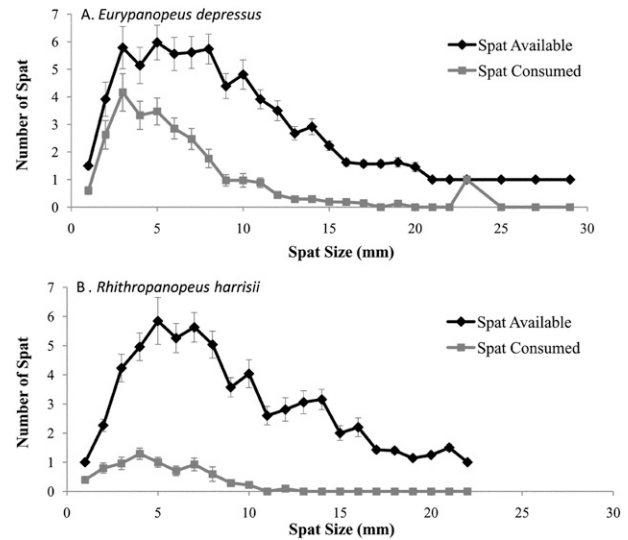| Species	Time Periods (h)			
	0–24	24–48	48–72	72–96
Eurypanopeus depressus	16.2 (±2.1)	13.6 (±2.0)	9.4 (±1.5)	7.9 (±7.7)
Rhithropanopeus harrisii	6.1 (±1.3)	3.03 (±0.8)	1.3 (±0.5)	0.9 (±1.7)

SEM is displayed in parentheses.

Figure 2. Mean frequency of *Crassostrea virginica* spat that were available and consumed by *Eurypanopeus depressus* and *Rhithropanopeus harrisii* based on spat size. (A) Mean frequency recorded for *E. depressus*. (B) Mean frequency recorded for *R. harrisii*. Error bars represent ±1 SEM. The mean frequency of spat eaten was negatively correlated with spat size for both species (*E. depressus*: Spearman's rho = −0.8488, $P < 0.0001$; *R. harrisii*: Spearman's rho = −0.8767, $P < 0.0001$).

size class results described later; for all size classes, Wilcoxon's rank sum test, $P < 0.0001$; *E. depressus, n = 38; R. harrisii, n = 34;* Fig. 3). Furthermore, in both species, the mean percentage of spat F3 consumed among the size classes was significantly different (for both species: $P < 0.0001$). In both species, the small size class (1–5 mm) showed the highest predation rate over 4 days and the large size class (>10 mm) showed the lowest. *E. depressus* consumed $61.9 \pm 4.5\%$ of available small spat over 4 days and *R. harrisii* consumed $19.7 \pm 3.4\%$. In contrast, *E. depressus* preyed on $11.9 \pm 2.5\%$ of available large spat and *R. harrisii* preyed on $0.9 \pm 0.8\%$. In addition, the highest percentages of available small and medium spat were consumed during the first 48 h (Table 2). T2 Within each time period, the crabs consumed spat in the small size class at approximately twice the rate as those in the medium size class. Alternatively, for the large size class, *E. depressus* consumed similar percentages in each time period, whereas *R. harrisii* consumed no large spat in the second and last day.

There were 22 *E. depressus* and *R. harrisii* individuals whose CWs were not significantly different, ranging from 10–13 mm (Wilcoxon's rank sum test, $P < 0.1228$; *E. depressus, n = 11; R. harrisii, n = 11*). Of these crabs, *E. depressus* consumed a significantly greater proportion of spat than *R. harrisii* in each size class (for the small size class, $P < 0.0017$; for the medium size class, $P < 0.0110$; for the large size class, $P < 0.0239$; *E. depressus, n = 11; R. harrisii, n = 11*). Specifically, *E. depressus* consumed $63.3 \pm 9.1\%$ of available small spat, $28.8 \pm 6.7\%$ of available medium spat, and $6.0 \pm 3.3\%$ of available large spat over 4 days, whereas *R. harrisii* consumed $12.9 \pm 4.8\%$, $9.4 \pm 4.5\%$, and 0%, respectively.

DISCUSSION

Based on the results of this study, *E. depressus* could be a substantial predator of spat in the Maryland portion of the Chesapeake Bay. Of the available spat, *E. depressus* preyed on
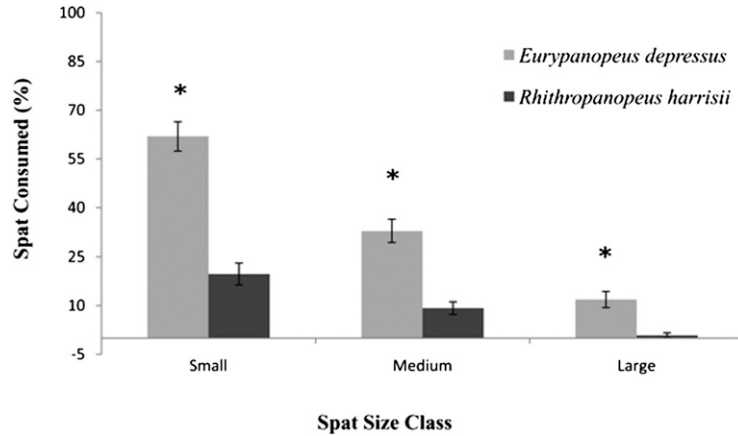
Figure 3. Percentage of available *Crassostrea virginica* spat consumed in each spat size class by *Eurypanopeus depressus* and *Rhithropanopeus harrisii*. The 3 size classes were small (1–5 mm), medium (6–10 mm), and large (>10 mm). The error bars were ±1 SEM. Asterisks designate that within a size class there was a significant difference between species (*P* < 0.05). Within each spat size, *E. depressus* consumed a significantly greater proportion of available spat than *R. harrisii* (Wilcoxon's sum rank test; for all spat size classes: *P* < 0.0001; *E. depressus*, *n* = 38; *R. harrisii*, *n* = 34). The proportion of available spat consumed was significantly different between spat size classes in *E. depressus* and *R. harrisii* (Wilcoxon's sum rank test; for both species: *P* < 0.0001; *E. depressus*, *n* = 38; *R. harrisii*, *n* = 34).

37%, whereas *R. harrisii* preyed on 9% of available spat within 96 h. Sizes of spat preyed on ranged from 1–23 mm, but the vast majority of the spat consumed were between 1 mm and 8 mm. Because the hatchery-based restoration program in Maryland typically plants spat within this size range, these two predators could have a significant influence on survivorship of juvenile oysters.

To assess the relative contribution *E. depressus* and *R. harrisii* have on spat mortality, results were compared with predation rates of two other important crab predators of spat: *C. sapidus* and *P. herbstii*. Daily predation rates by *C. sapidus* and *P. herbstii* were more than double the 4-day predation rate of either *E. depressus* or *R. harrisii* (Bisker & Castagna 1987). However, Bisker and Castagna (1987) used "cultchless" spat, which has been shown to be easier to handle and results in higher spat mortality (Krantz & Chamberlain 1978). Although *E. depressus* and *R. harrisii* did not prey on as many spat as *C. sapidus* and *P. herbstii*, *E. depressus* and *R. harrisii* could have a substantial impact on spat survival based on their abundances on oyster reefs in Maryland. From preliminary counts, *E. depressus* has been found in densities of 100 crabs/m^2 in the Patuxent River, whereas *R. harrisii* has been found in densities of 100 crabs/m^2 in the Severn River (Harwell, unpubl.). Based on the estimated predation rates from the current study, the *E. depressus* population within a 1-m^2 area could have the capacity to consume more than 2,000 spat in 4 days and *R. harrisii* could have the capacity to consume approximately 500 spat during the same time period. Because restoration efforts in Maryland plant about 250–500 spat/m^2, *E. depressus* and *R. harrisii* populations could reduce those spat densities by half or more, especially in areas where crab densities are high. In addition, population levels of *E. depressus* and *R. harrisii* have been shown to be four orders of magnitude higher on restored oyster reefs compared with nonrestored reefs, suggesting that crab population levels respond to the addition of shell and an increase in oyster reef complexity (Rodney & Paynter 2006).

Predation rates found in this study were also compared with those previously reported for *E. depressus* and *R. harrisii*. The percentage of available *C. virginica* spat consumed by *R. harrisii*

in 96 h was consistent with findings in the work by Newell et al. (2007), who had given individual crabs a choice of consuming either *C. ariakensis* or *C. virginica* spat over 30 days. Conversely, *E. depressus* in the current study had preyed on a greater percentage of available *C. virginica* spat than found in Newell et al. (2007). Although both species were shown to consume significantly more *C. ariakensis* than *C. virginica* in Newell et al. (2007), the added presence of *C. ariakensis* may have had more of an influence on the *C. virginica* predation potential for *E. depressus* than *R. harrisii*. In addition, our study observed a higher average daily *E. depressus* predation rate of 5.7 crabs per day compared with the 3.8 spat crabs per day reported by McDermott (1960). The difference in predation rates could be attributed to

TABLE 2.

Percentages of *Crassostrea virginica* spat preyed upon by *Eurypanopeus depressus* and *Rhithropanopeus harrisii* in each spat size class during each 24-h time period.

*Eurypanopeus depressus***	Time Periods (h)			
Size class	0–24	24–48	48–72	72–96
Small	26.5 (±3.5)	27.3 (±4.0)	24.7 (±4.5)	13.6 (±2.6)
Medium	13.9 (±1.9)	11.4 (±1.9)	8.0 (±1.4)	7.1 (±1.8)
Large	3.7 (1.2)	2.2 (±4.4)	3.0 (±0.9)	4.4 (±1.3)

Rhithropanopeus harrisii†	Time Periods (h)			
Size Class	0–24	24–48	48–72	72–96
Small	12.2 (±2.5)	11.0 (±4.4)	3.1 (±1.5)	2.9 (±1.8)
Medium	6.0 (±1.6)	2.6 (±0.7)	0.9 (±0.4)	0.7 (±0.4)
Large	1.6 (±1.5)	0 (±0)	0.5 (±0.5)	0 (±0)

* Spat consumption by *E. depressus*.
† Spat consumption by *R. harrisii*.
The 3 size classes were small (1–5 mm), medium (6–10 mm), and large (>10 mm). SEM is displayed in parentheses.

the influence of intraspecific competition, because McDermott (1960) did not separate crabs into individual containers.

The sizes of the crabs collected in this study likely reflect the natural size distribution found in the upper Chesapeake Bay. Typically, *E. depressus* grows to a larger CW than *R. harrisii* (Ryan 1956). Even though the CWs were significantly different between species, we do not believe the difference in crab size explains their differing predation rates. Among individuals that had similar CWs, *E. depressus* still consumed a significantly greater proportion of spat than *R. harrisii* in each size class. The differing predation rates may instead indicate that the two species have different resource preferences. Milke and Kennedy (2001) found a greater crusher claw mechanical advantage in *E. depressus* than *R. harrisii*, which may allow *E. depressus* to remove spat from the shell more effectively. This difference in claw strength may result in a shorter processing time for spat predation by *E. depressus* than *R. harrisii*, making *C. virginica* a more efficient food resource for *E. depressus*. Further investigations need to be conducted before the prey dynamics of *E. depressus* and *R. harrisii* are clearly understood.

Both crab species showed clear spat size preferences, preferring smaller spat (1–5 mm). The observed size frequency distribution cannot be explained purely by chelae mechanical limits because both mud crab species demonstrated an ability to open large spat (>10 mm). In addition, despite the ability of *E. depressus* to open larger spat than *R. harrisii*, *E. depressus* still preyed on the same mean spat size range as *R. harrisii*. Furthermore, our study found that both species were capable of preying on larger spat than found in Newell et al. (2007), suggesting that *E. depressus* and *R. harrisii* actively select smaller spat. Crab selection of smaller spat has been recorded in multiple predation studies, and may be a direct result of energetic costs (Elner & Lavoie 1983, Bisker & Castagna 1987, Eggleston 1990, Brown & Haight 1992, Juanes 1992). Shell strength and handling time need to be investigated further to uncover the underlying cause behind smaller spat selection in *R. harrisii* and *E. depressus*.

The patterns in the spat sizes preyed on could be used to estimate a size refuge from *E. depressus* and *R. harrisii* predation. Approximately 75% of spat preyed on were less than 8 mm in size. After spat grow to 8 mm in size, *E. depressus* and *R. harrisii* may become less efficient in their predation on spat, thus potentially decreasing predation pressure. Currently, the spat planted for restoration are approximately 1 mm in size (Paynter, pers. obs.). Although spat grow at different rates under different environmental conditions, spat have been shown to grow approximately 12 mm per month from July to October (Paynter & DiMichele 1990). Based on that growth rate, spat would be vulnerable to mud crab predation for at least 2 wk after planting and settlement. However, predation rates in the benthos could be very different from what has been measured in the laboratory. Additional predation experiments should be repeated in the field, which may provide a more realistic representation of spat predation in the Maryland portion of the Chesapeake Bay.

ACKNOWLEDGMENTS

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