

Predation rates on juvenile blue crabs in estuarine nursery habitats: evidence for the importance of macroalgae (*Ulva lactuca*)

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ABSTRACT: Rates of predation on juvenile blue crabs *Callinectes sapidus* (12 to 64 mm carapace width) in eelgrass *Zostera marina*, sea lettuce *Ulva lactuca*, and paired adjacent unvegetated substrates, and a *Spartina* marsh creek were compared using 24 h tethering experiments from July to October 1987. Vegetation provided the best cover from predation, with mean predation rates in sea lettuce of 9 % and in eelgrass of 20 %, compared with mean rates of 40 % or greater in unvegetated controls and the marsh creek. Seasonal changes in rates of predation on crabs occurred in eelgrass and sea lettuce habitats indicating that the refuge value of these macrophytes varied seasonally. Sea lettuce, previously considered a poor habitat for decapod crustaceans, provided effective refuge for blue crabs and should be considered a potential nursery habitat.

INTRODUCTION

The blue crab *Callinectes sapidus* occurs in estuarine waters of the east coast of the United States from New England to South Florida and the Gulf of Mexico and is the basis for large and important commercial and recreational fisheries in many of these areas (Kennish et al. 1984, Williams 1984). Adults occupy seagrass meadows, unvegetated sediments, *Spartina* marsh creeks, and macroalgae (Heck & Thoman 1984, Kennish et al. 1984, Williams 1984, Wilson et al. unpubl.), utilizing these habitats as sources of food, shelter, and refuge from predation (Orth et al. 1984, Williams 1984, Hines et al. 1987). Extensive research on adult biology (e.g. Pearson 1948, van Engel 1958, Williams 1965, Tagatz 1968, Hines et al. 1987), behavior (Jachowski 1974), and feeding ecology (Blundon & Kennedy 1982, Laughlin 1982, Lipcius & Hines 1986) has shown that, in systems where the blue crab is abundant, it is an important predator, controlling the abundance of some bivalves (Arnold 1984, Lipcius & Hines 1986), and the diversity and structure of parts of the benthic community (Virnstein 1977, Laughlin 1982, Holland et al. 1980).

Little is known, however, of the natural history of early juvenile blue crabs or their role in benthic communities. Only recently were detailed comparisons of

habitat utilization and seasonal abundance patterns of juveniles described for Chesapeake Bay (Orth & van Montfrans 1987) and southern New Jersey (Wilson et al. 1990).

Field and laboratory experiments have shown that seagrasses are effective refuges, reducing rates of predation on a variety of decapod crustaceans (Heck & Thoman 1981, Heck & Wilson 1987, Barshaw & Lavalli 1988) including the blue crab (Wilson et al. 1987). Several species of red drift algae have also been shown to reduce rates of predation on shrimps (Coen et al. 1981, Heck & Thoman 1981) and early juvenile spiny lobsters (Herrnkind & Butler 1986).

Although seagrass beds are extensive in much of the northern portion of the blue crab's range, associated drift algae (such as the rhodophytes *Laurencia* spp. and *Gracilaria* spp.) are less common and do not form the massive aggregations or beds seen in sub-tropical estuaries (Hooks et al. 1976, Thorhaug & Roessler 1977, Gore et al. 1981). In the mid-Atlantic states, however, estuaries lacking red drift algae commonly contain large quantities of the (attached or drifting) green macroalga *Ulva lactuca* (sea lettuce), on otherwise unvegetated substrate (Orris & Taylor 1973, Loveland et al. 1984). In addition, salt marshes are major components of these estuaries (Chizmadia et al. 1984) and may be

potential nursery habitats and refuge for juvenile blue crabs. There have been few experimental studies of the potential refuge value of marsh creeks for decapod crustaceans (Boesch & Turner 1984, Zimmerman & Minello 1984) and none for *U. lactuca* beds, and yet they comprise some of the most dominant shallow-water estuarine habitats of New Jersey and Delaware.

In this study we examined experimentally relative rates of predation on juvenile blue crabs among several dominant New Jersey estuarine habitats by estimating predation rates in eelgrass *Zostera marina*, sea lettuce *Ulva lactuca*, *Spartina* marsh creeks and unvegetated sediment. We confirm results from earlier studies that submerged aquatic vegetation serves as refuge from predation and provide evidence that *U. lactuca* may be a more effective seasonal refuge than eelgrass.

STUDY SITES

Tethering experiments were conducted in Little Egg Harbor and Great Bay (ca 39° N, 74° W) in southern New Jersey, USA (Fig. 1). The seagrass site is located in the eelgrass meadows of Little Egg Harbor which contain scattered patches of unvegetated substrate and small clumps of algae (*Gracilaria tikvahiae*, *Agardhiella* sp.). The macroalgae site is located ca 7 km from the eelgrass site, near the mouth of a marsh creek on Great Bay. Like much of Great Bay it has mats and drifting patches of *Ulva lactuca* over a sandy-mud

bottom. Other species of algae that occur in the area include *Gracilaria tikvahiae*, *Agardhiella* sp., and *Ceramium* sp. The *Spartina* marsh creek study site is a small tidal tributary of Hatfield Creek located off of Great Bay ca 1 km from the macroalgae site. The creek bottom is characterized by soft, flocculent mud overlying oyster shell hash. Occasionally, several species of algae (*Agardhiella* sp., *Ceramium* sp., *Polysiphonia* sp. and *U. lactuca*) drift in the creek. Juvenile and adult blue crabs occur in all of the field sites along with other common decapod crustaceans such as *Crangon septemspinosa*, *Palaemonetes vulgaris*, and *Dyspanopeus sayi* (Wilson et al. unpubl.).

Salinities at all sites were very similar, ranging from 27 to 32 ‰, but water temperatures at the sites were more variable and changed with the seasons (Table 1). Water depth at low tide ranged from 60 to 120 cm at all sites.

Table 1. Mean temperatures (°C) and salinities (‰) at the 3 study sites during 1987

Month	Eelgrass		Sea lettuce		Marsh creek	
	‰	°C	‰	°C	‰	°C
July mean	31.3	25.8	31.6	23.8	31.2	24.7
SD	1.2	3.4	1.4	2.8	1.0	2.3
September mean	27.8	20.8	29.3	20.7	29.0	21.1
SD	1.8	3.8	0.4	3.4	1.4	2.9
October mean	26.7	15.7	27.0	14.5	27.7	14.1
SD	0.6	1.0	1.4	1.0	1.6	1.6

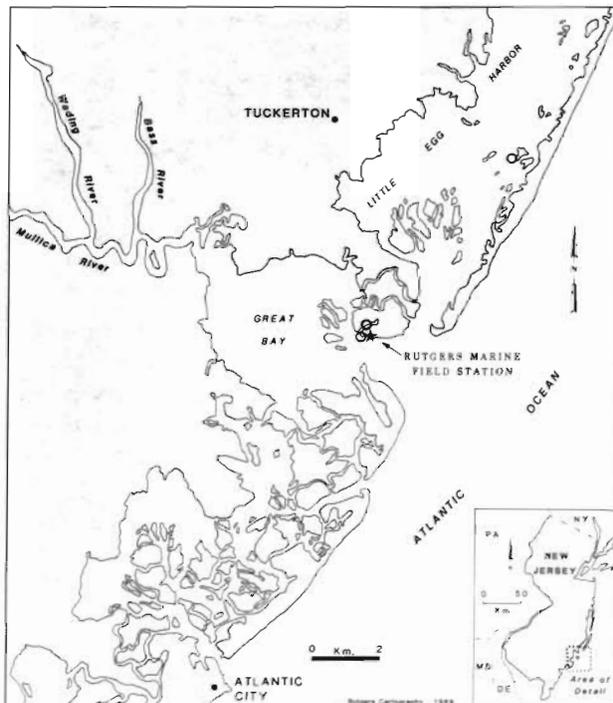


Fig. 1. Study area. (o) Study sites

METHODS AND MATERIALS

Relative rates of predation in eelgrass *Zostera marina*, macroalgae *Ulva lactuca*, unvegetated substrates adjacent to these habitats, and a *Spartina* marsh creek were estimated with tethering techniques similar to those used by Heck & Thoman (1981), Heck & Wilson (1987) and Wilson et al. (1987). Only hard, intermolt crabs were used. One end of a ½ m length of light-weight monofilament line was tied around the lateral spines and across the dorsal surface of the carapace. A drop of 'super' (cyanoacrylate) glue was placed at the knot on the carapace securing the line to the crab. Each crab was placed in the habitat tethered by the line to a J-shaped wire stake (one crab per stake) pushed completely into the sediment. A predation loss was scored when the crab was missing from the tether and a piece of the glued carapace remained on the line. Instances where crabs had molted or when it was not clear whether they might have escaped rather than being eaten were eliminated from consideration. These

cases made up 4 % of the total number of tethered crabs. Sixty-five of the crabs (7.4 % of all tethered crabs) recovered from experiments were used a second time in subsequent trials because of a shortage of small juveniles.

We have used this tethering technique to measure relative rates of predation among habitats, but do not contend that we are measuring absolute rates of predation. Our observations indicate that tethered crabs are able to swim, bury, or feed, and when placed in the habitat move immediately to the bottom and either bury in the substrate or hide in the vegetation.

Crabs were collected for tethering from eelgrass, *Ulva* patches and shallow-water unvegetated areas in the Little Egg Harbor–Great Bay estuary with seines and push nets. Sizes of tethered crabs thus closely resembled sizes of crabs in the field at the time of the experiment. In each trial 9 measured (carapace width at lateral spines, CW) crabs were tethered in each of the treatment habitats (eelgrass, sea lettuce, and *Spartina* marsh creek) and in 2 control areas (unvegetated substrates adjacent to the sea lettuce and eelgrass habitats) within 3 h of each other at low tide on the same day. At the 2 vegetated sites crabs were tethered in 3 densities (low, medium, high) of eelgrass and macroalgae (3 crabs per density) in order to determine if crabs in different densities of vegetation were eaten at different rates. The tethered crabs were left for 24 h (± 1 h) and then recovered and losses scored. Nineteen trials (with 45 crabs per trial and a total of 855 tethered individuals) were conducted from 25 June to 19 October 1987. However, because of loss of tethered crabs to storms, vandalism, and other events, results are presented from a total of 674 crabs. No tethering experiments were conducted between 28 July and 24 August. For ease of presentation and analysis, data from the end of June through July are termed 'July results', and data from the end of August through September are termed 'September results'.

Density of eelgrass in the tethering sites was estimated visually in the field at the time of the experiment. Subsequently, eelgrass biomass was measured by determining the mean dry weight of total plant biomass (above and below ground) from 3 replicate quadrats (0.063 m^2) taken twice (July and September) in each of the sites of visually estimated low, medium, and high density vegetation (a total of 6 replicates per density).

Ulva lactuca density was also estimated visually prior to each experimental trial. In July and September *U. lactuca* was collected near the macroalgae sites immediately before the trials to measure macroalgal biomass by dry weight. We noted, however, that *Ulva* often drifted through the area and densities sometimes changed over a few hours. We also found that our

unvegetated control sites adjacent to the *Ulva* beds were frequently disrupted by drifting macroalgae. To remedy this situation (after 25 August) we moved our *Ulva* site ca 50 m, away from the area where the *Ulva* drifted in large quantities, to an area where the macroalgae was less abundant, but the substrate was similar to the original site. Here, different sized clumps of *Ulva* were each held down with a 65 cm length of 0.64 cm reinforcing bar lying flat on the substrate to form stationary algal patches in which crabs could be tethered. One crab was tethered in each of the low, medium, and high density patches (3 replicates per density) as in July. The control consisted of crabs tethered in adjacent unvegetated substrate, with the sites marked by reinforcing bar (65×0.64 cm) resting on the substrate. This allowed us to test for differences in predation among densities of *Ulva*, and in the same area measure rates of predation on crabs in unvegetated sediment for the controls, with very little drifting algae confounding our control or treatment.

DATA ANALYSIS

A 1-way analysis of variance (ANOVA) was used on arcsin-transformed data to test for differences in predation rates among habitats. The data were analysed for each month separately because of the problems with disrupted controls in the unvegetated sites adjacent to the *Ulva* in July. Planned orthogonal comparisons were made among treatment means. Differences in rates of predation on size classes were tested for with Kolmogorov-Smirnov (KS) 2-sample tests on each of the habitats for the 3 mo of data combined, except for the unvegetated habitat adjacent to the macroalgae. Only September and October size data were tested for this habitat because of the disruption by drifting *Ulva* in July. Sizes of tethered crabs used in each habitat for each experimental period were tested to determine if the mean crab size was similar among habitats over time. Differences among low, medium, and high density vegetation were tested for with 1-way ANOVA and Student-Newman-Keul (SNK) tests as were differences among predation rates in the different densities of eelgrass and sea lettuce.

RESULTS

Rates of predation on juvenile blue crabs differed significantly among the habitats (Fig. 2). Overall, crabs tethered in eelgrass and macroalgae were preyed on at the lowest rates, and those in unvegetated and marsh creek substrates at the highest rates. Crabs that were recovered and used a second time in experiments were

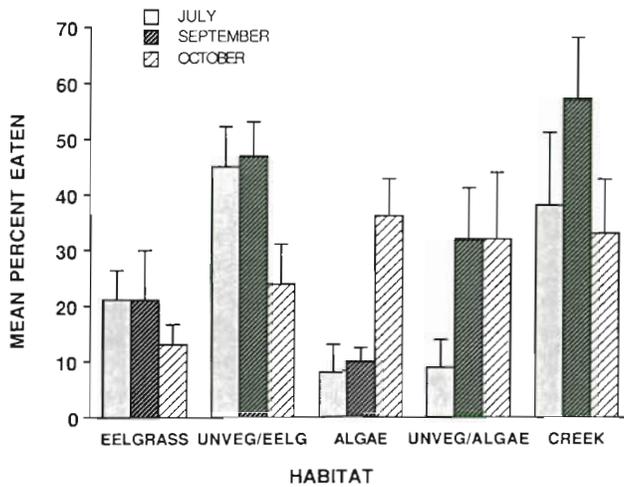


Fig. 2. *Callinectes sapidus*. Mean percent crabs eaten in eelgrass, adjacent unvegetated substrate, macroalgae (sea lettuce), adjacent unvegetated substrate, and marsh creek (+ 1 standard error)

not eaten at significantly different rates from crabs tethered only once (Mann-Whitney U-test, $U = 42$, $p > 0.10$).

Rates of predation also varied seasonally. In July, crabs in the vegetated habitats (eelgrass and macroalgae) exhibited significantly different predation rates compared to the unvegetated controls or the marsh creek (Table 2). Most striking was the significantly lower rate in sea lettuce (8 %) compared to the rates in eelgrass (21 %). For that time period it was difficult to distinguish between the unvegetated substrates and the marsh creek because of the presence of drifting algae across the unvegetated control adjacent to the macroalgae site. Of 9 trials in the unvegetated sub-

strate adjacent to the *Ulva*, 8 were disrupted by drifting algae. In essence, the unvegetated control acted as a second macroalgae treatment, and appears to confirm results from the planned *Ulva* treatment. Predation rates in the creek (38 %) are at least as high as those in the control unvegetated substrate adjacent to the eelgrass (45 %).

In September, crabs in the vegetated habitats were preyed on at significantly lower rates than those in unvegetated sites (Table 2), and predation rates were lower in *Ulva* (10 %) than in eelgrass (21 %), but the differences were not significant. There were no significant differences between the unvegetated controls and the marsh creek, all of which had rates greater than 31 %.

In October, there were no significant differences in predation intensity among the habitats (Table 2). Predation rates in the eelgrass dropped slightly (to 13 %), as did those in the unvegetated site adjacent to the eelgrass (to 24 %) (Fig. 2). The predation rate in *Ulva*, however, rose to 36 % and was not significantly different from the unvegetated sites.

Mean total biomass (above and below ground components) for visually estimated low density eelgrass was 185.6 g dry wt m^{-2} . This was significantly different from the visually estimated medium (428.3 g dry wt m^{-2}) and high (563.0 g dry wt m^{-2}) density eelgrass (SNK, $p < 0.001$), although medium and high density eelgrass were not significantly different in biomass. Rates of predation in the 3 densities of eelgrass (Table 3) differed significantly only between the rates in the low (29.5 % eaten) and high (13.2 % eaten) density treatments (SNK, $p < 0.05$).

Mean biomass of *Ulva lactuca* in low density treatments was 4.8 g dry wt m^{-2} and measurements of

Table 2. ANOVA and planned comparisons table for predation rate data from eelgrass, adjacent unvegetated substrate, sea lettuce, adjacent unvegetated substrate, and marsh creek habitats. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. NS: not significant

	Source	df	MS	F	p
July	Habitat	4	2163.44	9.89	<0.001
	Error	40	218.63		
September	Habitat	4	8.23	5.38	<0.005
	Error	20	166.80		
October	Habitat	4	184.40	0.69	<0.10
	Error	20	266.15		
Planned comparisons					
			Jul	Sep	Oct
<hr/>					
Vegetated vs Unvegetated			**	***	NS
(Eelgrass + sea lettuce vs unvegetated)					
Eelgrass vs sea lettuce			**	NS	NS
Unveg. sites adjacent to veg. vs marsh creek			*	NS	NS
Unvegetated/eelgrass vs unveg./sea lettuce			**	NS	NS

Table 3. Mean biomass of vegetation in high, medium, and low density treatments and the percent crabs *Callinectes sapidus* eaten

Eelgrass			Sea lettuce		
Biomass (g dry wt m ⁻²)		% Eaten	Biomass (g dry wt m ⁻¹)		% Eaten
\bar{x}	SD		\bar{x}	SD	
563.0	82.3	13.2	60.2	16.6	13.6
428.3	55.3	17.5	23.8	8.6	20.3
185.6	39.6	29.5	4.8	1.0	14.1

biomass in the low, medium, and high density *Ulva* patches were significantly different between all pairs (SNK, $p < 0.05$). However, the predation rate in the low density *Ulva* (Table 3) was not significantly different from rates in either medium or high density *Ulva* treatments.

The size frequency distributions of crabs eaten in eelgrass, adjacent unvegetated substrate, and the marsh creek were not significantly different from the size frequency distribution of crabs tethered in those habitats (Fig. 3a, b, e) (KS test, $p > 0.10$). Tests (KS 2-sample test) of size distributions of tethered crabs

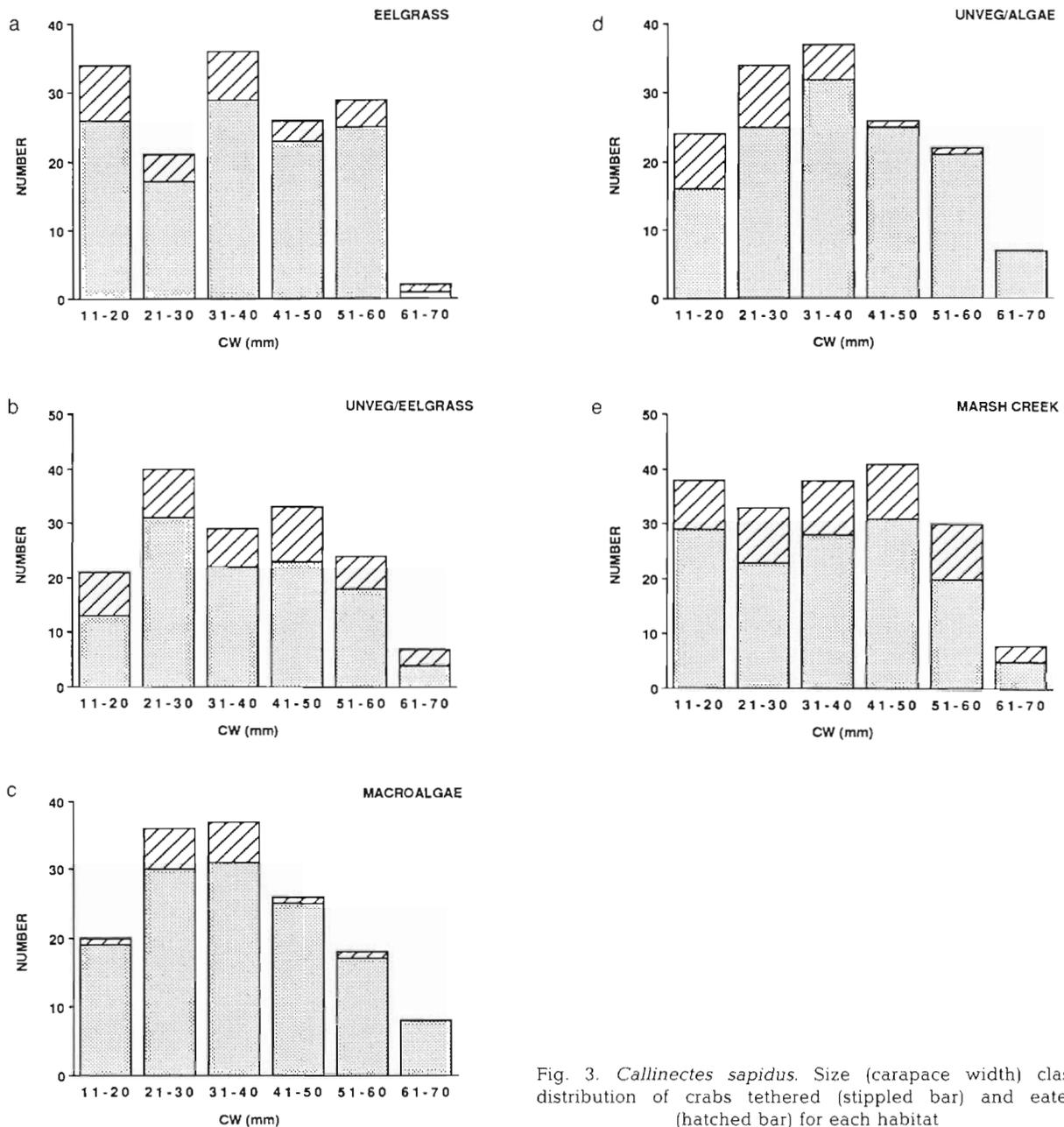


Fig. 3. *Callinectes sapidus*. Size (carapace width) class distribution of crabs tethered (stippled bar) and eaten (hatched bar) for each habitat

among habitats within each month found no significant differences between distributions. Differences were found, however, between months. Tethered crabs were smaller in October in all habitats (Table 4) reflecting the size of crabs in the field as a result of recruitment of small juveniles to the estuary. The mean size of crabs tethered in all habitats was similar in July and September (Table 4) although variation in size was greater in September. In the macroalgae it appears that the smallest and largest crabs were not eaten at the same rates (Fig. 3c), but this was not significant (KS test, $p > 0.10$). In the unvegetated substrate adjacent to the macroalgae, however, there was a significant difference in size classes that were preyed upon (KS test, $p < 0.01$), where the smallest crabs were eaten at a higher rate than larger crabs (Fig. 3d).

DISCUSSION

Our study demonstrates the importance of *Ulva lactuca* as a predator refuge, and that the refuge may vary seasonally. Its value as a refuge may exceed eelgrass at some times of the year. Enhanced survival of juveniles in *U. lactuca* patches is surprising considering the evidence for detrimental effects of sea lettuce on growth and survival of some invertebrates (Magre 1974, Edwards & Welsh 1982), particularly for larval stages of decapod crustaceans (Johnson & Welsh 1985). Toxic exudates from *Ulva* and low levels of dissolved oxygen associated with large *Ulva* beds have been suggested as the causes of morbidity and mortality of larval invertebrates and their avoidance of *Ulva* beds. We have found, however, that large numbers of decapod crustaceans and small fishes (Wilson et al. unpubl.) occur in *U. lactuca* patches in southern New Jersey. In addition, some invertebrates are closely associated with *Ulva* spp. Sea hares *Aplysia* spp. commonly live among and consume *U. lactuca* in Israeli coastal waters (Susswein et al. 1987), and amphipods *Eogammarus confervicolus* can potentially consume half the net production of *Ulva fenestrata* in False Bay, Washington, USA (Price & Hylleberg 1982).

Associations of invertebrates with green macroalgae in temperate estuaries are not well known, although tropical species such as *Halimeda opuntia* and *Penicillus capitatus* can harbor many macrocrustaceans (Stoner 1985, Stoner & Lewis 1985). High densities of animals associated with red macroalgae species (Gore et al. 1981) and the value of red algae as refuge from predators (Coen et al. 1981, Heck & Thoman 1981, Marx & Herrnkind 1985) have been reported. The refuge properties of red algae such as *Laurencia* spp. and *Gracilaria* spp. have been attributed to their foliose structure, which serves to increase surface area and structural complexity (Heck & Orth 1980). The structure of these algae may also provide a complex background which prey may match (cf. Orth et al. 1984). *Ulva lactuca*, however, grows in sheets, and would not seem to offer the complex background or have the structural complexity of foliose algae or seagrass. Instead, *Ulva* may act as an opaque barrier to visual predators (cf. Main 1987). Prey may then hide under the sheets of *Ulva* and be invisible to visual predators.

Other studies have suggested a positive correlation between macroalgae biomass and prey survivorship (Coen et al. 1981, Heck & Thoman 1984, Heck & Wilson 1987), but no such relationship was found between *Ulva* biomass and blue crab survivorship. If the *Ulva* does act as an opaque barrier, and functions differently from red algae or seagrasses, then small quantities might work as well as large simply by providing cover over the sediment surface.

Ulva lactuca may also serve as an associational defense for invertebrate prey (cf. Hay 1986). That is, some predators may find *Ulva* and its exudates distasteful or repulsive (Magre 1974) and avoid foraging in *Ulva* beds. Prey would gain some benefit from inhabiting an *Ulva* patch or bed, through lowered predation risk, even if there were some physiological costs to exposure to exudates or the low oxygen levels that may occur.

Juvenile blue crabs occur in a variety of vegetated and unvegetated habitats in southern New Jersey (Kennish et al. 1984) including marsh creeks and *Ulva lactuca* beds (Wilson et al. 1990). In Chesapeake Bay, after fall

Table 4. *Callinectes sapidus*. Mean carapace width (mm) of blue crabs tethered in field predation experiments from July to October 1987. Not included here are 9 % of the crabs which were not measured

Habitat	July		September		October	
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
Eelgrass	38.4	11.4	36.1	17.9	23.7	9.3
Unveg./eelgrass	36.8	11.5	38.2	17.3	25.8	11.6
Sea lettuce	38.4	11.0	38.6	18.3	24.3	8.3
Unveg./sea lettuce	37.5	11.1	39.0	17.4	27.0	11.6
Marsh creek	38.4	10.0	39.2	18.8	24.6	9.7

recruitment, juveniles can occur in very high densities in eelgrass beds (up to 90 m^{-2}) after fall recruitment and at lower densities (12 m^{-2}) in marsh creeks (Orth & van Montfrans 1987). Several coincident factors may be operating to produce such a pattern of abundance. Passive recruitment, habitat preference (Bell & Westoby 1986), physical factors, or predation may all influence the abundance of decapod crustaceans in particular habitats. Orth & van Montfrans (1987) suggest that predation and lack of suitable refuge in marsh creeks contributed to lower juvenile blue crab abundances relative to eelgrass beds in their study. Rates of predation in our New Jersey marsh creek were higher than the rates in eelgrass, lending support to the hypothesis that predation rates are greater in marsh creeks and that eelgrass has a higher refuge value. Certainly the data demonstrate differential rates of survival among habitat types, which could lead to different patterns of abundance. Other experiments are needed, however, to distinguish among the many factors and their interactions that may affect abundance.

Our tethering results in eelgrass and the adjacent unvegetated sediment are similar to an earlier study on predation in various densities of eelgrass (Wilson et al. 1987) in Manahawkin Bay, New Jersey. The overall predation rates are similar (within 2 to 3 percentage points) but rates in low, medium and high densities of eelgrass at Marsh Elder Island (this study) appear different. Biomasses of the visually estimated densities, however, are lower than those from the earlier study in Manahawkin Bay. The estimated high density ($563 \text{ g dry wt m}^{-2}$) of this study is closer to the medium density ($691.8 \text{ g dry wt m}^{-2}$) measured by Wilson et al. (1987). Thus, our experiments actually confirm earlier results that predation is intense in eelgrass of low biomass and is relatively less at biomass levels in the region of $500 \text{ g dry wt m}^{-2}$. Our experiments here did not test for predation rates in higher density eelgrass of total biomass over $1000 \text{ g dry wt m}^{-2}$ (Wilson et al. 1987).

Different types of predators may influence changing patterns of predation in habitats. This may be the case where seasonal changes in predation rates occur and in habitats where different size classes of crabs are being eaten. The size distribution of crabs eaten in the unvegetated control adjacent to the *Ulva* site (Fig. 3d) suggests that different predators or different size classes of predators are feeding in this habitat than in the adjacent *Ulva* habitat.

Smaller crabs might be expected to be more vulnerable to predation (Orth & van Montfrans 1987). Our results suggest, though, that in most of the habitats all sizes from 10 to 65 mm CW are vulnerable. Smaller crabs (< 40 mm CW) were preyed on at higher rates in the unvegetated site adjacent to the macroalgae. This may demonstrate the interaction of habitat type (lack of

vegetative cover) and the suite of predators that operates in that area. Smaller crabs were tethered in all habitats in October (Table 4) than in the previous months reflecting the size distribution of crabs in the field. Smaller size of tethered crabs in October might contribute to the change in predation rates and lack of differences among habitats, although other changes occur in the fall that could contribute to different predation rates. For example, water temperatures show a drop in October that might influence activity patterns of both prey and predators.

The October rise in predation rates in the *Ulva lactuca* site suggests that the habitat is effective as a refuge for only parts of the year. Seasonal movements of predators through the area may account for some of the changes in predation. For example, small (< 4 cm total length, TL) *Tautoga onitis* juveniles inhabit *Ulva* patches (Wilson & Able pers. obs.), and larger (20 to 30 cm TL) juveniles, which are known crustacean predators (Able pers. obs.), may become more active and move through habitats in the fall while migrating to overwintering sites (Olla et al. 1978). Further contributing to changes in refuge value of sea lettuce is the fact that, unlike eelgrass, this macroalga is ephemeral and unpredictable in abundance (Loveland et al. 1984, Wilson et al. unpubl.). On the other hand, the root/rhizome mat of eelgrass, which remains after exfoliation in the fall (Vaughan 1982), may still provide some shelter to small burying invertebrates through the winter (Wilson et al. 1987, cf. Orth et al. 1984). Thus, if refuge value of the various habitats is considered over the period of time in which the blue crab population may be most vulnerable to predation (fall to spring), then eelgrass might prove to be the more important habitat for survival.

We feel, however, that the data suggest the potential of *Ulva lactuca* as an important habitat and refuge for epibenthic invertebrates, especially in areas without seagrasses. Marsh creeks have been suggested as potential nursery areas, but the high rates of predation that we found indicate that juvenile blue crabs may suffer high mortality without some type of macrophyte shelter. The abundance and widespread distribution of *Ulva* spp. in estuarine waters suggest that this green macroalga should be more carefully studied for its nursery potential. Patches of *U. lactuca* in well-flushed areas, where accumulation of exudates and low dissolved oxygen are less likely to occur, may be important alternative refuge for juvenile blue crabs and other economically important species that utilize estuarine nurseries.

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LITERATURE CITED

- Arnold, W. S. (1984). The effects of prey size, predator size, and sediment composition on the rate of predation of the blue crab, *Callinectes sapidus* Rathbun, on the hard clam, *Mercenaria mercenaria* (Linne) J. exp. mar. Biol. Ecol. 80: 207-219
- Barshaw, D. E., Lavalli, K. L. (1988). Predation upon post-larval lobsters *Homarus americanus* by cunners *Tautogolabrus adspersus* and mud crabs *Neopanope sayi* on three different substrates: eelgrass, mud and rocks. Mar. Ecol. Prog. Ser. 48: 119-123
- Bell, J. D., Westoby, M. (1986). Abundance of macrofauna in dense seagrass is due to habitat preference, not predation. Oecologia (Berl.) 68: 205-209
- Boesch, D. F., Turner, R. E. (1984). Dependence of fishery species on salt marshes: the role of food and refuge. Estuaries 7 (4 A): 460-468
- Blundon, J. A., Kennedy, V. S. (1982). Refuges for infaunal bivalves from blue crab, *Callinectes sapidus* (Rathbun), predation in Chesapeake Bay. J. exp. mar. Biol. Ecol. 65: 67-81
- Chizmadia, P. A., Kennish, M. J., Otori, V. L. (1984). Physical description of Barnegat Bay. In: Kennish, M. J., Lutz, R. A. (eds.) Ecology of Barnegat Bay, New Jersey. Springer-Verlag, New York, p. 1-28
- Coen, L. D., Heck, K. L., Jr, Abele, L. G. (1981). Experiments on competition and predation among shrimps of seagrass meadows. Ecology 62 (6): 1484-1493
- Edwards, S. F., Welsh, B. L. (1982). Trophic dynamics of a mud snail (*Ilyanassa obsoleta* [Say]) population on an intertidal mudflat. Estuar. cstl Shelf Sci. 14: 663-686
- Gore, R. H., Gallaher, E. E., Scotto, L. E., Wilson, K. A. (1981). Studies on decapod crustacea from the Indian River region of Florida. XI. Community composition, structure, biomass and species-area relationships of seagrass and drift algal-associated macrocrustaceans. Estuar. cstl Shelf Sci. 12: 485-508
- Hay, M. E. (1986). Associational plant defenses and the maintenance of species diversity: turning competitors into accomplices. Am. Nat. 128: 617-641
- Heck, K. L. Jr, Orth, R. J. (1980). Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. pp. 449-464. In: Kennedy, V. S. (ed.) Estuarine perspectives. Academic Press, New York, p. 449-464
- Heck, K. L. Jr, Thoman, T. A. (1981). Experiments on predator-prey interactions in vegetated aquatic habitats. J. exp. mar. Biol. Ecol. 53: 125-134
- Heck, K. L. Jr, Thoman, T. A. (1984). The nursery role of seagrass meadows in the upper reaches of the Chesapeake Bay. Estuaries 7 (1): 70-92
- Heck, K. L. Jr, Wilson, K. A. (1987). Predation rates on decapod crustaceans in latitudinally separated seagrass communities: a study of spatial and temporal variation using tethering techniques. J. exp. mar. Biol. Ecol. 197: 87-100
- Herrnkind, W. F., Butler, M. J. IV (1986). Factors regulating postlarval settlement and juvenile microhabitat use by spiny lobsters *Panulirus argus*. Mar. Ecol. Prog. Ser. 34: 23-30
- Hines, A. H., Lipcius, R. N., Haddon, M. (1987). Population dynamics and habitat partitioning by size, sex, and molt stage of blue crabs *Callinectes sapidus* in a subestuary of central Chesapeake Bay. Mar. Ecol. Prog. Ser. 36: 55-64
- Holland, A. F., Mountford, N. K., Hiegel, M. H., Kaumeyer, K. R., Mihursky, J. A. (1980). Influence of predation on infaunal abundance in upper Chesapeake Bay, USA. Mar. Biol. 57: 221-235
- Hooks, T. A., Heck, K. L. Jr, Livingston, R. J. (1976). An inshore marine invertebrate community: structure and habitat associations in the northeastern Gulf of Mexico. Bull. mar. Sci. 26: 99-109
- Jachowski, R. L. (1974). Agonistic behavior of the blue crab, *Callinectes sapidus* Rathbun. Behaviour 50 (3-4): 232-253
- Johnson, D. A., Welsh, B. L. (1985). Detrimental effects of *Ulva lactuca* (L.) exudates and low oxygen on estuarine crab larvae. J. exp. mar. Biol. Ecol. 86: 73-83
- Kennish, M. J., Vouglitois, J. J., Danila, D. J., Lutz, R. A. (1984). Shellfish. In: Kennish, M. J., Lutz, R. A. (eds.) Ecology of Barnegat Bay, New Jersey. Springer-Verlag, New York, p. 171-200
- Laughlin, R. (1982). Feeding habits of the blue crab, *Callinectes sapidus* Rathbun, in the Appalachicola estuary, Florida. Bull. mar. Sci. 32 (4): 807-822
- Lipcius, R. N., Hines, A. H. (1986). Variable functional responses of a marine predator in dissimilar homogeneous microhabitats. Ecology 67: 1361-1371
- Loveland, R. E., Brauner, J. F., Taylor, J. E., Kennish, M. J. (1984). Macroflora. In: Kennish, M. J., Lutz, R. A. (eds.) Ecology of Barnegat Bay, New Jersey. Springer-Verlag, New York, p. 78-94
- Magre, E. J. (1974). *Ulva lactuca* L. negatively affects *Balanus balanoides* (L.) (Cirripedia: Thoracica) in tidepools. Crustaceana 27: 231-234
- Main, K. L. (1987). Predator avoidance in seagrass meadows: prey behavior, microhabitat selection, and cryptic coloration. Ecology 68: 170-180
- Marx, J. M., Herrnkind, W. F. (1985). Macroalgae (Rhodophyta: *Laurencia* spp.) as habitat for young juvenile spiny lobsters, *Panulirus argus*. Bull. mar. Sci. 36 (3): 423-431
- Olla, B. L., Bejda, A. J., Martin, A. D. (1978). Seasonal dispersal and habitat selection of cunner, *Tautogolabrus adspersus*, and young tautog, *Tautoga onitis*, in Fire Island Inlet, Long Island, New York. Fish. Bull. U.S. 77: 255-261
- Orris, P. K., Taylor, J. E. (1973). A floristic and ecological survey. The benthic algae of Rehoboth Bay, Delaware, Botanica mar 16: 180-192
- Orth, R. J., Heck, K. L. Jr, van Montfrans, J. (1984). Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries 7 (4 A): 339-350
- Orth, R. J., van Montfrans, J. (1987). Utilization of a seagrass meadow and tidal marsh creek by blue crabs, *Callinectes sapidus*. I. Seasonal and annual variations in abundance with emphasis on post-settlement juveniles. Mar. Ecol. Prog. Ser. 41: 283-294
- Pearson, J. C. (1948). Fluctuations in the abundance of the blue crab in Chesapeake Bay. U.S. Fish Wildl. Serv. Res. Rep. 14, p. 1-26
- Price, L. H., Hylleberg, J. (1982). Algal-faunal interactions in a mat of *Ulva fenestrata* in False Bay, Washington. Ophelia 21: 75-88
- Stoner, A. W. (1985). *Penicillus capitatus*: an algal island for macrocrustaceans. Mar. Ecol. Prog. Ser. 26: 279-287
- Stoner, A. W., Lewis, F. G. III. (1985). The influence of quantitative and qualitative aspects of habitat complexity in tropical sea-grass meadows. J. exp. mar. Biol. Ecol. 94: 19-40
- Susswein, A. J., Achituv, Y., Markovich, S. (1987). *Aplysia* from shallow water along the coasts of Israel. Cah. Biol. mar 28: 97-110
- Tagatz, M. E. (1968). Biology of the blue crab, *Callinectes sapidus* Rathbun, in the St. Johns River, Florida. Fish. Bull. U.S. 67 (1): 17-33
- Thorhaug, A., Roessler, M. A. (1977). Seagrass community

- dynamics in a subtropical estuarine lagoon. *Aquaculture* 12: 253–277
- van Engel, W. A. (1958). The blue crab and its fishery in Chesapeake Bay. *Comml Fish. Rev.* 20: 6–17
- Vaughan, D. E. (1982). Production ecology of eelgrass (*Zostera marina* L.) and its epiphytes in Little Egg Harbor, New Jersey. Ph. D. thesis, Rutgers University, New Brunswick, New Jersey
- Virnstein, R. W. (1977). The importance of predation by crabs and fishes on benthic in fauna in Chesapeake Bay. *Ecology* 58 (6): 1199–1217
- Williams, A. B. (1965). Marine decapod crustaceans of the Carolinas. *Fish. Bull. U.S.* 65 (1): i–xi
- Williams, A. B. (1984). Shrimps, lobsters, and crabs of the Atlantic coast of the Eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, D.C.
- Wilson, K. A., Able, K. W., Heck, K. L. Jr, (1990). Habitat utilization of juvenile blue crabs: a comparison among habitats of southern New Jersey. *Bull. mar. Sci.* 46 (1): in press
- Wilson, K. A., Heck, K. L. Jr, Able, K. W. (1987). Juvenile blue crab, *Callinectes sapidus*, survival: an evaluation of eelgrass *Zostera marina*, as refuge. *Fish. Bull. U.S.* 85 (1): 53–58
- Zimmerman, R. J., Minello, T. J. (1984). Densities of *Penaeus aztecus*, *Penaeus setiferus*, and other natant macrofauna in a Texas salt marsh. *Estuaries* 7 (4 A): 421–433

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