Effects of anthropogenic shoreline hardening and invasion by *Phragmites australis* on habitat quality for juvenile blue crabs (*Callinectes sapidus*)

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ABSTRACT

Unvegetated, shallow water habitats adjacent to marshes are an important nursery for juvenile blue crabs, *Callinectes sapidus*, in Chesapeake Bay. Alteration of the shoreline, either through the replacement of marshes with anthropogenic structures, such as riprap and bulkheads, or through the replacement of the native marsh grass *Spartina* sp. (*Spartina*) with the invasive *Phragmites australis* (*Phragmites*), may affect the value of this habitat as a nursery. In this study, we compared the effects of four common shoreline types, bulkheads, riprap, *Phragmites* marshes, and *Spartina* marshes, on food availability, feeding, growth, and survival of juvenile blue crabs in adjacent subtidal areas, as well as on the abundance and size of predators in the South River, Maryland. Sites with each shoreline type were randomly selected. We used benthic cores to sample macrobenthic prey and performed gut content analysis on caged crabs to examine food availability and feeding. Growth was estimated using caged crabs. Survival was assayed with a tethering experiment and predators were sampled with a seine net. Riprap had a lower abundance of macrofaunal prey, and the macrofaunal community differed from both marsh types in that it had it had smaller an more opportunistic species such as nematodes and small polychaetes compared to more bivalves and larger polychaetes at the marsh sites; however, gut contents and growth did not vary among shoreline types. Predation pressure on juvenile blue crabs was highest at bulkhead sites and lowest at riprap. Predator abundance did not vary among the shoreline types, though piscine predators were smaller in size near *Spartina* marshes compared to the other shorelines. We conclude that shoreline hardening substantially reduced the value of shoreline habitats for juvenile blue crabs, but that *Spartina* and *Phragmites* are functionally equivalent.

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1. Introduction

In Chesapeake Bay and elsewhere, shallow, unvegetated habitats, especially those adjacent to salt marshes, are important secondary nursery habitats for many macrofaunal species (e.g. Minello et al., 2003) including the ecologically (Baird and Ulanowicz, 1989) and economically (Lipcius and Stockhausen, 2002) important blue crab, *Callinectes sapidus* (Lipcius et al. 2005). These areas provide a refuge from predation (Clark et al., 2003; Dittel et al., 1995; Hines and Ruiz, 1995; Minello et al., 2003; Ruiz et al., 1993), especially for vulnerable molting crabs (Hines et al., 1987; Ryer et al., 1997), and offer a high abundance of macrofaunal prey, which contributes to high growth rates (Seitz et al., 2005, 2006). However, these habitats are changing, both through human development of coastal areas,

which includes the alteration of the shoreline (Peterson and Lipcius, 2003), and through replacement of native salt marsh grasses, especially *Spartina* sp. (hereafter *Spartina*) by the invasive common reed *Phragmites australis* (hereafter *Phragmites*) along the US Atlantic coast (Fell et al., 1998).

Although coastal development, land-use patterns, and eutrophication influence large-scale abundance and distribution of blue crabs and their prey resources (e.g. Kemp et al., 2005; King et al., 2005), relatively little is known about small-scale effects of shoreline development. Fragmentation of marshes through costal development may alter shoot density and faunal abundance (Long and Burke, 2007). Hardened shorelines, such as riprap and bulkheads, are associated with a lower abundance of macrofaunal organisms in the adjacent subtidal habitats when compared to marsh shorelines (Seitz et al., 2006; Weis et al., 1998). In the case of bulkheads, this may be due to toxic chemicals leaching from treated lumber (Weis et al., 1998). However, because marshes can supply substantial amounts of allochthonous carbon to subtidal habitats (Quan et al., 2007; Roman and Daiber, 1989; Wainright et al., 2000), replacing them with riprap or bulkheads, which cannot supply such resources, may lower macrofaunal densities (Seitz et al., 2006). Additionally, hardened shorelines are frequently associated with lower densities and smaller sizes of

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nektonic species (Hendon et al., 2000; Peterson et al., 2000), though not in all cases (Seitz et al., 2006). However, in Southern California, riprap is functionally equivalent to the local natural rocky habitats indicating that effect is not always detrimental (Pister 2009).

Extensive research has been conducted on the ecological effect of *Phragmites* invasions. In general, *Phragmites* differs little from *Spartina* as a habitat for macrofauna (Weis and Weis, 2003). Most nektonic species use both marsh types similarly (Hanson et al., 2002; Jivoff and Able, 2003; Meyer et al., 2001; Osgood et al., 2003; Robertson and Weis, 2007), and macrofaunal densities are equivalent (Osgood et al., 2003; Posey et al., 2003). However, epifaunal abundance is lower in *Phragmites* than in *Spartina* (Robertson and Weis, 2005) and the abundance of some nektonic species, such as juvenile *Fundulus heteroclitus*, may be lower (Able et al., 2003). Also, the hydrology and topology of the marsh differ with *Phragmites* having reduced tidal flooding that may limit use by nekton (Osgood et al., 2003). Taken together, these studies suggest that the replacement of a *Spartina* marsh with *Phragmites* is unlikely to have a significant effect on habitat quality for juvenile blue crabs.

We designed this study to examine the effects of biological and anthropogenic shoreline changes on the value of the habitats as a nursery for juvenile blue crabs. We hypothesized that hardened shorelines would be associated with lower densities of macrofaunal organisms, leading to decreased crab growth rate. Also, we expected that unstructured bulkheads would be associated with higher predation rates than structured habitats such as riprap and salt marshes. Finally, we anticipated that *Phragmites* and *Spartina* marshes would differ little in their functioning as nursery habitats for blue crabs.

2. Materials and methods

2.1. Sampling area

The study was conducted July–September, 2008 in the South River, Maryland, USA, a heavily urbanized tributary of Chesapeake Bay. We investigated four types of shorelines common to the river: Bulkhead, Riprap, *Spartina* marsh, and *Phragmites* marsh. Although this is not a comprehensive set of shoreline types, these were among the most common and represent ~70% of the total shoreline in the system (Table 1). Using data from the Comprehensive Coastal Inventory Program (Berman et al., 2006), we identified all stretches of each shoreline type in the river that had >200 m of continuous shoreline. We verified all sites by visiting them and rejected those that had changed type in such a way as to reduce the length of continuous shoreline to <~100 m by visual estimation. Marsh areas that had a mixture of *Spartina* and *Phragmites* along the shoreline were also rejected although we retained those that had *Spartina* alone along the shore with *Phragmites* upland, well away from the shore. We randomly selected 10 of each of the shoreline types that met our criteria (Fig. 1). At each site, we measured bottom temperature, salinity (using the practical salinity scale), and dissolved oxygen using a DO probe (YSI Model 85, Yellow
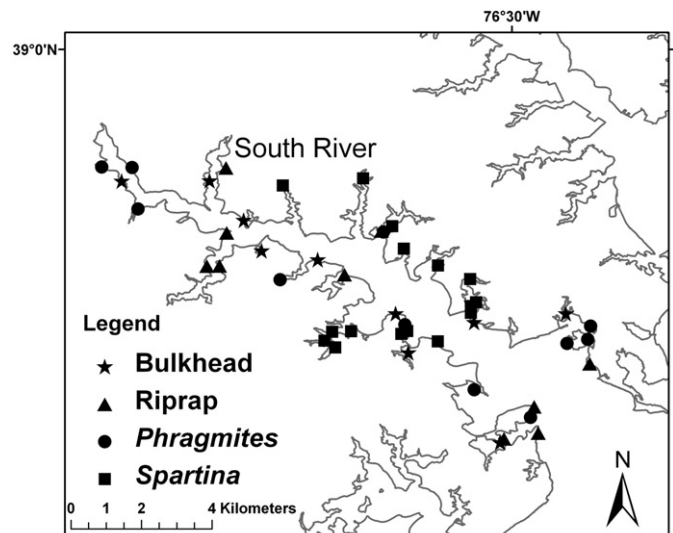

Fig. 1. Map of the South River, Chesapeake Bay, Maryland. Symbols represent sampling sites.

Springs Instruments, Dayton, Ohio, USA[3]). One of the *Spartina* marshes was later discovered to be a mixture of the two species and was excluded from all analyses.

2.2. Crab feeding, growth, and benthic prey availability

Hatchery crabs reared at the Center for Marine Biotechnology were used in all experiments (Zmora et al., 2005). Cages used for both the feeding and growth experiments were constructed with galvanized hardware cloth with a mesh size of 6.5 mm. Cages were 50 cm by 50 cm and 14 cm tall and open at the bottom, with a latchable door cut in the top. At each site, a cage was inserted several cm into the sediment at approximately the central point of the shoreline. One juvenile blue crab, carapace width (cw) 26.3 mm ± 3.0 (SD), was enclosed in each cage and allowed to feed for at least 24 h (Dittel et al., 1995). Crabs were starved for at least 2 days prior to the experiment. Crabs were resampled by enclosing the cage with a stainless steel frame inserted into the sediment. The top of the frame was encircled with vexar plastic mesh to keep the crabs from escaping. The cage was removed and a 10.16 cm diameter benthic core was taken from the center of the caged area. We sampled from within the caged area because we wanted to ensure that a direct comparison between the benthic assemblage in the core and the gut contents of the crab would be possible. The core was sieved on a 0.5 mm mesh screen, frozen, and stored at −20 °C. The caged area was then swept with nets until the crab was found. Digestion was stopped immediately by placing the crab on dry ice until frozen. The crab was then placed on ice before being stored at −20 °C.

Benthic cores were stained with rose Bengal, a vital stain, all animals were removed and identified to the lowest taxonomic level possible (usually species), and the density of each taxa (m^{-2}) was calculated. All crabs were dissected to remove the foreguts. Percent gut fullness was estimated, and the wet mass of the foregut was determined. The contents of the foreguts were identified to the lowest level possible under a stereo-microscope, and percent composition (by volume) of each food type was estimated.

Crab growth rate was determined at each of the four shoreline types by caging a juvenile blue crab, cw 12.0 mm ± 1.5 (SD), as above, and remeasuring them after 4 and 12 weeks. The growth experiment was run immediately after the feeding study using the

Table 1
Length and percent of the total length of bulkhead, riprap, *Spartina* marshes, and *Phragmites* marshes along the shoreline in the South River, MD. Total indicates the length of the entire shoreline and Total Developed includes bulkhead, riprap, and other man-made structures such as groin fields, jetties, and marinas. Data is from the Comprehensive Coastal Inventory Program (Berman et al., 2006).

Shoreline type	Length (km)	Percent
Bulkhead	28.5	21
Riprap	20.5	15
Spartina	30.4	23
Phragmites	12.3	9
Total developed	57.0	43
Total	133.3	

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[3] Use of trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

same cages. After 4 weeks, the crabs were resampled as described previously, and the cw of each was measured. The cage was then moved to a different location at the same site (to minimize caging effects and because resampling disturbed the site), and the crab was re-caged. After a further 8 weeks (12 weeks total), the crabs were resampled, and the cw of each was measured.

2.3. Predation risk and predator abundance

Predation risk was estimated by tethering (see Hines and Ruiz, 1995; Lipcius et al., 2005). Intermolt crabs had a 1 m long monofilament line glued to their carapaces using cyanoacrylate glue. The tethered crab was tied to a stake that was inserted fully into the sediment. A small marker float was also tied to the stake to aid in relocation. At each site, two juvenile blue crabs were tethered. Crabs were placed within 0.5 m of the shoreline at each site to allow the crabs to utilize any available structure, as long as they remained submerged at low tide. Otherwise, they were placed as close to the shore as possible. The crabs were checked daily until they were missing, molted, or dead. Crabs were deployed and checked in approximately the same order each day so while they were deployed and checked at different points during the day and tidal cycle, they were each checked after about 24 h of deployment and experienced the same number of tidal cycles. Survival of wild and hatchery crabs does not differ in tethering experiments (Johnson et al. 2011).

Predators of juvenile blue crabs were sampled with a 30.5 m long seine. At each site, the seine was pulled in a quarter arc up to the shoreline. All potential crab predators were identified, and the lengths or carapace widths were measured of up to 10 haphazardly selected individuals of each species. All other species that were not potential predators were identified and their presence noted.

2.4. Statistical analyses

Temperature, salinity, and dissolved oxygen were analyzed among shoreline type with a one-way analysis of variance (ANOVA). In all ANOVA/ANCOVA analyses, homogeneity of variance was verified using Levene's test and normality with an Anderson-Darling test. When the data did not meet these assumptions, the data were transformed. If transformed data failed to satisfy assumptions a Kruskal–Wallis test was used. Differences in benthic community structure among the shoreline types were analyzed using a non-metric multidimensional scaling analysis (MDS) and an analysis of similarity (ANOSIM; Primer v6.1.6; Clarke and Gorley, 2001; Clarke and Warwick, 2001). Where shoreline types differed significantly, a similarity percentages (SIMPER) analysis was performed to determine which species contributed most to that difference. Species richness and benthic abundance were analyzed with a one-way ANOVA. Differences in gut contents among the shoreline were also analyzed using ANOSIM. Percent gut fullness was analyzed with a one-way ANOVA.

Crab growth was calculated as the change in cw per day between the initial cw and the cw at 4 and 12 weeks after caging, square-root transformed to achieve homogeneity of variance, and then analyzed with an analysis of covariance (ANCOVA) with shoreline as a factor and initial size as a covariate. Growth after 4 and 12 weeks were analyzed separately.

We modeled predation by assuming an exponential distribution of survival times, and used maximum likelihood to fit our tethering data and calculate the predation rates. To prevent pseudoreplication we averaged the survival times for two crabs at each site. We tested four models: 1) No difference among the shoreline types; 2) Structured habitats (Riprap, *Spartina*, and *Phragmites*) differ from unstructured shoreline (Bulkhead); 3) The marshes (*Spartina* and *Phragmites*), Riprap, and Bulkhead all differ; 4) Each shoreline type differs from the others. The best model was selected using the Akaike's information criterion corrected for small sample size (AIC$_c$) of each model (Burnham and

Anderson 2002). Differences were analyzed among the shoreline types in total predator abundance and the average length of each of the most abundant predator species with a one-way ANOVA. The pelagic community, i.e. all species caught in the seine including both predators and non-predators, was analyzed as a whole with ANOSIM using a presence-absence transformed matrix.

3. Results

3.1. Physical variables

The average temperature at the sites was 27.7 °C and did not vary among shoreline types (ANOVA; $F_{3,35} = 1.36$, $p = 0.271$). Salinity and dissolved oxygen measurements were strongly heteroscedastic, and transformation did not help so they were analyzed with a Kruskal-Wallis test. Salinity ranged from 3.6 to 8.5 (mean 7.3) and did not vary among shoreline types (Kruskal–Wallis; test statistic = 1.196, df = 3, $p = 0.754$). Dissolved oxygen averaged 5.7 mg L^{-1} and also did not vary among shoreline types (Kruskal–Wallis; test statistic = 1.043, df = 3, $p = 0.791$).

Table 2
Average density (ind. m^{-2}) of macrofaunal organisms in benthic cores adjacent to each shoreline type. B = bivalve, G = gastropod, C = crustacean, I = insect, P = polichaete, O = other.

| Species	Bulkhead	Riprap	Phragmites	Spartina
Mya arenaria (B)	0	0	0	46
Macoma balthica (B)	12	46	25	15
Macoma mitchelli (B)	62	46	49	293
Mulinia lateralis (B)	25	31	25	0
Rangia cuneata (B)	0	15	0	0
Mytilus edulis (B)	0	0	0	15
Hydrobia miniata (G)	0	15	0	0
Hydrobia neglecta (G)	0	0	0	15
Cyathura polita (C)	0	0	37	0
Leptochelia spp. (C)	49	31	271	293
Edotea triloba (C)	37	0	12	15
Cassidisca lunifrons (C)	0	0	12	0
Corophium lacustre (C)	25	0	12	0
Neohaustorius schmitzi (C)	0	0	25	46
Gammarus mucronatus (C)	12	31	148	0
Gammarus tigrinus (C)	210	62	136	123
Leptocheirus plumulosus (C)	0	31	160	15
Palaemonetes pugio (C)	0	0	12	0
Crab megalopae (C)	12	0	12	0
Eurypanopeus depressus (C)	25	0	0	15
Semibalanus balanoides (C)	37	0	0	0
Mysidopsis bigelow (C)	0	0	0	15
Cumacea spp. (C)	0	31	0	0
Lynceus sp. (C)	0	0	12	62
Chironomidae spp. (I)	444	62	407	802
Culicidae spp. (I)	0	0	49	15
Heteromastus filiformis (P)	111	139	123	154
Notomastus spp (P)	0	0	25	31
Mediomastus californiensis (P)	37	0	0	0
Mediomastus ambiseta (P)	12	0	0	0
Capitella capitata (P)	0	0	37	0
Opheliidae sp. (P)	432	308	247	586
Ophelia bicornis (P)	12	31	0	0
Spionidae spp. (P)	0	0	12	0
Neanthes succinea (P)	62	31	123	46
Laonereis culveri (P)	185	15	222	262
Eteone heteropoda (P)	222	123	62	262
Leitoscoloplos fragilis (P)	0	46	0	0
Potamilla neglecta (P)	0	15	0	0
Ampharetidae sp. (P)	12	15	12	108
Cirratulidae spp. (P)	0	0	25	0
Glycera americana (P)	0	0	12	0
Demonax microphthalmus (P)	12	0	0	0
Tubificidae spp.	0	0	25	0
Nematoda spp.	0	62	25	0
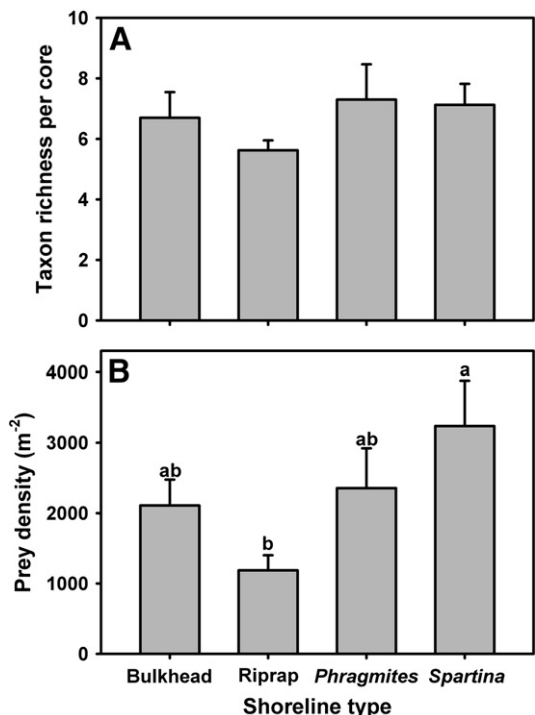
Fig. 2. Taxon richness (A) and density of benthic macrofaunal prey (B) in cores (10 cm diameter) taken at each of the four shoreline types. Bars are mean + SE. Bars with different letters above them differ at an α level of 0.05 (Fisher's least significant difference test).

3.2. Crab feeding and growth and benthic prey availability

The benthic community structure differed among the shoreline types (ANOSIM; Global $R = 0.082$, $p = 0.0503$). In pairwise comparisons, Riprap

and *Spartina* (Global $R = 0.264$, $p = 0.009$) and Riprap and *Phragmites* (Global $R = 0.205$, $p = 0.024$) had significantly different community structures (Table 2). The average dissimilarity between Riprap and *Spartina* was 78.45% and between Riprap and *Phragmites* was 84.04% (SEMPER). *Spartina* had higher densities of Chironomidae spp. larvae, the polychaetes *Opheliidae* sp., *Laonereis culveri*, and *Eteone heteropoda*, *Ampharetidae* sp., the isopod *Leptochelia* sp., the amphipod *Gammarus tigrinus*, and the bivalve *Macoma mitchelli* than did riprap, while Riprap had higher densities of *Nematoda* spp.(SIMPER, Table 2). *Phragmites* had higher densities of *Chironomidae* spp. larvae, the polychaetes *Laonereis culveri* and *Neanthes succinea*, the isopod *Leptochelia* sp., and the amphipods *Gammarus tigrinus*, *G. mucronatus*, and *Leptocheirus plumulosus* than did Riprap, while Riprap had higher densities of the polychaetes *Heteromastus filiformis* and *Onuphidae* sp., and *Nematoda* spp. (SEMPER, Table 2). Both prey density and taxon richness were square-root transformed to meet the assumptions of ANOVA. Shoreline types differed in prey density (ANOVA; $F_{3,32} = 2.983$, $p = 0.046$) but not taxon richness (ANOVA; $F_{3,32} = 0.443$, $p = 0.724$; Fig. 2). Prey density was higher in *Spartina* than in Riprap (Fig. 2).

Twenty-nine out of 39 crabs were recovered for gut content analysis (N: Bulkhead = 8, Riprap = 6, *Spartina* = 7, *Phragmites* = 8). Foregut fullness was square root transformed to meet assumptions of ANOVA. Average foregut fullness was $44 \pm 6.6\%$ (SE) and did not differ among shoreline types (ANOVA; $F_{3,25} = 0.582$, $p = 0.632$). There was no difference in the gut contents (ANOSIM; Global $R = -0.043$, $p = 0.791$). Major food items included polychaetes, plant material (including detritus and benthic micro-algae), chronomid larvae, and amphipods (Fig. 3).

Eighteen out of 39 crabs were recovered for growth analysis after 4 weeks (N: Bulkhead = 6, Riprap = 3, *Spartina* = 4, *Phragmites* = 5), and 10 crabs (out of the recaged 18) after 12 weeks (N: Bulkhead = 3, Riprap = 1, *Spartina* = 3, *Phragmites* = 3). As Riprap had only one crab recovered after 12 weeks we did not include it in the analysis. Growth after 4 weeks was square root transformed to meet assumptions of ANOVA. Growth did not vary among shoreline types after either
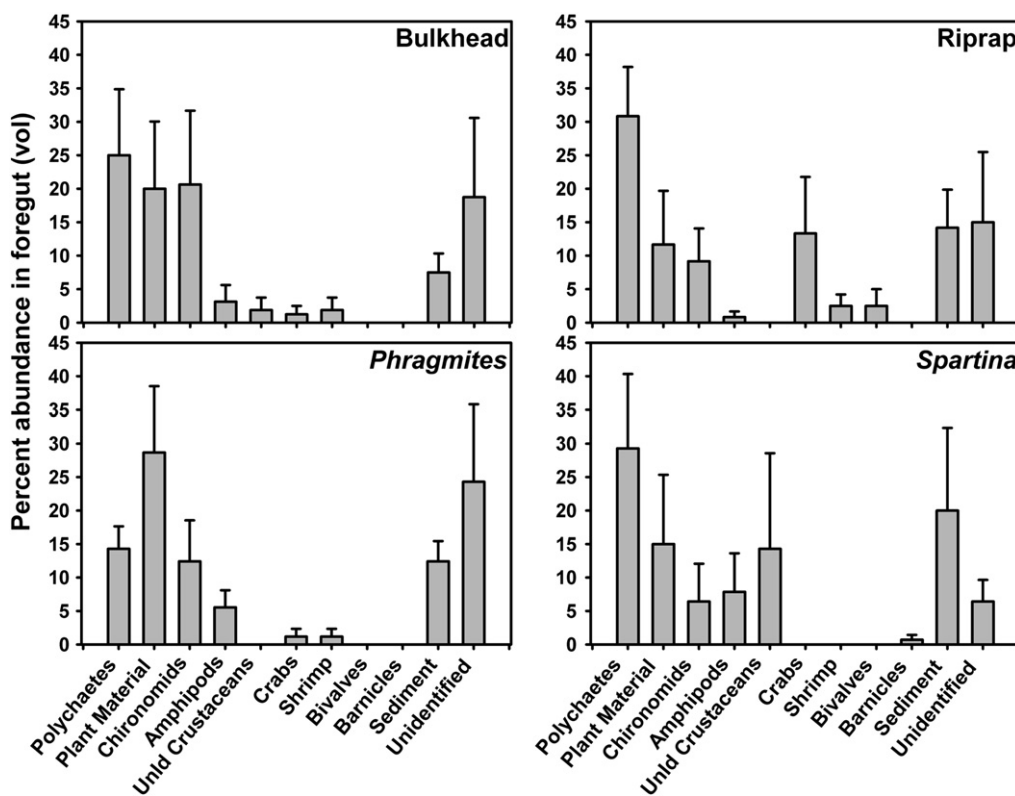

Fig. 3. Percent abundance by volume of prey in the foreguts of juvenile blue crabs from each of the four shoreline types. Bars are means + SE.
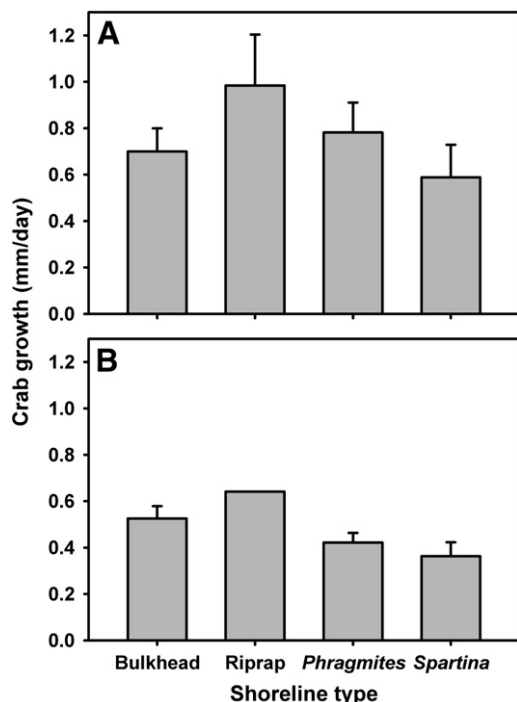
Fig. 4. Juvenile blue crab growth after 4 weeks (A) and 12 weeks (B) along each of four shoreline types. Bars are mean + SE.

4 weeks (ANCOVA; $F_{3,12} = 0.851$, $p = 0.490$) or 12 weeks (ANCOVA; $F_{2,5} = 2.220$, $p = 0.204$; Fig. 4).

3.3. Predation risk and predator abundance

In the best model, the loss rates of tethered crabs differed among the Marshes, Riprap, and Bulkhead; however, there was almost equivalent support for the model with the loss rate differing among all shoreline types and for the model contrasting structured and unstructured habitats (Table 3, Fig. 5A). The loss rate was highest at Bulkhead sites and lowest at Riprap sites. The marshes were intermediate, with *Spartina* having a slightly lower loss rate than *Phragmites*. Potential predators of juvenile blue crabs caught in the seines included white perch, *Morone americana*, Atlantic croaker, *Micropogonias undulates*, striped bass, *Morone saxatilis*, blue crab, and brown bullhead, *Ameiurus nebulosus*. Predator abundance was $\ln(N + 0.1)$ transformed to meet assumptions of ANOVA. Predator abundance did not vary among the marsh types (ANOVA: $F_{3,35} = 1.406$, $p = 0.257$.; Fig. 5B). The lengths of Atlantic croaker were heavily heteroscedastic and transformation did not help so we analyzed differences with a Kruskal–Wallis test. The size of predators did vary among the marsh types for white perch (ANOVA: $F_{3,58} = 3.216$, $p = 0.029$) and Atlantic croaker (Kruskal–Wallis test statistic = 14.120, df = 3, $p = 0.003$) but not for blue crabs (ANOVA: $F_{3,13} = 2.009$, $p = 0.162$; Fig. 6). In general,

Table 3
Ranking of exponential loss rate models for tethered juvenile blue crabs in four different shoreline types using Alkaike's information criterion with small sample size correction (AIC$_c$). The models are as follows: No Difference— all habitats are the same; Structure— Bulkhead differs from structured shorelines (riprap and marshes); M,R,B — Marshes, riprap, and bulkhead all differ from each other; All Different— all four shorelines differ. Bold font indicates the best fit model(s).

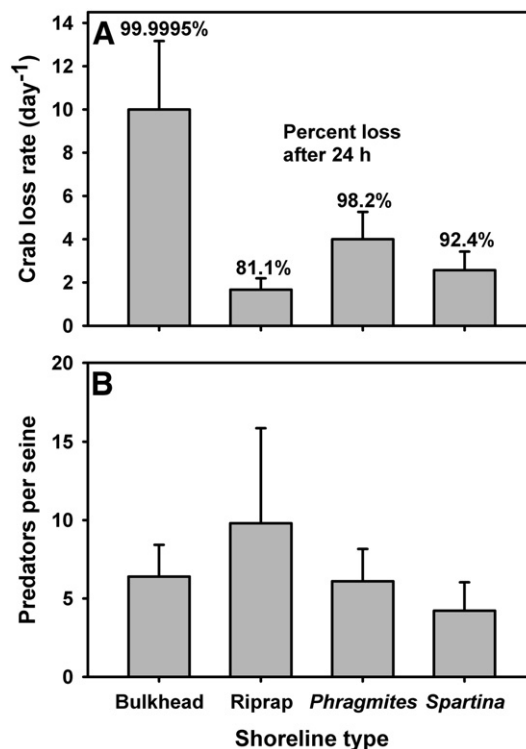| Model	Parameters	AIC$_c$	ΔAIC$_c$	Likelihood	AIC$_c$ weights
No difference	1	−5.58	9.80	0.01	0.00
Structure	**2**	**−14.90**	**0.49**	**0.78**	**0.35**
M,R,B	**3**	**−15.38**	**0.00**	**1.00**	**0.44**
All different	**4**	**−13.82**	**1.57**	**0.46**	**0.20**

Fig. 5. A) Maximum likelihood estimates of loss rates (+SE) of tethered crabs at each of four shoreline types assuming an exponential loss. The number above each bar represents predicted percent of tethered crabs lost after 24 h. B) Average abundance of predators (+SE) at each of the shoreline types. Predators include only species likely to prey upon blue crabs (see text for species included).

predators were smaller at *Spartina* sites and larger at Riprap sites. Also, white perch were larger at *Phragmites* sites than at *Spartina* sites. The nekton community structure sampled by the seine did not differ among the shoreline types (ANOSIM, Global $R = 0.018$, $p = 0.313$) and included species such as the silverside, *Menidia menidia*, Atlantic menhaden, *Brevoortia tyrannus*, *Funduls* spp., and grass shrimp *Palaemonetes sp.*

4. Discussion

As hypothesized anthropogenic alteration of shorelines can have a substantial effect on the value of the habitat as a secondary nursery for juvenile blue crabs, especially in terms of food availability and predation risk. We also found that the invasive marsh grass, *Phragmites australis*, can have a similar value as a nursery habitat to the native, *Spartina* sp.

One of the primary differences among the habitat types was in the abundance and structure of the benthic infauna. This higher abundance of infauna adjacent to natural marsh habitats as compared to anthropogenically altered shorelines also occurs in the York and Elizabeth-Lafayette Rivers (Seitz et al., 2006). This is most likely driven by differences in allochthonous carbon inputs between the marshes and the hardened shorelines (Quan et al., 2007; Roman and Daiber, 1989; Seitz et al., 2006; Wainright et al., 2000), though differences in water flow (which we did not measure) may also have contributed (Seitz et al., 2006). Additionally, bulkheads are often made of CCA-treated wood, which can have a negative effect on benthic organisms (Weis et al., 1998); however, in this system, riprap, not bulkheads, had the lowest density of benthic macrofauna, and its benthic community differed more from the marshes. The community structure in riprap was characterized by higher densities of smaller, more opportunistic species, such as nematodes and the cappitellid polychaete *Heteromastus filiformis*, whereas, the marsh habitats had larger, longer-lived species such as *Neanthes succinea* and *Macoma mitchelli*. This shift in community structure towards smaller
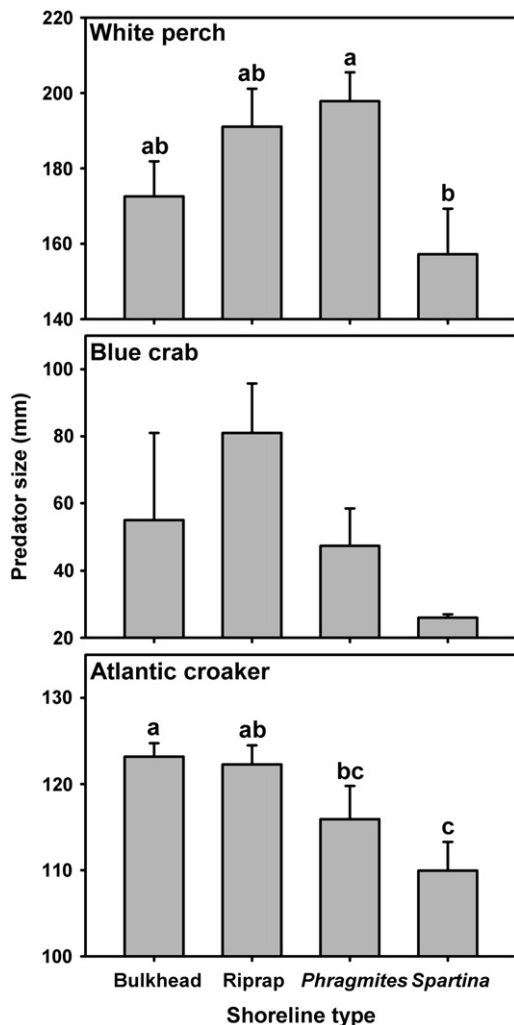
Fig. 6. Sizes of the most abundant juvenile blue crab predators at each of four shoreline types. Sizes are total length for piscine species and carapace width for crustaceans. Bars are mean + SE. Bars with different letters above them differ at an α level of 0.05 (Fisher's least significant difference test for white perch; Kruskal–Wallis multiple comparison for croaker). The scale of the x-axis varies among the plots.

organisms is similar to what occurs in Chesapeake Bay under stressors such as hypoxia (Llansó, 1992; Long and Seitz, 2009).

The lower density and shift in community structure did not have a significant effect on juvenile blue crab feeding. The crabs in this study primarily consumed small benthic invertebrates, especially polychaetes, chronomid larvae, and amphipods, as well as plant material, which is a typical diet for this size class of blue crabs (Dittel et al., 2006; Hines, 2007; Laughlin, 1982; Lipcius et al., 2007). Although no significant difference existed, there was a trend for a higher abundance of plant material in the diet of crabs at *Phragmites* plots, which is not surprising given the abundance of plant material in the sediment adjacent to that habitat. Also, crabs, probably xanthid crabs, accounted for a substantial portion of the diet in riprap habitats only, likely because xanthid crabs of Chesapeake Bay are often associated with hard structured habitats such as oyster reefs (Grabowski et al. 2005; Meyer, 1994).

Despite the variation in prey abundance among the shoreline types, there was no difference in crab growth either after 4 or 12 weeks. This differs from previous studies in which juvenile blue crab growth was correlated with food availability (Seitz et al., 2005; Terwin, 1999). However, this is likely due to the differences between the studies. Our crabs (9.0–14.7 mm cw) were much smaller than those used in the previous

studies (65–80 mm cw; Terwin, 1999; 25–52 mm cw; Seitz et al., 2005) and thus were feeding on a different set of prey items (Dittel et al., 2006; Hines, 2007; Lipcius et al., 2007). Additionally, in both studies, crab growth was positively correlated with the density of the clam *Macoma balthica* (Seitz et al., 2005; Terwin, 1999). Because clams are longer lived members of the infauna and only recruit in the fall and spring, the possibility of short-term local depletion due to predation is much greater than for smaller polychaetes and amphipods, which recruit many times during the summer (Holland et al., 1977, 1987; Virnstein, 1977), and which constituted the primary food source for our size class of crabs. Higher growth rates at 4 weeks than at 12 weeks are probably due to our resampling at different times during the molt cycle of the crabs.

Although the lower prey density at the riprap sites in this study did not seem to inhibit crab growth on a small temporal and spatial scale, it nevertheless indicates that the carrying capacity of these habitats for juvenile blue crabs, in terms of food availability, is likely lower than the Marsh shorelines. The distribution of blue crabs in Chesapeake Bay is strongly influenced by bottom up factors (King et al., 2005, Seitz et al., 2003), supporting this conclusion. However, as the current blue crab population in Chesapeake Bay is recruit limited (Lipcius and Stockhausen, 2002) and therefore below carrying capacity even in the southern portion of the bay where recruitment is highest (Seitz et al., 2008) this is currently of little practical concern.

Predation risk for juvenile blue crabs varied greatly among the shoreline types. The clear difference between the unstructured bulkhead habitats and the structured marsh and riprap habitats was unsurprising given the predation refuge structured habitats offer in aquatic systems (Everett and Ruiz, 1993; Heck et al., 2003; Minello et al., 2003). Among the structured habitats, riprap offered the most protection from predation, and surviving crabs were often found actively using the structure. This may be partially due to the fact that the structure is available to juvenile crabs at all times during the tidal cycle, whereas the marshes were only available at high tide. Additionally, hard, submerged substrate, such as oyster reefs and cobble habitats, generally provides better refuge than marsh habitat (Stunz and Minello, 2001), even when the marsh habitat is available throughout the tidal cycle (Barshaw et al., 1994). In the best model, the *Spartina* and *Phragmites* marshes had the same loss rate, though there was support for *Spartina* having a lower loss rate than *Phragmites*. There is little evidence that juvenile blue crabs use *Spartina* and *Phragmites* marshes differently; the abundance of blue crabs both within (Able and Hagan, 2000; Meyer et al., 2001) and near (Jivoff and Able, 2003) the two marshes is equivalent, as is the use of both marshes by molting crabs (Jivoff and Able, 2003). In our study there was no evidence that the crabs ever moved into the marshes; tethered crabs were always found in the water nearby the marshes regardless of tidal cycle. Indeed in many of the marshes, especially the *Phragmites*, the stem density is so high it is unlikely that the crabs would have been able to use it at all.

The differences in crab loss rates among the habitat types cannot be explained by predator abundance, which did not vary among the shoreline types. This is similar to patterns in the York and Elizabeth-Lafayette Rivers in the southern portion of Chesapeake Bay, where predator densities did not differ among *Spartina*, riprap, and bulkhead shorelines (Seitz et al., 2006). In contrast, the abundance of blue crabs was lower along altered (bulkhead or riprap) shorelines than along marsh shorelines in Mississippi estuaries, though this was not true of the Atlantic croaker (Peterson et al., 2000). In general, the size of piscine predators was lower at *Spartina* marshes compared to the other shorelines, which may partially explain the slight difference in predation rate between the *Spartina* and *Phragmites* shorelines. This is the opposite of trends in Mississippi, where the size of fish tended to be lower at altered habitats (Peterson et al., 2000). The reason for the difference between the studies is not clear and could be related to geographic, physical, sampling, or seasonal differences.

5. Conclusions

Our findings suggest that *Spartina* and *Phragmites* are approximately equivalent in terms of the nursery habitat they provide for juvenile blue crabs. Although the invasion of *Phragmites* does not seem to affect blue crab other aspects of the ecosystem are affected (Able et al., 2003; Osgood et al., 2003; Robertson and Weis, 2005) so this study should not be taken to indicate that the invasion is of no ecological concern. In contrast, we show that replacement of marsh shorelines with riprap or bulkheads substantially reduces the habitat value of shallow water areas through a reduction in prey density, with a concurrent decrease in the habitat carrying capacity, and, in the case of bulkheads, the removal of a refuge from predation. This adds to the growing evidence that anthropogenic shoreline hardening can substantially reduce the ecosystem services provided by the habitat (Peterson et al., 2000; Seitz et al., 2006). Although more research into the effects and mechanisms of shoreline hardening is needed, land owners, policy makers and managers should consider alternative methods of stabilizing shorelines.

Acknowledgments

References

Able, K.W., Hagan, S.M., 2000. Effects of common reed (*Phragmites australis*) invasion on marsh surface macrofauna: response of fishes and decapod crustaceans. Estuaries 23, 633–646.

Able, K.W., Hagen, S.M., Brown, S.A., 2003. Mechanisms of marsh habitat alteration due to *Phragmites australis*: response of young-of-the-year mummichog (*Fundulus heteroclitus*) to treatment for *Phragmites* removal. Estuaries 26, 484–494.

Baird, D., Ulanowicz, R.E., 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. Ecol. Monogr. 59, 329–361.

Barshaw, D.E., Able, K.W., Heck, K.L., 1994. Salt marsh peat reefs as protection for postlarval lobsters *Homarus americanus* from fish and crab predators: comparisons with other substrates. Mar. Ecol. Prog. Ser. 106, 203–206.

Berman, M.R., Berquist, H., Killeen, S., Nunez, K., Rudnicky, T., Schatt, D.E., Weiss, D., Reay, K., 2006. Anne Arundel County, Maryland — Shoreline Situation Report, Comprehensive Coastal Inventory Program. Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, Virginia. 23062.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach, Second edition. Springer Science, New York, New York, USA.

Clark, K.L., Ruiz, G.M., Hines, A.H., 2003. Diel variation in predator abundance, predation risk and prey distribution in shallow water estuarine habitats. J. Exp. Mar. Biol. Ecol. 287, 37–55.

Clarke, K.R., Gorley, R.N., 2001. Primer v. 5, User Manual. Plymouth Marine Laboratory, Plymouth, UK.

Clarke, K.R., Warwick, R.M., 2001. Change in Marine Communities: an Approach to Statistical Analysis and Interpretation, 2nd edition. Plymouth, UK, Plymouth Marine Laboratory.

Dittel, A.I., Hines, A.H., Ruiz, G.M., Ruffin, K.K., 1995. Effects of shallow water refuge on behavior and density-dependant mortality of juvenile blue crabs in Chesapeake Bay. Bull. Mar. Sci. 57, 902–916.

Dittel, A.I., Epifanio, C.E., Fogel, M.L., 2006. Trophic relationships of juvenile blue crabs (*Callinectes sapidus*) in estuarine habitats. Hydrobiologia 568, 379–390.

Everett, R.A., Ruiz, G.M., 1993. Coarse woody debris as a refuge from predation in aquatic communities: an experimental test. Oecologia 93, 475–486.

Fell, P.E., Weissbach, S.P., Jones, D.A., Fallon, M.A., Zeppieri, J.A., Faison, E.K., Lennon, K.A., Newberry, K.J., Reddington, L.K., 1998. Does invasion of oligohaline tidal marshes by reed grass, *Phragmites australis* (Cav.) Trin. Ex Steud., affect the availability of prey resources for the mummichog, *Fundulus heteroclitus* L.? J. Exp. Mar. Biol. Ecol. 222, 59–77.

Grabowski, J.H., Hughes, A.R., Kimbro, D.L., Dolan, M.A., 2005. How habitat setting influences restored oyster reef communities. Ecology 86, 1926–1935.

Hanson, S.R., Osgood, D.T., Yozzo, D.J., 2002. Nekton use of a *Phragmites australis* marsh on the Hudson River, New York, USA. Wetlands 22, 326–337.

Heck, K.L., K.L., Hays, G., Orth, R.J., 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. Mar. Ecol. Prog. Ser. 253, 123–136.

Hendon, J.R., Peterson, M.S., Comyns, B.H., 2000. Spatio-temporal distribution of larval *Gobiosoma bosc* in waters adjacent to natural and altered marsh-edge habitats of Mississippi coastal waters. Bull. Mar. Sci. 66, 143–156.

Hines, A.H., 2007. Ecology of juvenile and adult blue crabs. In: Kennedy, V.S., Cronin, L.E. (Eds.), The Blue Crab, *Callinectes sapidus*. Maryland Sea Grant, College Park, MD, pp. 565–654.

Hines, A.H., Lipcius, R.N., Haddon, A.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.

Hines, A.H., Ruiz, G.M., 1995. Temporal variation in juvenile blue crab mortality: nearshore shallows and cannibalism in Chesapeake Bay. Bull. Mar. Sci. 57, 884–901.

Holland, A.F., Mountford, N.K., Mihursky, J., 1977. Temporal variation in upper bay and mesohaline communities: I. The 9-m mud habitat. Ches. Sci. 18, 370–378.

Holland, A.F., Shaughnessy, A.T., Hiegel, M.H., 1987. Long-term variation in mesohaline Chesapeake Bay macrobenthos: spatial and temporal patterns. Estuaries 10, 227–245.

Jivoff, P.R., Able, K.W., 2003. Blue crab, *Callinectes sapidus*, response to the invasive common reed, *Phragmites australis*: abundance, size, sex ratio, and molting frequency. Estuaries 26, 587–595.

Johnson, E.G., Young, A.C., Hines, A.H., Kramer, M.A., Bademan, M., Goodison, M.R., Aguilar, R., 2011. Field comparison of survival and growth of hatchery-reared versus wild blue crabs, *Callinectes sapidus* Rathbun. J. Exp. Mar. Biol. Ecol. 402, 35–42.

Kemp, W.M., Boynton, W.R., Adolf, J.E., Boesch, D.F., Boicourt, W.C., Brush, G., Cornwell, J.C., Fisher, T.R., Glibert, P.M., Hagy, J.D., Harding, L.W., Houde, E.D., Kimmel, D.G., Miller, W.D., Newell, R.I.E., Roman, M.R., Smith, E.M., Stevenson, J.C., 2005. Eutrophication of Chesapeake Bay: historical trends and ecological interactions. Mar. Ecol. Prog. Ser. 303, 1–29.

King, R.S., Hines, A.H., Craige, F.D., Grap, S., 2005. Regional, watershed and local correlates of blue crab and bivalve abundances in subsuaries of Chesapeake Bay, USA. J. Exp. Mar. Biol. Ecol. 319, 101–116.

Laughlin, R.A., 1982. Feeding habits of the blue crab, *Callinectes sapidus* Rathbun, in the Apalochicola estuary, Florida. Bull. Mar. Sci. 32, 807–822.

Lipcius, R.M., Stockhausen, W.T., 2002. Concurrent decline of the spawning stock, recruitment, larval abundance, and size of the blue crab *Callinectes sapidus* in Chesapeake Bay. Mar. Ecol. Prog. Ser. 226, 45–61.

Lipcius, R.N., Seitz, R.D., Seebo, M.S., Colon-Carrion, D., 2005. Density, abundance and survival of the blue crab in seagrass and unstructured salt marsh nurseries of Chesapeake Bay. J. Exp. Mar. Biol. Ecol. 319, 69–80.

Lipcius, R.N., Eggleston, D.B., Heck, K.L., Seitz, R.D., Van Montfrans, J., 2007. Ecology of postlarvae and young juvenile blue crabs. In: Kennedy, V.S., Cronin, L.E. (Eds.), The Blue Crab, *Callinectes sapidus*. Maryland Sea Grant, College Park, MD, pp. 535–564.

Llansó, R.J., 1992. Effects of hypoxia on estuarine benthos: the lower Rappahannok River (Chesapeake Bay), a case study. Estuarine Coastal Shelf Sci. 359, 491–515.

Long, W.C., Burke, R.P., 2007. Habitat size, flora, and fauna: interactions in a tidal saltwater marsh. J. Exp. Mar. Biol. Ecol. 353, 80–88.

Long, W.C., Seitz, R.D., 2009. Hypoxia in Chesapeake Bay tributaries: worsening effects on macrobenthic community structure in the York River. Estuaries Coast 32, 287–297.

Meyer, D.L., 1994. Habitat partitioning between the xanthid crabs *Panopeus herbstii* and *Eurypanopeus depressus* on intertidal oyster reefs (*Crassostrea virginica*) in Southeastern North Carolina. Estuaries 17, 674–679.

Meyer, D.L., Johnson, J.M., Gill, J.W., 2001. Comparison of nekton use of *Phragmites australis* and *Spartina alterniflora* marshes in the Chesapeake Bay, USA. Mar. Ecol. Prog. Ser. 209, 71–84.

Minello, T.J., Able, K.W., Weinstein, M.P., Hays, C.G., 2003. Salt marshes as nurseries for nekton: testing hypotheses on density, growth and survival through meta-analysis. Mar. Ecol. Prog. Ser. 246, 39–59.

Osgood, D.T., Yozzo, D.J., Chambers, R.M., Jacobson, D., Hoffman, T., Wnek, J., 2003. Tidal hydrology and habitat utilization by resident nekton in *Phragmites* and non-*Phragmites* marshes. Estuaries 26, 522–533.

Peterson, C.H., Lipcius, R.N., 2003. Conceptual progress towards predicting quantitative ecosystem benefits of ecological restorations. Mar. Ecol. Prog. Ser. 264, 297–307.

Peterson, M.S., Comyns, B.H., Hendon, J.R., Bond, P.J., Duff, G.A., 2000. Habitat use by early life-history stages of fishes and crustaceans along a changing estuarine landscape: differences between natural and altered shoreline sites. Wetlands Ecol. Manage. 8, 209–219.

Pister, B., 2009. Urban marine ecology in southern California: the ability of riprap structures to serve as rocky intertidal habitat. Mar. Biol. 156, 861–873.

Posey, M.H., Alphin, T.D., Meyer, D.L., Johnson, J.M., 2003. Benthic communities of common reed *Phragmites australis* and marsh cordgrass *Spartina alterniflora* marshes in Chesapeake Bay. Mar. Ecol. Prog. Ser. 261, 51–61.

Quan, W., Fu, C., Jin, B., Luo, Y., Li, B., Chen, J., Wu, J., 2007. Tidal marshes as energy sources for commercially important nektonic organisms: stable isotope analysis. Mar. Ecol. Prog. Ser. 252, 89–99.

Robertson, T.L., Weis, J.S., 2005. A comparison of epifaunal communities associated with the stems of salt marsh grasses *Phragmites australis* and *Spartina alterniflora*. Wetlands 25, 1–7.

Robertson, T.L., Weis, J.S., 2007. Interactions between the grass shrimp *Palaemonetes pugio* and the salt marsh grasses *Phragmites australis* and *Spartina alterniflora*. Biol. Invasions 9, 25–30.

Roman, C.T., Daiber, F.C., 1989. Organic carbon flux through a Delaware Bay salt marsh: tidal exchange, particle size distribution, and storms. Mar. Ecol. Prog. Ser. 54, 149–156.

Ruiz, G.M., Hines, A.H., Posey, M.H., 1993. Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. Mar. Ecol. Prog. Ser. 99, 1–16.

Ryer, C.H., van Montfrans, J., Moody, K.E., 1997. Cannibalism, refugia and the molting blue crab. Mar. Ecol. Prog. Ser. 147, 77–85.

Seitz, R.D., Lipcius, R.N., Stockhausen, W.T., Delano, K.A., Seebo, M.S., Gerdes, P.D., 2003. Potential bottom-up control of blue crab distribution at various spatial scales. Bull. Mar. Sci. 72, 471–490.

Seitz, R.D., Lipcius, R.N., Seebo, M.S., 2005. Food availability and growth of the blue crab in seagrass and unvegetated nurseries of Chesapeake Bay. J. Exp. Mar. Biol. Ecol. 319, 57–68.

Seitz, R.D., Lipcius, R.N., Olmstead, N.H., Seebo, M.S., Lambert, D.M., 2006. Influence of shallow-water habitats and shoreline development on abundance, biomass, and diversity of benthic prey and predators in Chesapeake Bay. Mar. Ecol. Prog. Ser. 326, 11–27.

Seitz, R.D., Lipcius, R.N., Knick, K.E., Seebo, M.S., Long, W.C., Brylawski, B.J., Smith, A., 2008. Stock enhancement and ecosystem carrying capacity in blue crab nursery habitats of Chesapeake Bay. Rev. Fish. Sci. 16, 1–9.

Stunz, G.W., Minello, T.J., 2001. Habitat-related predation on juvenile wild-caught and hatchery-reared red drum *Sciaenops ocellatus* (Linnaeus). J. Exp. Mar. Biol. Ecol. 260, 13–25.

Terwin, J.R., 1999. Blue crab, Callinectes sapidus, foraging in Chesapeake Bay: the importance of intra-specific interactions and prey distributions. Ph.D. Dissertation. University of Maryland, College Park, MD.

Virnstein, R.W., 1977. The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. Ecology 58, 1199–1217.

Wainright, S.C., Weinstein, M.P., Able, K.W., Currin, C.A., 2000. Relative importance of benthic microalgae, phytoplankton and the detritus of smooth cordgrass *Spartina alterniflora* and the common reed *Phragmites australis* to brackish-marsh food webs. Mar. Ecol. Prog. Ser. 200, 77–91.

Weis, J.S., Weis, P., 2003. Is the invasion of the common reed, *Phragmites australis*, into tidal marshes of the eastern US an ecological disaster? Mar. Pollut. Bull. 46, 816–820.

Weis, J.S., Weis, P., Proctor, T., 1998. The extent of benthic impacts of CCA-treated wood structures in Atlantic coast estuaries. Arch. Environ. Contam. Toxicol. 34, 313–322.

Zmora, O., Findiesen, A., Stubblefield, J., Frenkel, V., Zohar, Y., 2005. Large-scale juvenile production of the blue crab, *Callinectes sapidus*. Aquaculture 244, 129–139.