Exotic macroalga *Gracilaria vermiculophylla* provides superior nursery habitat for native blue crab in Chesapeake Bay

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ABSTRACT: Exotic species often reduce the abundance or diversity of species in marine ecosystems, but some exotics may benefit native species, such as when habitat is enhanced. In Chesapeake Bay, the exotic macroalga *Gracilaria vermiculophylla* (Rhodophyta) has flourished and dispersed widely, yet the consequences for native species diversity and abundance are not well known. We experimentally examined the capacity of the structurally complex *G. vermiculophylla* to provide nursery habitat for the blue crab *Callinectes sapidus* in Chesapeake Bay, where native eelgrass nursery habitat has dwindled. We also examined ontogenetic shifts in survival across alternative nursery habitats. In field surveys, juvenile density was similar in macroalgae and eelgrass, but lower in unvegetated mud habitat. In field experiments, juvenile survival was positively related to crab size in mud but negatively in eelgrass, confirming the paradigm of a predation-induced ontogenetic shift from seagrass to unvegetated habitat. In contrast, irrespective of crab size, survival was higher in macroalgae than in either native habitat. Thus, exotic habitat-forming macroalgae can compensate for severe declines in seagrass nurseries, and facilitate the emergence of a novel ecosystem.

KEY WORDS: Exotic species · Ontogenetic habitat shift · Predation · Prey size refuge · Novel ecosystem · Emerging ecosystem · Macroalgae · Seagrass

INTRODUCTION

Exotic species and novel ecosystems

Exotic species have predominantly severe, negative effects on the diversity and abundance of native species (Mooney & Cleland 2001, Goodenough 2010). Recently, however, potentially beneficial effects of exotic species have been identified (e.g. Rodriguez 2006, Martin & Valentine 2011, Schlaepfer et al. 2011). For example, although exotic species may outcompete native species, in degraded ecosystems they may fill ecological roles left vacant by declining native species (Rodriguez 2006). Various species of macroalgae are often viewed as perilous invaders, because they thrive under eutrophic conditions and may outcompete or exclude seagrasses, yet they can also be integral to estuarine nutrient cycling and ecosystem function (Penhale & Thayer 1980, Sand-Jensen & Borum 1991, Duarte 1995, Schlaepfer et al. 2011).

Gracilaria vermiculophylla is a macroalga native to eastern Asia (Ohmi 1956, Bellorin et al. 2004) that has colonized the coasts of North America and Europe (Bellorin et al. 2004, Thomsen et al. 2006a,b, 2007, Freshwater et al. 2006). Its spores attach to natural or

anthropogenic substrates in estuaries and bays, and it may form extensive beds in the intertidal and shallow sublittoral zones (Bellorin et al. 2004, Freshwater et al. 2006). Although high macroalgal biomass >100 g m^{-2} can lead to anoxia beneath dense mats and subsequent reductions in diversity and faunal biomass (Thomsen et al. 2006b), intermediate levels of *G. vermiculophylla* biomass may benefit shelter-dependent species by adding complexity to unvegetated habitats such as mud and sand flats (Thomsen et al. 2010, Byers et al. 2012).

Throughout the world, there has been increasing recognition of novel (=emerging) ecosystems, which are characterized by altered species assemblages, often due to anthropogenic impacts such as species introductions (Hobbs et al. 2006, 2009). Moreover, widespread human influence on natural systems can cause such severe degradation that restoration of historical ecosystem function is impractical (Jackson & Hobbs 2009, Schlaepfer et al. 2011). However, where vacant niches of native species are filled by exotic species, some ecosystems can re-emerge and function effectively, perhaps benefiting imperiled native species (Hobbs et al. 2009, Schlaepfer et al. 2011).

Here we experimentally examined whether the exotic habitat-forming macroalga *Gracilaria vermiculophylla* provides effective nursery habitat for the imperiled native blue crab *Callinectes sapidus* (Lipcius & Stockhausen 2002) in a marine ecosystem compromised by severe declines of seagrass (Orth & Moore 1984). Consequently, *G. vermiculophylla* may serve as a beneficial species in an emerging novel ecosystem. Furthermore, because it has been proposed that blue crab juveniles exhibit an ontogenetic habitat shift between alternative nursery habitats (Lipcius et al. 2007), we also examined the effect of juvenile crab size upon survival in the exotic macroalga and in 2 native nursery habitats.

in determining habitat preference (Werner & Gilliam 1984).

Such analyses have been conducted for various mobile aquatic species through the use of field survival and growth studies. In bluegill sunfish *Lepomis macrochirus* populations, discrete size-dependent dispersal events between littoral and pelagic habitats depended upon both predation risk and growth rate; predation pressure was, however, the primary determinant of habitat choice (Werner & Hall 1988). Similarly, habitat preference of mummichog *Fundulus heteroclitus* was positively associated with the availability of refuges from predation, regardless of growth potential within a habitat (Halpin 2000). The smallest size class of juvenile Nassau grouper *Epinephelus striatus* preferred habitats that minimized predation risk, and the largest juveniles only underwent growth-dependent dispersal once predation was minimized (Dahlgren & Eggleston 2000). In damselflies (*Enallagma* and *Ischnura* spp.), growth rates of the 2 genera varied in different habitats, but these alterations were primarily driven by dragonfly and fish predation (McPeek et al. 2001). These studies collectively demonstrated that relative habitat suitability and size-specific habitat shifts could be identified through experimental analysis of mortality and growth in the field, and that predation pressure played a predominant role in determining tradeoffs associated with habitat choice.

Given that *Gracilaria vermiculophylla* may serve as nursery habitat, where tradeoffs in predation risk and growth rate can drive ontogenetic habitat shifts (Craig & Crowder 2000), we also experimentally compared survival as a function of size in 2 native nursery habitats (eelgrass *Zostera marina* and unvegetated mud flats) and in *G. vermiculophylla*, to assess whether blue crabs encounter similar ontogenetic tradeoffs in native and exotic juvenile habitats.

Ontogenetic tradeoffs in nursery habitats

As individuals grow, fitness may be maximized by dispersing between habitats that offer different size-dependent costs and benefits (i.e. tradeoffs in growth rate and predation risk; Werner & Gilliam 1984). Thus, experimentally analyzing mortality (μ) risk and growth rate (g) allows identification of shifts in habitat choice, the factor(s) determining those choices, and the suitability of each habitat as a nursery (Beck et al. 2001). Such species may display patterns that minimize mortality, maximize growth or minimize μ/g, depending on which factors are most important

Blue crab use of nursery habitat

Small and large juveniles of *Callinectes sapidus* differentially inhabit vegetated primary nurseries and unvegetated secondary nurseries, respectively (Pardieck et al. 1999, Lipcius et al. 2007). This has been proposed to be due to a size-specific habitat shift during ontogeny, given that crabs <30 mm carapace width (CW) are abundant within seagrass beds, whereas larger juveniles inhabit sublittoral mudflats, where they may escape density-dependent growth reduction, cannibalism and predation (Pile et al. 1996, Hovel & Lipcius 2001, Lipcius et al. 2007).

Small, pre-dispersal juveniles benefit from the structural refuge provided by seagrass. However, Chesapeake Bay has experienced severe declines in *Zostera marina*, including mass defoliations (Orth & Moore 1984, Orth et al. 2010), which may partly explain the inability of the blue crab population to recover from an 80% decline in biomass since the early 1990s (Lipcius & Stockhausen 2002). Thus, if *Gracilaria vermiculophylla* is effective as alternative nursery habitat, as Thomsen and colleagues have posited for invertebrates including the blue crab (Thomsen et al. 2009, Thomsen 2010), then it may compensate for the detrimental effects of eelgrass loss on blue crab population recovery.

Experimental rationale and objectives

Due to the dominant influence of predation pressure on habitat choice and based on earlier findings that blue crab food availability is similar between primary and secondary nursery habitats (Seitz et al. 2005), we exclusively assessed survival of juvenile blue crabs in *Gracilaria vermiculophylla*, *Zostera marina* and mud. We hypothesized that as eelgrass becomes scarce in Chesapeake Bay, juvenile crabs will readily use *G. vermiculophylla* as an alternative nursery habitat. We further hypothesized that the growth of structurally complex *G. vermiculophylla* on characteristically unvegetated mud habitat would alter the dynamics of blue crab ontogenetic habitat use. Essentially, as macroalgae (potential primary nursery) grows on extensive mud flats (secondary nursery), the increase in vegetated habitat availability will likely broaden the size range of juveniles in macroalgal habitats by supplying refuge for both primary and secondary nursery-phase individuals, thereby diminishing any size-specific habitat shift during development (Lipcius et al. 2007).

The variables that we examined included (1) crab size, which affects vulnerability to predation (Hines & Ruiz 1995), (2) habitat type, which alters juvenile survival and habitat choice (Lipcius et al. 2007), and (3) trial duration, which may affect crab survival due to variation in the predator assemblage by time of day and tidal fluctuations. Modeling these 3 factors individually and in combination, multiple alternative patterns of survival could be expected. Larger crabs were anticipated to live longer than small crabs since larger crabs have a more limited predator assemblage and are less susceptible to cannibalism (H_1: crab size) (Hines & Ruiz 1995, Lipcius et al. 2007). Due to the refuge provided by heterogeneous struc-

ture, we expected juvenile survival to be higher in both vegetated habitats when no effect of size was considered (H_2: habitat). Taking into account habitat and size effects separately, we expected large juveniles in vegetated habitats to survive best (H_3: habitat, size). However, by adding the interaction between size and habitat, based on previous findings that small juveniles inhabit seagrass whereas larger juveniles predominate in mud flats, we predicted a complementary pattern in which small juveniles survive best in structured habitats whereas larger individuals survive best in unvegetated habitat (H_4: size × habitat) (Pile et al. 1996, Lipcius et al. 2007). Within each habitat, juvenile survival was expected to decline with time until only crabs with a size-based refuge from predation survived almost indefinitely (H_5: duration, size, habitat) (Heck & Spitzer 2001). Using experimental studies and field sampling, we analyzed the survival and distribution of early juvenile (5 to 45 mm CW) blue crabs in *Zostera marina*, *Gracilaria vermiculophylla* and mud to detect size-dependent habitat shifts and determine the relative suitability of each habitat.

MATERIALS AND METHODS

Study sites

Studies were conducted in vegetated and unvegetated habitats in the York River, a tributary of lower Chesapeake Bay, during July 2007. Sandy Point (37° 15′ 52.00″ N, 76° 23′ 49.46″ W) and the mouth of Perrin's Creek (37° 15′ 43.78″ N, 76° 25′ 22.14″ W) each contained one *Zostera marina* site. Habitats of *Gracilaria vermiculophylla* and mud were both investigated near the mouth of Perrin's Creek and in a cove adjacent to Carmine's Island (37° 17′ 04.55″ N, 76° 31′ 59.95″ W). Patterns of survival were consistent across habitat type, regardless of site; thus we considered samples spatially independent. All sites were consistently submerged but <2 m deep with a tidal range of 0.7 m. The studied reach of the York River is ~11 km from the mouth, where it joins Chesapeake Bay. The reach is consistently polyhaline; in summer 2007, salinity ranged from 18 to 23 psu, dissolved oxygen ranged from 3 to 10 mg l⁻¹, turbidity ranged from 10 to 30 NTU, and temperature increased from 20 to 30°C from June until September (Virginia Estuarine & Coastal Observing System data from summer 2007, Gloucester Point Continuous Monitoring Station). Both seagrass beds consisted primarily of *Z. marina* at 70–100% cover but with small propor-

tions of widgeon grass *Ruppia maritima* scattered throughout (Orth et al. 2008). Although macroalgal abundance was not assessed at the time of this study, beds of *G. vermiculophylla* were consistently present at our sites (C.A.J. pers. obs.).

Crab density and size distribution

To determine natural juvenile density and distribution in the 3 habitats, crabs were sampled using trawls and standard ring suction methods, and corrected for 21 and 78% efficiencies, respectively (Orth & van Montfrans 1987). Trawling was conducted with a 4.9 m otter trawl of 2.5 cm mesh lined with 0.6 cm mesh. Rings covered 1.68 m^2 and were suctioned for 6 min each. We conducted 14, 25 and 16 sampling operations in *Gracilaria vermiculophylla*, mud and eelgrass, respectively. Captured crabs were counted and measured, and the volume of *G. vermiculophylla* in the samples was measured by volumetric displacement. Only juvenile crabs (≤100 mm CW) were included in this analysis.

Survival

Juvenile crabs were collected by trawling and seining along coves and creeks adjacent to our study sites in the York River. Crabs were held in flow-through seawater tanks for no longer than 24 h before experimental deployment. Each crab was measured to the nearest 0.1 mm spine-to-spine CW with calipers and then tethered by adhering 30 cm of monofilament fishing line to the carapace with cyanoacrylate superglue. Tethering estimates the relative differences in survival between experimental treatments, and does not produce treatment-specific bias (Peterson & Black 1994) when comparing vegetated and unvegetated habitats (Pile et al. 1996, Hovel & Lipcius 2001, Lipcius et al. 2005).

Small crabs (5 to 25 mm CW) were tethered to 3.6 kg test line with a single drop of glue. For larger crabs (26 to 45 mm CW), a noose of 9.1 kg test line was glued around their carapace spines. Visual observations during tethering and deployment verified that tethered crabs had sufficient freedom of movement (e.g. the ability to swim, walk and burrow).

To ensure that molting and escape from tethers did not cause overestimates of predation, we conducted tether retention studies on 24 crabs in the laboratory. Tethered crabs were secured in flow-through seawater tanks and checked for tether retention over 36 h.

Retention rates were high across all sizes (small = 9/10, large = 14/14). Since tethered crabs were never deployed in the field for longer than 25 h during survival studies, estimates of survival were considered accurate.

In the field, the end of each crab tether was connected to a staple that was secured with 9.1 kg test line to a PVC marker pole 1 m away. Crabs were sufficiently distant from the marker poles to prevent biases due to the pole structure, either as a crab refuge or predator attractant. Tethered crabs were deployed in *Gracilaria vermiculophylla* (n = 51), *Zostera marina* (n = 35) and mud (n = 54). In *G. vermiculophylla* treatments, a large handful (<1 l) of *G. vermiculophylla* was secured beneath the staple to ensure that the vegetation was consistently available to the tethered crab. To maintain independence, tethers were located >3 m apart, which placed crabs at or below natural densities, potentially preventing unnaturally high predation rates due to induced search by motile predators.

Tethered crabs were checked for survival within 12 to 25 h of deployment. This time interval ensured that each crab was tethered through a full tide cycle and either dawn or dusk, which should smooth differences in predation pressure based on water depth and time of day. The actual time interval was used as a covariate in statistical analyses, but did not affect survival significantly (see 'Results'). Predation was determined by the presence of carapace pieces on the line, a chewed line or a cut line (Lipcius et al. 2005).

Statistical analysis

Based on each of our 5 hypotheses, we developed models $g_1–g_5$ following an information-theoretic approach (Burnham & Anderson 2002, Anderson 2007). Within these models, crab size (mm) and trial duration (h) were continuous variables, whereas habitat type was a categorical factor with 3 levels (mud, *Zostera marina* and *Gracilaria vermiculophylla*).

Model-specific crab survival, recorded as 1 (alive) or 0 (dead), was analyzed for probability of survival under the various experimental treatments and conditions (i.e. habitat, crab size, time since deployment) using logistic regression. The resulting log-likelihood values from each model were used to calculate Akaike's information criterion (AIC) values (Burnham & Anderson 2002, Anderson 2007), specifically AIC$_c$, a second-order bias correction estimator. The

Δ_i values were used to rank the different models (g_i) against the model with the lowest AIC$_c$. Model probabilities (w_i) for each model estimated the probability that a particular model g_i was the best model; these were used to rank models. Any model with w_i less than 0.05 was eliminated. To further distinguish between competing models, individual parameter estimates were examined.

Subsequently, parameter estimates of models warranting further consideration were used to calculate binomial survival probabilities as:

$$\theta = \frac{e^{(\alpha+\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_i x_i)}}{1 + e^{(\alpha+\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_i x_i)}} \quad (1)$$

where θ is the probability of survival, α is a parameter (constant) for the baseline condition and β_i comprises parameters representing increases or decreases in survival due to the effects of corresponding independent variables x_i. Crab size (x_1) and trial duration (x_4) were represented by single variables since they are continuous. Each habitat type within the categorical habitat factor was represented by a dummy variable (x_2, x_3). Mud was designated the constant (α) due to its relative lack of structure. For mud, $x_2 = x_3 = 0$; for *Zostera marina*, $x_2 = 1$ and $x_3 = 0$; and for *Gracilaria vermiculophylla*, $x_2 = 0$ and $x_3 = 1$.

Natural density and size distribution were also compared across the different habitats from the field collections, and the relationship between crab density and *Gracilaria vermiculophylla* volume was analyzed using non-linear least-squares regression.

RESULTS

Natural density and size distribution

Blue crab density (Table 1) was high and approximately equal in *Zostera marina* (5.7 crabs m^{-2}) and *Gracilaria vermiculophylla* (5.6 crabs m^{-2}), and nearly 30-fold higher than that in unvegetated mud habitat (0.2 crabs m^{-2}). Mean densities in seagrass and *G. vermiculophylla* did not differ significantly from each other, but both were significantly higher than density in mud (ANOVA, p < 0.05; Student-Newman-Keuls post hoc tests, p = 0.05).

Both *Zostera marina* and *Gracilaria vermiculophylla* harbored mostly young juveniles <30 mm CW (Fig. 1), the size at which juveniles disperse to unvegetated mud and sand habitats (Lipcius et al. 2007). There was a positive correlation between crab density and *G. vermiculophylla* volume (r^2 = 0.44, p < 0.1), but the sample size was relatively low (n = 11), such that the relationship requires further verification in the field. However, the positive relationship has been repeated elsewhere (Thomsen 2010, Thomsen et al. 2010), suggesting that there is a significant positive relationship between blue crab density and *G. vermiculophylla* volume.

Table 1. *Callinectes sapidus*. Natural densities of juvenile blue crab by habitat in samples taken in July 2007 at York River, Chesapeake Bay. Mean crab densities in eelgrass (*Zostera marina*) and *Gracilaria vermiculophylla* did not differ significantly from each other, but both were significantly higher than density in mud (ANOVA, p < 0.05; Student-Newman-Keuls post hoc tests, p = 0.05)

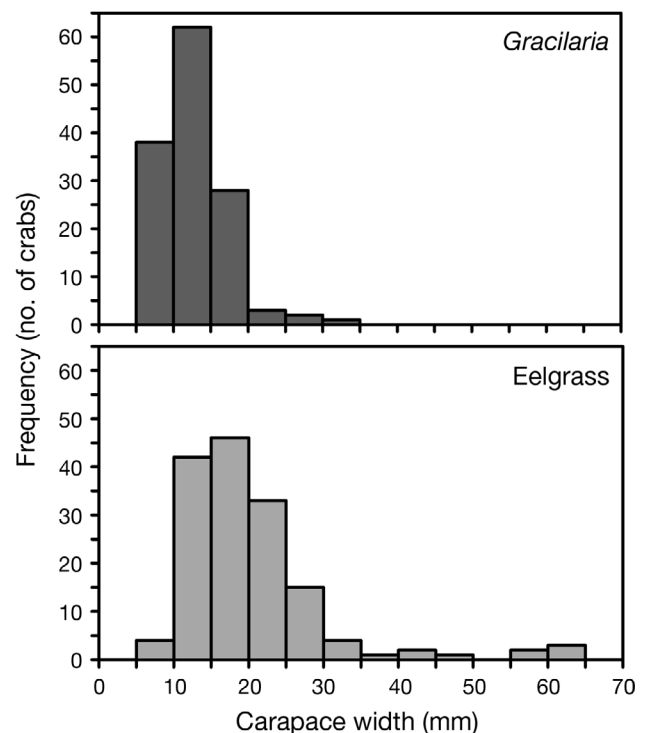| Habitat	n	Mean density ± SEM (ind. per m^2)	95% CI
Eelgrass	16	5.74 ± 0.97	3.66, 7.79
Gracilaria	14	5.61 ± 1.25	2.90, 8.31
Mud	25	0.17 ± 0.07	0.02, 0.32

Fig. 1. *Callinectes sapidus*. Size (carapace width) distribution of juvenile blue crab by habitat (*Gracilaria vermiculophylla* and eelgrass) from data gathered in July 2007 at York River, Chesapeake Bay. Mud was not included because the total number of blue crabs caught was too low to portray a histogram

Survival

Model g_1 (size only) was eliminated from further consideration because its probability was less than 0.05 (Table 2) and its effect size was negligible (Table 3). For the remaining models (g_2–g_5), Δ_i values were <5 and w_i probabilities were >0.05, such that they could not be excluded from consideration (Anderson 2007). Thus, we examined the significance of the model parameter estimates. Model g_3 was not considered further because its addition of a single variable (size) to g_2 increased the AIC_c value by approximately 2, which is indicative of an insignificant 'pretend' variable (Anderson 2007), and it did not have a major effect on the response variable (Table 3). Similarly, model g_4 was eliminated because it also increased the AIC_c value by approximately 2 after the addition of one variable (trial duration), and because the parameter estimate for trial duration had a statistically non-significant ($p \gg 0.05$) and inconsequential effect size (Table 3).

Table 2. Akaike's information criterion (AIC) calculations for the logistic regression models corresponding to the different hypotheses represented by the models g_i. k is the number of parameters, including variance (σ^2), in model i; $\boldsymbol{L}(g_i \mid X=x)$ is the log-likelihood; AIC_c is the corrected AIC value; Δ_i is the difference between model i and the best model in the set; and w_i is model probability of fitting the observed data

Model	k	$\boldsymbol{L}(g_i \mid X=x)$	AIC_c	Δ_i	w_i
g_1	3	−86.241	178.658	11.116	0.01
g_2	4	−79.623	167.542	0	0.62
g_3	5	−79.560	169.568	2.026	0.23
g_4	6	−79.550	171.732	4.190	0.08
g_5	7	−78.503	171.854	4.312	0.07

Of the 2 remaining models (g_2 and g_5), we chose g_5 as the optimal model because it included the variables in model g_2 and because the interaction effect sizes were statistically significant ($p < 0.05$) and substantial (Table 3), indicating that the relationship between the probability of survival and crab size differed significantly by habitat type (sigmoid non-linear regression, $r^2 = 0.40$, $p = 0.041$; Fig. 2). For the unvegetated (mud) habitat, survival probability was positively related to crab size, whereas for *Zostera marina*, survival was inversely related to crab size (Fig. 2), as predicted by the hypothesis of an ontogenetic shift in habitat from seagrass to mud as juveniles grow. In contrast, survival was generally higher and independent of
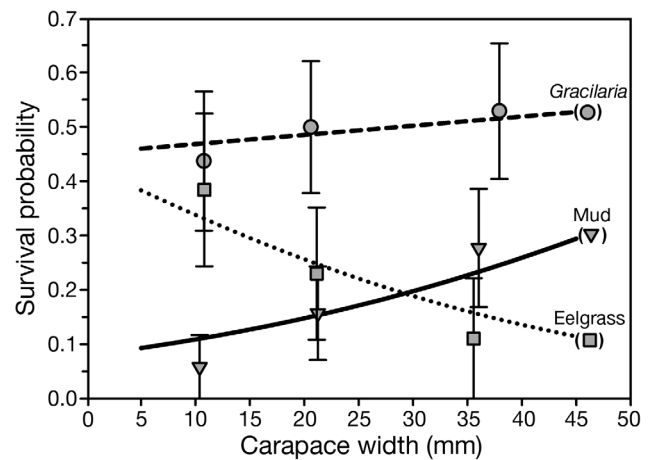

Fig. 2. *Callinectes sapidus*. Juvenile blue crab probability of survival by size (carapace width) within each habitat (*Gracilaria vermiculophylla*, mud and eelgrass) from survival probability models and field survival experiments during summer 2007 in the York River, Chesapeake Bay. The functions are derived from model g_5 (habitat type × crab size). The survival probability points are from the field experimental data. Means ±1 SE

Table 3. Parameter estimates with 95% confidence intervals (in parentheses) from logistic regression models (g_1–g_5)

Model k	Intercept	x_1 size	x_2 eelgrass	x_3 macroalgae	x_4 trial duration	x_5 eelgrass × size	x_6 macroalgae × size
g_1	−0.99 (−1.40,−0.57)	0.01 (−0.01,0.02)					
g_2	−1.61 (−2.34,−0.88)		0.55 (−0.51,1.61)	1.57 (0.65,2.49)			
g_3	−1.75 (−2.83,−0.67)	0.01 (−0.024,0.044)	0.56 (−0.50,1.62)	1.57 (0.65,2.49)			
g_4	−1.91 (−4.2,−0.65)	0.01 (−0.10,0.12)	0.55 (−0.52,1.62)	1.57 (0.65,2.49)	0.01 (−0.11,0.13)		
g_5	−2.45 (−4.22,−0.68)	0.04 (−0.02,0.10)	2.17 (−0.35,4.69)	2.26 (1.17,3.35)		−0.07 (−0.12,−0.02)	−0.03 (−0.07,0.01)

crab size in *Gracilaria vermiculophylla*, indicating that *G. vermiculophylla* served as an effective nursery habitat for a wider range of juvenile crab sizes.

DISCUSSION

Due to an extensive eelgrass decline and the spread of the exotic macroalga *Gracilaria vermiculophylla* in Chesapeake Bay, we suspected that *G. vermiculophylla* could be forming a novel ecosystem (sensu Hobbs et al. 2006, 2009) by providing structured nursery habitat for the blue crab and many other species reliant on seagrass for refuge (Beck et al. 2001, Lipcius et al. 2007). Our field surveys and experiments confirmed that *G. vermiculophylla* is utilized by blue crab juveniles, and that juveniles survive in *G. vermiculophylla* patches as well as or better than in eelgrass *Zostera marina* patches or unvegetated mud habitat. In addition, there appears to be a positive relationship between density of juvenile crabs and volume of *G. vermiculophylla*. Consequently, recovery of the blue crab from a major decline (Lipcius & Stockhausen 2002) may be facilitated by an exotic macroalgal species. Furthermore, we validated the role of predation-induced changes in survival in mediating an ontogenetic shift of juveniles from seagrass to unvegetated mud habitats as they grow, and that *G. vermiculophylla* supersedes the need for an ontogenetic habitat shift by providing suitable refuge for a wider size range of juvenile blue crabs than either eelgrass or unvegetated mud habitats.

We posit that the Chesapeake Bay ecosystem is transitioning into a functionally novel ecosystem due in part to the emergence of an exotic, habitat-forming species that is replacing the disappearing native eelgrass as nursery habitat. This situation can be conceptualized for an array of ecosystems and their restoration potential under various environmental and biotic conditions, such as the loss of native species or addition of exotic species (Fig. 3), as originally suggested by Hobbs et al. (2009). The Chesapeake Bay ecosystem similarly experienced an alteration from a 'historical' ecosystem state within its natural range of variability (lower left quadrant, Fig. 3) to a degraded 'altered' state (lower right quadrant), in which a substantial fraction of the bay's eelgrass beds have been destroyed (Orth & Moore 1984, Orth et al. 2010). We postulate that the system is moving from the lower right quadrant towards the intersection of the upper left and right quadrants, such that the functional role of nursery habitats will, in the future, be filled by a mix of seagrass and *Gracilaria ver-*
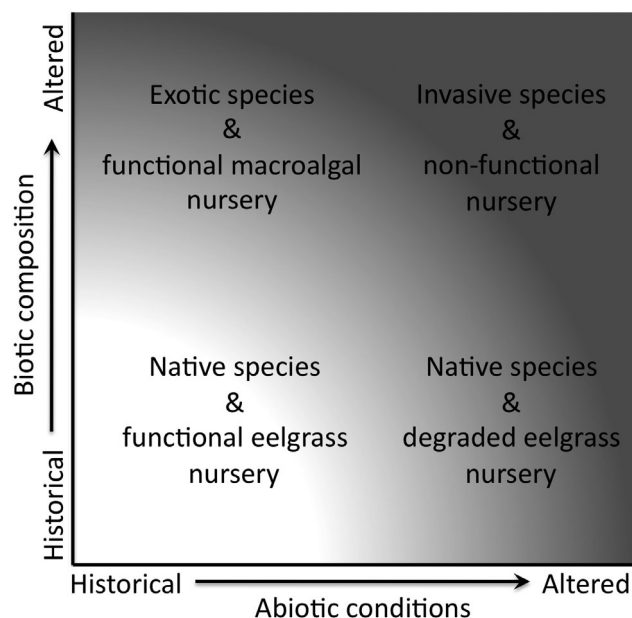

Fig. 3. Ecosystem types and their restoration potential under various conditions of biotic composition (loss of native species or addition of exotic species) and the abiotic environment (e.g. eutrophication), as adapted from Hobbs et al. (2009; their Fig. 1d). Each axis grades from a 'historical' ecosystem state within its natural range of variability to an 'altered' or 'novel' state where the ecosystems have experienced substantial modifications in abiotic conditions or biotic composition. In the case of Chesapeake Bay, the system initially shifted from the lower left (native species, suitable environment, functional eelgrass *Zostera marina* nursery habitat) to the lower right (eutrophication, degraded eelgrass nursery habitat). We postulate that the system is shifting towards the intersection of the upper left and right quadrants, with a mix of seagrass and *Gracilaria vermiculophylla* nursery habitats for the blue crab and other species. Note that the upper left quadrant lists beneficial 'exotic' species in a functional ecosystem, whereas it is assumed that a degraded ecosystem will contain deleterious 'invasive' species (upper right quadrant)

miculophylla nursery habitats for the blue crab and other species under a different set of environmental conditions than those that historically occurred in Chesapeake Bay. Through the establishment and spread of an exotic species, the ecosystem is therefore becoming more efficient at supporting a diverse suite of marine and estuarine species than in the absence of eelgrass habitat (e.g. Thomsen et al. 2010, Byers et al. 2012).

Ontogenetic tradeoffs in nursery habitats

Our field experiments demonstrated that juvenile survival was positively related to crab size in mud but negatively in seagrass, which corroborated the para-

digm of a predation-induced ontogenetic shift from seagrass to unvegetated habitat. The interaction effect between crab size and habitat type most likely relates to disparate preferences for structured and unstructured habitats by different juvenile size classes (Orth & van Montfrans 1987, 2002, Pile et al. 1996, Hovel & Lipcius 2001, Lipcius et al. 2007). Young, small juvenile blue crabs may require the structural refuge of vegetation, whereas larger juveniles that have reached a size refuge in unvegetated mud habitats can escape cannibalism in structured nurseries and safely exploit productive foraging grounds in unvegetated mud habitat (Seitz et al. 2005). Equally, the interaction may originate from effective scaling of structural refuge to prey body size such that different types of structural refuge are effective for different juvenile size ranges. For example, although large Nassau grouper juveniles remain at the periphery of macroalgae, they outgrow the finer refuge of algal interstices and shift to larger crevices provided by patch corals (Dahlgren & Eggleston 2000). Predator suites may also vary by habitat and prey size, which could produce an interaction effect, especially if the predators within each habitat vary in prey size limitation (Orth & van Montfrans 1987).

The graphical intersection in survival probability from the size × habitat model (g_5) indicates that a size-specific habitat shift of blue crab juveniles should occur at about 20 to 30 mm CW from seagrass to mud, which was corroborated by natural juvenile densities and size distributions. In various field studies, juvenile survival in mud and seagrass habitats converged when crabs reached 20 to 30 mm CW (Pile et al. 1996, Hovel & Lipcius 2001, Lipcius et al. 2005, 2007). Similar patterns have been observed for other marine species (finfish and crustaceans: Ruiz et al. 1993; ribbed mussel: Lee & Kneib 1994; Nassau grouper: Dahlgren & Eggleston 2000). In contrast to the pattern for survival, growth of juvenile blue crabs was comparable between seagrass and mud habitats (Seitz et al. 2005), suggesting that growth has a minimal influence on habitat preference. Thus, blue crab ontogenetic habitat preference supports the 'minimize mortality risk (μ)' hypothesis (Werner & Hall 1988).

Suitability of *Gracilaria vermiculophylla* as nursery habitat

In the field experiments, *Gracilaria vermiculophylla* generated the highest probability of survival for all juvenile sizes of the 3 habitats tested. In the field sampling of *G. vermiculophylla* patches, crab densities were high, crab size structure was typical of that occurring in native seagrass habitat, and crab density appeared to be positively correlated with *G. vermiculophylla* volume, indicating that it is effective as both primary (early juvenile) and secondary (late juvenile) nursery habitat. Most importantly, the comparatively high survival of juveniles in *G. vermiculophylla* indicates that this vegetation can serve as an alternative to the structural refuge provided by previously abundant eelgrass *Zostera marina* beds. This is in keeping with the hypothesis that shelter-seeking species use structural complexity rather than evolutionary familiarity to determine their use of habitat-forming vegetation (Duffy & Baltz 1998, Jackson & Hobbs 2009, Martin & Valentine 2011, Schlaepfer et al. 2011). In addition, prey items occurring in macroalgae such as *G. vermiculophylla* provide the necessary food quality to support juvenile crab growth (Epifanio et al. 2003, Thomsen et al. 2009, Byers et al. 2012).

The mechanism by which *Gracilaria vermiculophylla* produces higher survival in a wider range of juvenile sizes than seagrass remains unexplored. If the branching structure of *G. vermiculophylla* provides more rugosity than seagrass blades, then the inverse relationship between habitat complexity and predation pressure may explain the wider array of juvenile sizes surviving in its refuge (Coull & Wells 1983, Tupper & Boutilier 1997, Martin & Valentine 2011). Similarly, the branching structure of *G. vermiculophylla* may functionally scale to a broader array of body sizes, as documented in Nassau grouper, whose small juveniles inhabited macroalgal branch interstices, whereas large juveniles resided along algal clump edges (Dahlgren & Eggleston 2000).

Although *Gracilaria vermiculophylla* provides refuge for juvenile blue crab and other estuarine species, its benefits will likely vary temporally due to seasonal patterns in abundance, disturbances such as storms, and hydrodynamic conditions (Thomsen et al. 2010). In addition, it may be harmful to the ecosystem in places where it forms dense beds that foster hypoxia (Gray et al. 2002, Bell & Eggleston 2005). In the mainstem tributaries of Chesapeake Bay, we have observed only a few places where *G. vermiculophylla* formed dense beds, typically in small coves lacking sufficient water flow. This is in contrast to the coastal bays and seaside lagoons adjoining the Chesapeake, where dense beds are common (Thomsen et al. 2010). Hence, the effects of *G. vermiculophylla* in the ecosystem may generally be positive, though additional field surveys on its wide-scale effects in Chesapeake Bay are necessary, as done previously in the coastal bays and lagoons (Thomsen et al. 2010).

Implications for conservation

The positive effects of the exotic *Gracilaria ver-miculophylla* in fostering survival of the native blue crab, in addition to the poor prognosis for recovery of eelgrass in Chesapeake Bay, indicate that a novel ecosystem is emerging with *G. vermiculophylla* as a critical habitat-forming species. Native, shelter-seeking species are apparently more influenced by refuge structural complexity than vegetation origin (i.e. native versus exotic), as observed in other terrestrial and aquatic ecosystems (Schlaepfer et al. 2011). Consequently, the exotic *G. vermiculophylla* should be included in conservation assessments of structured benthic habitat availability, especially in areas already impacted by native habitat degradation. In today's rapidly changing ecosystems, the future of effective conservation may lay in the reassessment of novel ecological relationships (Hobbs et al. 2006, 2009), especially our understanding of native–exotic interactions. While preservation of historical native ecosystems remains the primary goal, recognition and assessment of novel ecosystems may provide powerful new conservation approaches (Jackson & Hobbs 2009, Schlaepfer et al. 2011).

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