FEATURE ARTICLE

Mangrove expansion into temperate marshes alters habitat quality for recruiting *Callinectes* spp.

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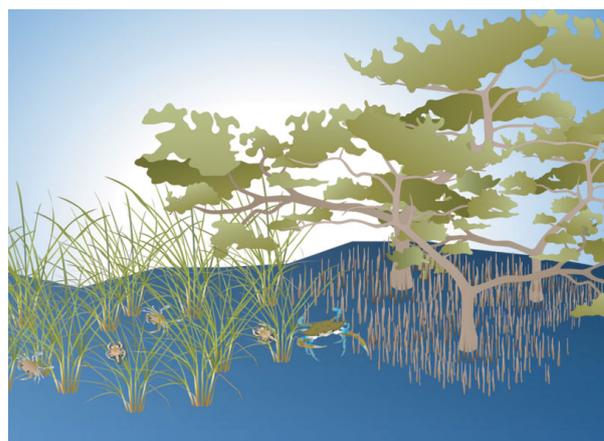[1]**Department of Entomology, University of Maryland, College Park, MD 20742, USA**
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ABSTRACT: Beyond direct habitat loss, climate change can alter habitat quality and availability by stimulating shifts in foundation species ranges. Tropical mangroves are proliferating at the intersection with temperate saltmarshes and continue moving poleward with unknown consequences for inhabitant marine fauna. We expected that mangrove and marsh foundation species differ in habitat quality, due at least in part to differences in their structural attributes, such that shifts from marsh to mangrove wetlands alter habitat availability for wetland inhabitants. We coupled recruitment surveys and laboratory experiments to assess the influences of foundation species' structural and non-structural attributes on *Callinectes* spp. recruitment, preference, and survival among mangrove and marsh habitats. Recruitment was evident in *Spartina alterniflora* and *Rhizophora mangle* intertidal habitats but not in *Avicennia germinans*. In laboratory trials, *S. alterniflora* was preferred in the presence of predation risk and provided the highest probabilities of survival, indicating that settlers can distinguish among ecotone vegetation types and that their choices correspond to habitat quality. Survival probability and recruit persistence were comparatively low in mangrove habitats. The differences in habitat use, preference, and survival identified in this study suggest that mangrove expansion is diminishing wetland habitat for *Callinectes* spp. It also reveals that changes between habitat-forming species, and not just the loss of structure *per se*, can affect habitat quality, such that foundation species may not replace one another functionally where they displace each other spatially.

KEY WORDS: Foundation species · Climate change · Biogenic habitat · Range shifts · Recruitment · Survival

Recruiting *Callinectes* spp. distinguish between mangrove and marsh vegetation.

Image: C. Chenery, T. Saxby, J. Thomas, Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/).

INTRODUCTION

Population dynamics depend on the habitat that a species occupies, such that recruitment, survival, and growth often vary even among co-occurring habitat types (Minello et al. 2003, Grol et al. 2011, Johnston & Lipcius 2012). Thus, changes in habitat availability can alter inhabitant population dynamics. Climate change and anthropogenic stressors are modifying marine habitats by reducing the abundance of habitat-forming species (Harley et al. 2006, Hoegh-Guldberg & Bruno 2010). Where foundation species are lost, secondary declines of inhabitant fauna are attributed

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to reduced habitat quality with the loss of structural complexity (e.g. transitions from coral reef to algal turf and kelp forest to urchin barrens; Knowlton 2001, Steneck et al. 2002, Feary et al. 2007, Ling 2008). Climate change is also redistributing species geographically, which can cause foundation species to replace one another without a loss of biogenic habitat *per se* (Stachowicz et al. 2002, Poloczanska et al. 2013). Accordingly, inhabitant fauna have declined less markedly where one structurally complex habitat is replaced by another (e.g. seagrass to macroalgae; Johnston & Lipcius 2012). With an increasing recognition of wide-spread shifts in species distributions, there is a growing need to understand how habitat use and inhabitant population dynamics differ between shifting foundation species.

Throughout the world, coastal wetlands are being reshaped by the poleward shift of tropical mangroves into temperate saltmarshes (Osland et al. 2013, Cavanaugh et al. 2014, Saintilan et al. 2014). Many macrofauna species use mangroves or saltmarshes as nursery habitat, but the vegetation types likely differ as habitat because their intertidal components differ in growth form (Robertson & Duke 1987, Minello et al. 2003, Friess et al. 2012). The ecotone along the Atlantic coast of Florida (USA) is dominated by 3 plant species with distinct intertidal growth structures: *Spartina alterniflora* (smooth cordgrass) forms tall shoots of flat-bladed leaves that branch upward from a central stem; *Rhizophora mangle* (red mangrove) prop roots are tall, with secondary roots branching downward from primary roots; *Avicennia germinans* (black mangrove) produce shorter, simple emergent pneumatophores (Fig. 1). We hypothesize that these mangrove and marsh vegetation types provide non-equivalent wetland habitats, due in part to influences of their structural attributes on habitat use and inhabitant survival (Friess et al. 2012, Sepúlveda-Lozada et al. 2015).

To better understand how climate-driven shifts in foundation species affect inhabitant species, we studied the distribution of *Callinectes* spp. (Decapoda: Portunidae) recruits among mangrove and marsh biogenic habitats where they co-occur, paying particular attention to the effects of differences in vegetation structural attributes on habitat use. Specifically, we (1) monitored a recruiting cohort of *Callinectes* spp. on an experimental array deployed in patches of mangrove and marsh vegetation in the ecotone and (2) tested the underlying drivers of habitat use patterns with settling *Callinectes* spp. in the laboratory. We expected recruits to use mangrove and marsh vegetation differently, and that differ-
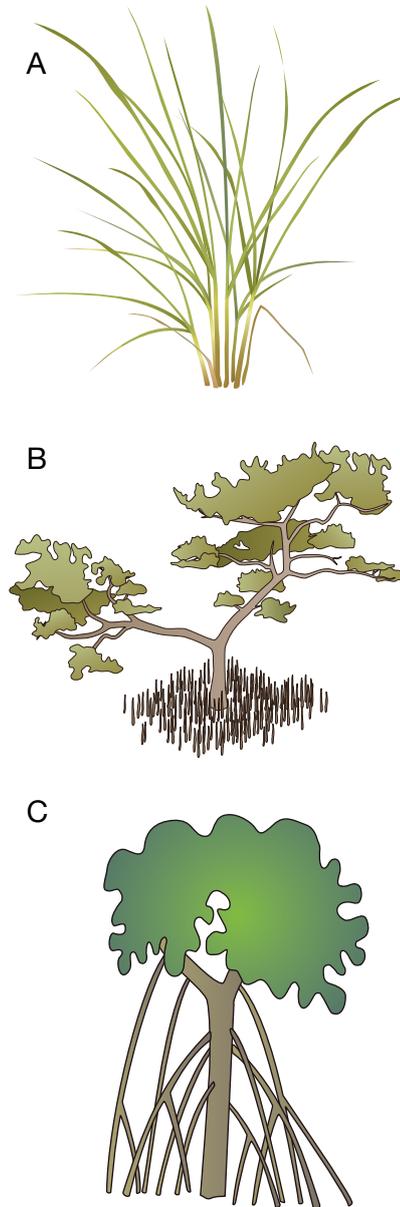

Fig. 1. The 3 vegetation types studied are (A) *Spartina alterniflora* (cord grass) shoots, (B) *Avicennia germinans* (black mangrove) pneumatophores, and (C) *Rhizophora mangle* (red mangrove) prop roots. Vegetation illustrations: T. Saxby and J. Thomas, Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/)

ences in habitat use originate from active habitat selection (hereafter 'preference') or from subsequent post-settlement mortality (Houde 1987, Etherington & Eggleston 2000, Heck et al. 2001). The differences in habitat use, preference, and survival identified in this study suggest that shifts in foundation species and their structural attributes alter habitat quality and availability for *Callinectes* spp.

MATERIALS AND METHODS

Study system

An undifferentiated mix of *Callinectes sapidus* and *Callinectes similus* (hereafter *Callinectes*) were the focal organisms in all study components. These swimming crabs settle as megalopae in near-shore environments in the southeast USA, and are dependent on wetlands as nursery habitat (Orth & van Montfrans 1987, Hsueh et al. 1993, Epifanio 1995, Etherington & Eggleston 2000). To evaluate changes in habitat quality for *Callinectes* with mangrove expansion, we examined habitat formed by temperate *Spartina alterniflora* (saltmarsh cordgrass), tropical *Avicennia germinans* (black mangroves) and *Rhizophora mangle* (red mangroves), hereafter referred to by generic names.

Specifically, we evaluated habitat value and crab use of the vegetation components that occupy the intertidal water column—grass shoots and aerial mangrove roots. To parameterize our experimental units, we first measured structural attributes of naturally occurring vegetation at 4 sites spanning the ecotone (27.8–30.4° N). Each vegetation type was surveyed in at least 3 sites. Sampling areas (n = 20) were identified by selecting a randomly drawn number that corresponded to a point along a haphazardly chosen strip of shoreline. Within a 1 m^2 plot at each sampling area, we recorded vegetation cover and composition, the presence of branching, and the number of elements: roots or shoots. Within a 0.25 m^2 subplot, we measured angles of articulation and element diameters 10 cm above the substrate. Experimental vegetation units were then constructed to match field measures of vegetation density, diameter, and articulation.

Field studies: recruitment

We established a landscape-scale field experiment to assess habitat associations of recruiting *Callinectes* in the mangrove-marsh ecotone throughout the recruitment season (May to November 2014). We used an array of retrievable panels to conduct equal sampling with a single method across emergent shoot and pneumatophore and overhanging prop root vegetation structures. The experiment was designed to test recruitment response both (1) by habitat type at the scale of 10s of meters and (2) by physical structure at the scale of 10s of centimeters. Retrievable panels were fitted with artificial vegetation mimics and deployed in patches of each habitat type, such that comparisons by panel indicate the influences of physical structure, while grouping by habitat type indicates responses to broader habitat attributes such as chemical cues, production, or shading (Fig. 2A). Recruitment was monitored across 2 sites, Halifax River and Matanzas River, Florida, within the mixed vegetation ecotone (Fig. 2B). Halifax River (29.09° N, 80.94° W) is a mangrove-dominated site north of Cape Canaveral that has small stands of *Spartina* that persist along shallow, sandy banks. Some 70 km further north, Matanzas River (29.67° N, 81.21° W) is a historically saltmarsh-dominated site south of St. Augustine where mangroves have been proliferating since at least the 1980s (Cavanaugh et al. 2014, Rodriguez et al. 2016); *Avicennia* are abundant, while *Rhizophora* are still rare.

At each site, habitat patches were selected adjacent to main waterways within 4.5 km of the inlet to minimize spatial variation in larval supply and environmental conditions (Etherington & Eggleston 2000, Paula et al. 2001). Across sites, habitat patches were selected to provide a continuous edge of a single vegetation type with a total intertidal patch area >15 m^2. All patches had mixed sand, mud, and oyster substrates. A total of 4 patches per vegetation type were selected (n = 12 patches total), with 6 patches at each site allocated according to the natural abundance of each vegetation type (3 *Spartina*, 2 *Avicennia*, and 1 *Rhizophora* patch at Matanzas; 1 *Spartina*, 2 *Avicennia*, and 3 *Rhizophora* patches at Halifax).

To conduct the study, retrievable 61 × 61 cm panels were constructed from ½ inch (~1.27 cm) non-pressure treated plywood and populated with artificial vegetation structures. Vegetation structures were affixed to the central 50 × 50 cm (0.25 m^2), leaving a 5 cm outer border for anchoring and retrieval. *Avicennia* pneumatophores were constructed from 0.64 cm diameter birch dowels (24–27 cm tall). *Rhizophora* prop roots were constructed from a variety of 1.3 and 1.9 cm diameter birch dowels, composed of 6–7 'mainstems' with 2–3 lateral roots each affixed at ~60°. *Spartina* shoots were composed of 3 mm diameter PVC rod with polyester leaves glued at regular intervals (5 blades per shoot); green plastic straws were placed over the lower stem to increase the diameter to ~4.6 mm. Within the 0.25 m^2 center of each panel, 1 of the 3 vegetation types was added at natural densities (mean ± SD: 227 ± 99 pneumatophores, 85 ± 35 prop roots, or 150 ± 41 shoots per m^2).

Panels were deployed along the periphery of habitat patches in a balanced design across sites. Panels, anchored flush with the benthos, were
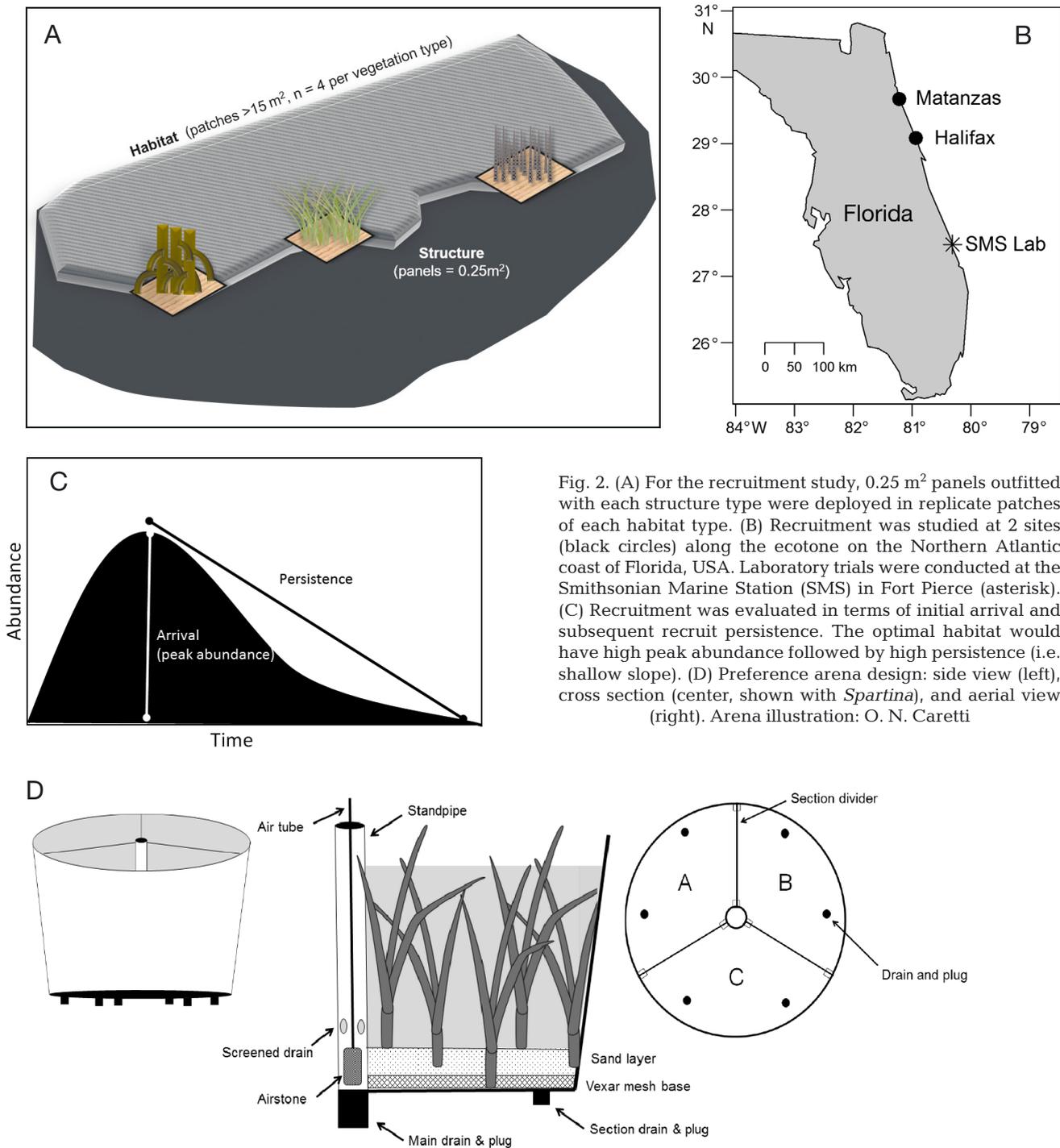
Fig. 2. (A) For the recruitment study, 0.25 m² panels outfitted with each structure type were deployed in replicate patches of each habitat type. (B) Recruitment was studied at 2 sites (black circles) along the ecotone on the Northern Atlantic coast of Florida, USA. Laboratory trials were conducted at the Smithsonian Marine Station (SMS) in Fort Pierce (asterisk). (C) Recruitment was evaluated in terms of initial arrival and subsequent recruit persistence. The optimal habitat would have high peak abundance followed by high persistence (i.e. shallow slope). (D) Preference arena design: side view (left), cross section (center, shown with *Spartina*), and aerial view (right). Arena illustration: O. N. Caretti

deployed in triplicate, with one panel of each vegetation structure placed within each habitat type in a fully crossed design (n = 36 panels total or 12 per structure type across habitats and 12 within each habitat type; method as in Lindsey et al. 2006, Pardo et al. 2007; Fig. 2A). During panel sampling, a cube lined with 1 × 2 mm mesh on all but one side — edged with foam-rubber — was placed over a panel, pressed down to create a seal, and secured (Brainard et al. 2009). The entire unit was retrieved, and the contents were rinsed through a 500 µm sieve and examined for *Callinectes* recruits. Recruits were measured and released. Panels were immediately redeployed. The panels were deployed in May 2014 and monitored

every 2 wk within 3 d of full and new moons to maximize recruitment detection. Once recruitment began in late summer, monitoring continued until early November; at which time water temperatures fell, abundance returned to pre-recruitment levels, and crabs reached 15–20 mm carapace width (CW), when secondary dispersal is expected (Lipcius et al. 2007, Johnston & Lipcius 2012). We used the resultant 10 weeks of cohort occurrence data to examine differences in recruitment dynamics, especially arrival and persistence, by habitat type (Fig. 2C).

For analysis, data was constrained to samples from late August through early November to characterize the recruiting cohort. All models of recruitment by habitat type included a random effect of patch identity to account for replicate panels within each patch. Generalized additive models (GAM) were used to fit smoothing functions to recruitment abundance in each habitat and each structure type across dates ('mgcv' package in R; Wood 2006, R Core Team 2015). We identified a recruitment pulse as the significant fit of a smoother to a change in recruit abundance over time. A smoother of salinity was also included in each model to account for variation in recruit abundance with salinity fluctuations throughout the study period.

To further characterize recruitment dynamics, we analyzed abundance during peak recruitment in late September and at subsequent dates until differences in abundance by habitat type or structure type were no longer significant ($p > 0.05$). Differences in abundance were analyzed with generalized linear mixed effects models with a Poisson distribution using the 'glmer' function in the 'lme4' package in R (Bates et al. 2015). Predictor level responses were assessed with Tukey post-hoc comparisons using the 'glht' function in the 'multcomp' package (Bretz et al. 2016). Together, recruit arrival and persistence were used as indicators of habitat use and quality (Fig. 2C). Also, in all study components (recruitment, preference, and survival), *Spartina* was specified as the intercept for all linear model analyses based on the logic that mangroves are encroaching on the saltmarsh landscape.

Laboratory experiments

We conducted habitat preference and survival studies with settling crabs during peak *Callinectes* recruitment in May, August, and September 2015 and May 2016. Both studies were conducted at the Smithsonian Marine Station in Fort Pierce, Florida,

USA. Seawater was provided via a flow-through system that delivers sand-filtered water directly from the adjacent Indian River Lagoon. During the study dates, lagoon waters near the study site had a mean salinity (± SD) of 33 ± 4 and mean temperature of 25 ± 3°C (sensor 0054, Harbor Branch Oceanographic Institute Land/Ocean Biogeochemical Observatory). Vegetation used in each study was collected fresh, scrubbed, and rinsed with fresh water to remove biofilms and epibionts (van Montfrans et al. 2003).

To populate the studies, megalopae and early juvenile (hereafter J1) *Callinectes* were collected by plankton net in Fort Pierce Inlet (27.48° N, 80.31° W) during incoming night tides within a week of full or new moon. Each study was populated with high but realistic densities of settlers (110–120 megalopae or 65–88 J1 per m² in preference trials and 75–94 megalopae or J1 per m² in survival trials; maximum documented natural recruitment is ~150 megalopae per m²: Moksnes 2002, van Montfrans et al. 2003). Developmental stage did not influence results in any trial, thus megalopae and J1 data are analyzed and presented together. We used sub-adult portunid crabs, which readily cannibalize conspecific recruits and first instar juveniles, as the predators in survival and risk trials (Smith 1995, Hines & Ruiz 1995, Moksnes et al. 1997, Aumann et al. 2006). Small portunids (16–36 mm CW) were collected with a push net in shallow flats adjacent to the laboratory, then held in separate ~2 l tanks until each experiment (<48 h holding time).

Preference

Settler preference for mangrove and marsh vegetation with and without risk (predator cues) was tested at night in ambient outdoor conditions with a pair of multi-section arenas. In preference tests, we simultaneously offered each vegetation type to settling crabs within a subdivided circular arena (van Montfrans et al. 2003). Each 200 l arena (bottom surface = 0.28 m²; 64 cm bottom width [77 cm top width] × 42 cm height) contained a center stand pipe for infrastructure, aeration, and drainage (Fig. 2D). Removable dividers split each arena into 3 individually draining 900 cm² sections. Sections were outfitted with freshly harvested mangrove or marsh vegetation that was fixed haphazardly to plastic mesh screens at low but realistic densities (55 prop roots, 110 pneumatophores, or 92 grass shoots per m²). Vegetation was assigned to random-

ized arena sections, then sand pre-washed and sieved to <500 μm grain size was added until the mesh was covered and the vegetation stood upright (~5 cm sand depth). The arenas were filled to 30 cm with sand-filtered ambient seawater. To assess the influence of risk on habitat preference, 2 portunid predators (described in the previous section) were added to each standpipe in half the trials. Mesh-covered openings between the standpipe and each section allowed predator chemical cues to enter the arena without any risk of actual predation (Griffiths & Richardson 2006, Smee & Weissburg 2006). Aeration within each standpipe increased water flow, circulating predator cues from the pipe into the broader arena. Arenas, sand, and vegetation were thoroughly rinsed with fresh water between trials.

At the start of each trial, dividers were placed between the vegetation types. Equal numbers of settling crabs (6–8 J1 or 10–11 megalopae) were added to each section to simulate a random distribution, the expected condition for no preference (van Montfrans et al. 2003). After 5 min of acclimation, dividers were removed to allow crabs to freely move about the arena for 12–14 h between 18:30–09:30 h, when megalopae are most active due to natural nocturnal ingress behavior (Epifanio 1995, Tankersley et al. 2002, van Montfrans et al. 2003, Moksnes & Heck 2006). At the end of each trial, dividers were simultaneously returned to each arena and water was drained down to ~10 cm depth through the central standpipe (lined with <500 μm mesh to prevent settler loss). Section plugs were then removed simultaneously so that the remaining water, sand, and settlers drained in unison from each section into a corresponding bucket below. Vegetation was rinsed and visually inspected for settlers. Finally, the drained contents of each section were filtered through a 710 μm sieve, allowing the <500 μm sand to pass through while retaining the ~1 mm settled crabs. Preference and avoidance were evaluated as changes in the number of crabs per section from the initial even distribution using a repeated G-test (chi-square framework) in R version 3.2.3 (R Core Team 2015). Only trials with ≥80% recapture efficiency were included in final analyses. Expected values for each habitat per trial were calculated as 1/3 (3 habitats per tank) of the total number of recovered settlers per trial. For significant G-test results, the habitats driving overall differences were identified as those with standardized residuals >|2| from corresponding chi-square tests, indicating significant deviation from the null expectation for a given habitat (Sharpe 2015).

Survival

Settler survival was assessed during the day under ambient conditions in an open air flow-through laboratory. Each sub-adult predator was fasted for 12 h prior to survival trials (8–10 h stomach clearing time; McGaw & Reiber 2000). Satiation trials were conducted to ensure that juvenile portunids are effective megalopae predators and that consumption in survival trials was not limited by predator satiation. To test satiation, individual fasted portunid predators (n = 32) were added to tanks containing only seawater, an airstone, and 4 J1 or 6 megalopae (4–5 maximum used in survival trials). After 7 h (comparable to survival trial duration), predators were removed and surviving settlers counted. Ninety percent of prey was consumed on average, with 100% consumed in 70% of satiation trials, indicating that predator satiation is not a limiting factor in our survival trials.

Differences in survival by vegetation type were tested in a series of 530 cm² circular tanks (26 cm width × 44.28 cm height) containing only one vegetation type each. Tanks were haphazardly assigned to each vegetation type or an unvegetated sand treatment. Treatment tanks were outfitted with mangrove or marsh vegetation fixed to plastic mesh screens as in preference trials. Pre-sieved and rinsed sand (<500 μm grain size) was added until the mesh was covered and the vegetation stood upright (~5 cm sand depth). The unvegetated control treatment received only 5 cm of sand. Tanks were filled to 30 cm with sand-filtered ambient seawater and aerated with a single air stone. Four J1 or 5 megalopae were placed in each tank and given 20 min to acclimate before 1 portunid predator (described in 'Laboratory experiments' above, 22 ± 0.4SE mm mean CW) was added to each tank. Trials ran for ~6 h in ambient daylight between 09:00 and 19:00 h. At the end of each trial, predators were removed and tanks were drained, rinsed, and sieved as in preference trials. A series of predator-free control trials (n = 10 sets) revealed that settler recovery was 95–100% efficient in the absence of predators, indicating no vegetation-specific recovery bias. Thus, all settlers missing from predation trials were considered depredated. Survival probability was measured as the proportion of settlers recovered. Based on our hypotheses, survival was analyzed relative to habitat type using generalized linear models in the 'mass' package in R with a quasibinomial family to account for overdispersion (Venables & Ripley 2002, R Core Team 2015). Treatment level responses were assessed with Tukey post-hoc comparisons between predictor levels with the 'glht' function in the 'multcomp' package (Bretz et al. 2016).

RESULTS

Recruitment

We evaluated *Callinectes* recruitment responses to both (1) habitat type of large patches and (2) physical structure of vegetation mimics within patches. A recruiting cohort was first detected in early September 2014 and reached peak abundance in late September. Recruits were twice as abundant, on average, at the Halifax River site (mangrove dominated; 7.6 recruits per m² on average compared to 3.6 at Matanzas River); nonetheless, site did not significantly contribute to model fit, and habitat associations remained consistent when standardized by recruit availability for each site and sampling date. Thus, results are presented for raw data, un-standardized by site.

Significant recruitment pulses were detectable in *Spartina* (GAM temporal smoother $\chi^2 = 18.8$, edf = 3.3, p = 0.0009) and *Rhizophora* habitat patches ($\chi^2 = 24.6$, edf = 3.8, p < 0.0001) but not in *Avicennia* habitat patches ($\chi^2 = 3.3$, edf = 1.4, p = 0.24; Fig. 3A). In recruitment comparisons by date, late September peak abundance in *Rhizophora* habitat (mean ± SE: 32 ± 8 settlers per m²) was marginally higher compared to *Spartina* (13 ± 4 settlers per m², GLMER residual df = 3, p = 0.0837) and significantly higher than in *Avicennia* (8 ± 3 settlers per m², p = 0.0106; Likelihood Ratio Test $\chi^2 = 36.8$, n = 4 patches per habitat type, with recruits sampled on 3 panels in each patch; Fig. 3B). Recruit persistence from peak abundance to the subsequent sampling date was lowest in *Rhizophora* habitat (0.28), with higher persistence in *Avicennia* (0.57) and *Spartina* (0.45), such that within 2 wk (early October) recruit occupancy
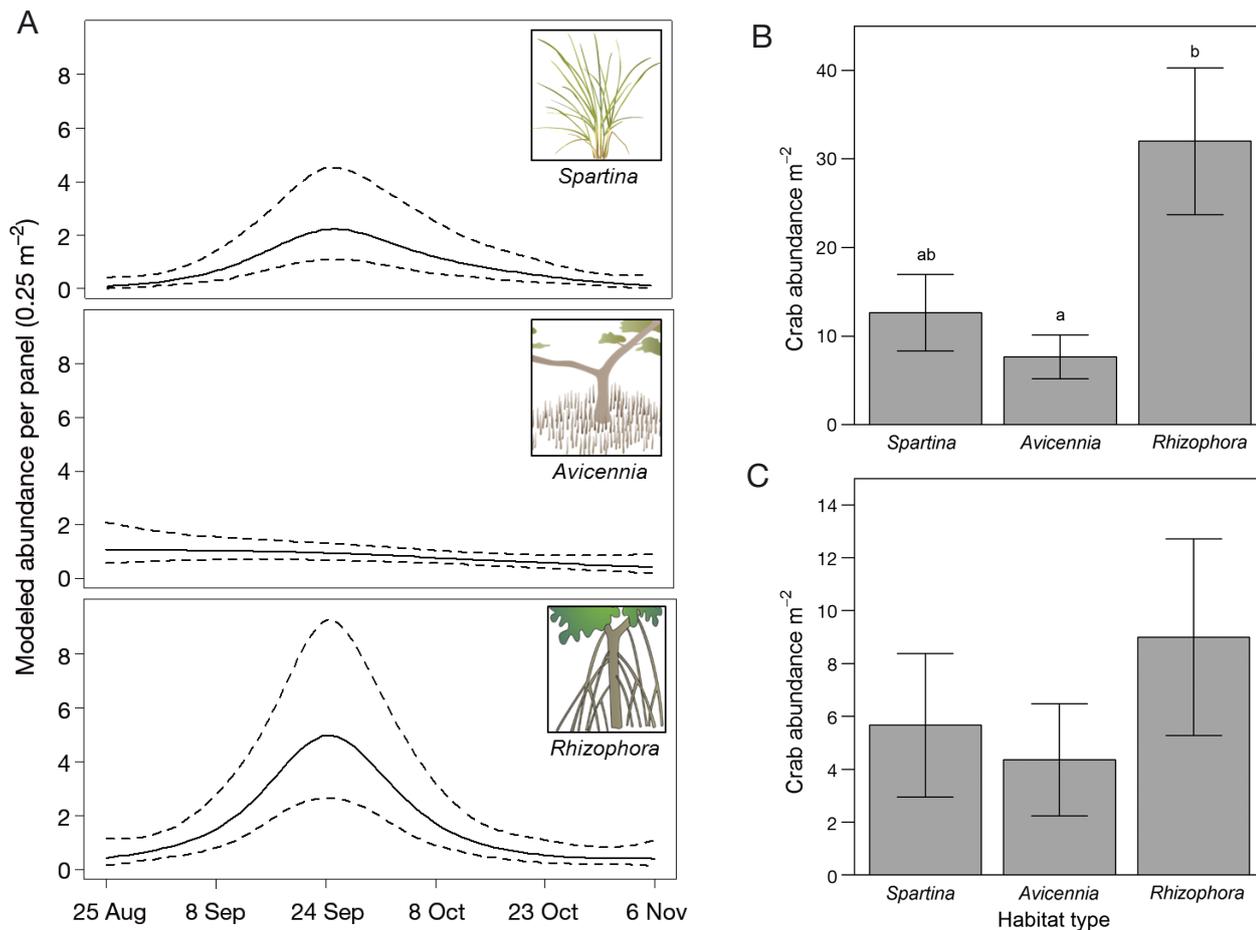

Fig. 3. (A) Modeled abundance of settling *Callinectes* in patches of 3 vegetation types in the field. Solid lines plot the fitted smoother (generalized additive model); dashed lines represent ± 2 SE. (B) Settling *Callinectes* abundance by vegetation type at initial (peak) abundance in late September. (C) *Callinectes* abundance 2 wk after peak recruitment (early October) demonstrates differences in recruit persistence. Lettering indicates significant differences at p < 0.05. Note difference in abundance scales between September (B) and October (C). Credits for vegetation illustrations: see Fig. 1

was no longer significantly different by habitat type (GLMER residual df = 29, p = 0.075; Fig. 3C).

Recruits also responded to isolated vegetation structures. Recruitment pulses occurred in grass shoot (GAM temporal smoother χ^2 = 23.34, edf = 3.8, p = 0.0001) and prop root structures (χ^2 = 13.32, edf = 2.9, p = 0.0077) but not in pneumatophores (χ^2 = 6.57, edf = 2.3, p = 0.11; Fig. 4A). During peak abundance in late September, recruit abundance was highest on grass shoots (30 ± 9 settlers per m^2) and significantly lower on pneumatophores (13 ± 4 settlers per m^2, GLMER residual df = 30, p < 0.0001) and prop roots (10 ± 3 settlers per m^2, p < 0.0001; χ^2 = 6.8, n = 12 panels per structure type; Fig. 4B). As with habitat patches, differences in persistence eliminated any difference in abundance by physical structure type within 2 wk (GLMER residual df = 29, p = 0.775; Fig. 4C).

Preference

To determine whether recruitment patterns in the field are driven by active preference, we tested settler habitat preference in the laboratory. In the absence of predation risk, settlers did not display a preference between habitat types (individual G-test for no risk: n = 16 trials, df = 2, p = 0.58). Although they remained non-significant, differences in habitat preference strengthened markedly in the presence of predation risk (heterogeneity G-test by risk presence/absence: df = 2, p = 0.09). In risk trials, *Spartina* shoots were preferred marginally over mangrove vegetation (individual G-test for risk: n = 16 trials, df = 2, p = 0.07). Unexpected variation in preference by season emerged, with settlers distinguishing between habitat significantly more in the fall than
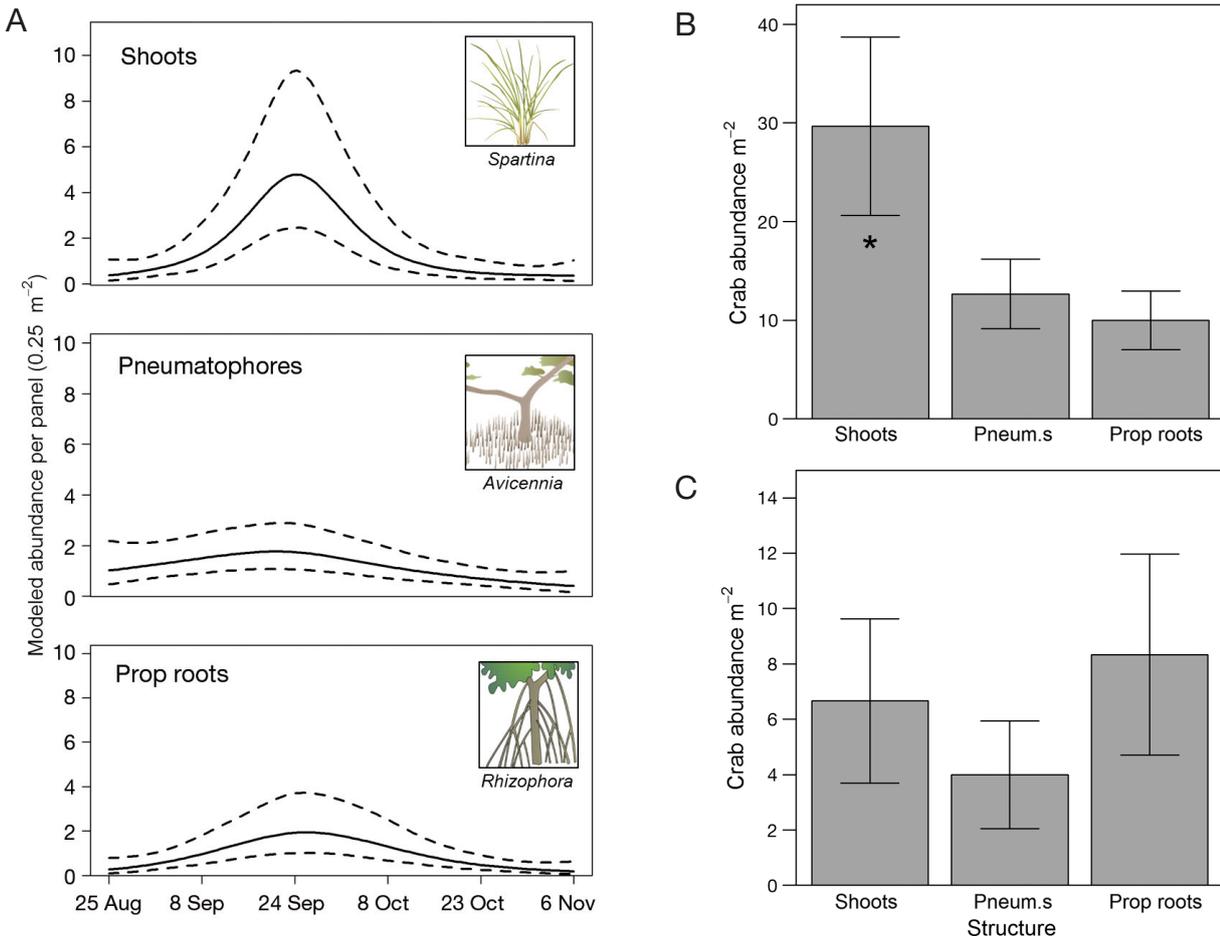

Fig. 4. (A) Modeled abundance of settling *Callinectes* in structural mimics of each vegetation type in the field. Solid lines plot the fitted smoother (generalized additive model); dashed lines represent ± 2 SE. (B) Settling *Callinectes* abundance by structural mimic type at initial (peak) abundance in late September. (C) *Callinectes* abundance by structure type 2 wk after peak recruitment (early October) demonstrates differences in recruit persistence. Asterisk indicates significant differences at p < 0.05. Note difference in abundance scales between September (B) and October (C). Credits for vegetation illustrations: see Fig. 1
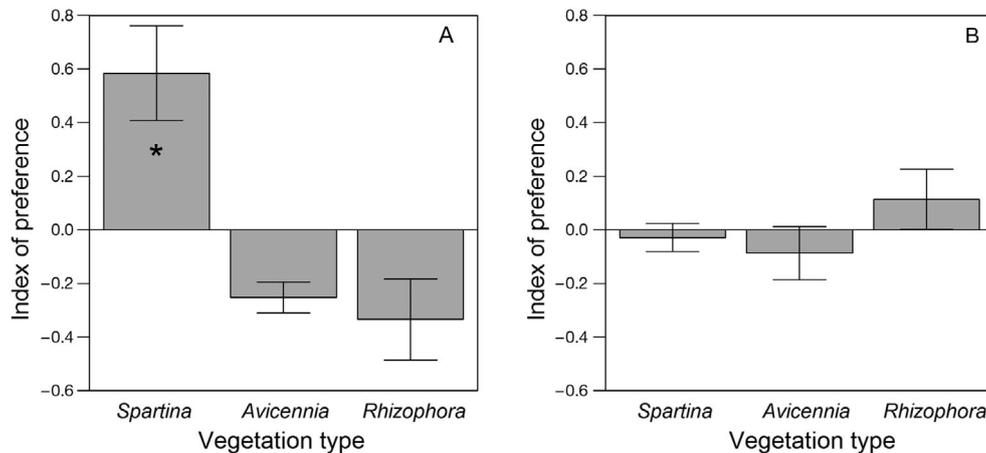
Fig. 5. *Callinectes* preference for vegetation types in the presence of predator cues during (A) fall (August and September) and (B) spring (May) laboratory studies. Values >0 indicate preference; values <0 indicate avoidance. Asterisks indicate significant differences at p < 0.05

spring (heterogeneity G-test by season: df = 2, p = 0.005, Fig. 5). In the fall and in the presence of risk, *Spartina* shoots were preferred over mangrove vegetation (individual G-test for fall: n = 11 trials, df = 2, p = 0.009, Fig. 5A). No preference was evident in the spring (individual G-test for spring: n = 21 trials, df = 2, p = 0.24, Fig. 5B).

Survival

Stronger preference in the presence of predator cues suggests that preferred habitats confer higher survival, so we also evaluated settler survival in each vegetation type. Among the 3 vegetation types tested, only *Spartina* shoots provided a probability of survival (0.54 ± 0.07SE) that was significantly higher than the unvegetated treatment (0.23 ± 0.06SE; residual df = 56, p = 0.028; Fig. 6).
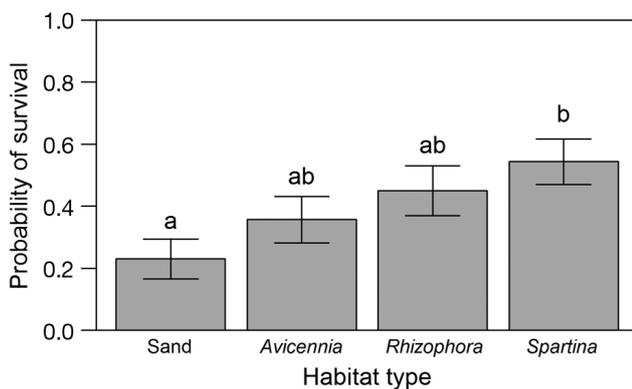

Fig. 6. *Callinectes* settler survival by vegetation type in the presence of a portunid predator. Lettering indicates significant differences at p < 0.05

DISCUSSION

Climate change is redistributing foundation species, with the potential to affect the population dynamics of inhabitant species if alternative habitats differ in quality. We used studies of recruitment, preference, and survival to determine the suitability of mangrove and marsh vegetation as habitat for post-settlement stage *Callinectes*. We expected habitat use to be vegetation-dependent, with use reflecting differences in preference for and survival in a given vegetation type. Habitat use in the field revealed that recruits favor *Rhizophora* habitat and *Spartina* shoot structures. Independent experimentation in the laboratory demonstrated that recruits preferred *Spartina* in the presence of predation risk, and that it was the only vegetation that significantly increased recruit survival compared to unvegetated conditions. Our results confirm that habitat use is vegetation-dependent and reveal that *Spartina* provides superior habitat; the driver of high recruitment into apparently unfavorable *Rhizophora* habitat remains to be identified, but vegetation structural attributes are likely influential (see the Supplement at www.int-res.com/articles/suppl/m573p001_supp.pdf).

Recruitment

Patchy recruitment has the potential to reduce settlement-based population attrition if recruits preferentially settle in habitats that provide higher probability of survival (Dahlgren & Eggleston 2000, Halpin 2000, Johnston & Lipcius 2012). The evolution of transient, mobile settler stages (e.g. megalopae) is

attributed in part to the importance of finding and recruiting to optimal habitat by recognizing and choosing among cues for structure, food, and reduced predation (Welch et al. 1997, Rittschof et al. 1998, Tapia-Lewin & Pardo 2014). Settling recruits responded to both patch-level habitat cues and isolated vegetation structures. Recruitment was 4-fold higher in patches of *Rhizophora* and 2-fold higher in *Spartina* compared to neighboring *Avicennia*. Although recruitment was higher at the mangrove-dominated site, recruitment was high to *Rhizophora* habitat regardless of its prevalence in the surrounding landscape (i.e. mangrove- or marsh-dominated sites). Recruitment was also 3-fold higher in grass shoots than in either other vegetation structure. Recruitment peaked simultaneously across the landscape, indicating that initial differences in abundance arose immediately upon recruitment, rather than due to secondary dispersal (Heck et al. 2001, Moksnes 2002, Moksnes & Heck 2006). These patterns of *Callinectes* habitat use suggest that recruits respond most positively to non-structural attributes provided by *Rhizophora* and to structure formed by *Spartina*.

Callinectes often distinguish between habitats upon initial settlement (Welch et al. 1997, Moksnes & Heck 2006, Johnston & Lipcius 2012); however, settlement patterns are not always indicative of later population distribution, which is more readily attributed to juvenile survival and secondary dispersal (Heck et al. 2001, Moksnes 2002, Moksnes & Heck 2006). Thus, recruit persistence was expected to vary by habitat according to quality. Often, recruit arrival alone may indicate sufficient differences in habitat quality to impact population dynamics, especially for species that are vulnerable to predation (Levin & Stunz 2005, Almany & Webster 2006, Baker et al. 2014). For *Callinectes*, the benefit of selecting one habitat over another may be relatively short lived, such that recruit persistence likely provides additional insight into habitat quality through duration of habitat use and as a proxy for post-settlement mortality (Houde 1987, Etherington & Eggleston 2000, Heck et al. 2001). Between peak recruitment in late September and the next sampling event in early October, recruit persistence in *Rhizophora* was only half that documented in the neighboring habitat types. Thus, within 2 wk, lower persistence in *Rhizophora* habitat eliminated differences in settler abundance between *Rhizophora* and *Spartina* habitat. A comparable trend emerged across vegetation structures, reducing structure-based differences in habitat use within 2 wk, though mean *Callinectes* abundance remained

nearly double in favored prop root and shoot structures compared to pneumatophores. Continued recruit loss over time could be explained by a number of mechanisms. (1) Mortality would lead to decreasing recruit abundance over time. (2) Redistribution could also lead to decreased occurrence, but secondary dispersal is unlikely to be confounding because the sampled crabs did not exceed 20 mm CW, the expected size at secondary dispersal (Lipcius et al. 2007, Pardo et al. 2007, Johnston & Lipcius 2012). (3) It is possible that recruit attrition was due in part to less effective capture of large or fast-swimming individuals with the panel retrieval method; however, finfish and swimming crabs ranging in size from 0.5 to 100 mm were regularly captured. Thus, some combination of mortality and local redistribution are the most likely explanations for recruit attrition. Ultimately, optimal habitat should host high initial arrival, followed by recruit persistence; these conditions were most apparent in *Spartina* habitat. The differences in habitat use between vegetation types may originate from some combination of active preference and post-settlement mortality, so we evaluated each in turn.

Preference

Juvenile habitat use is driven foremost by mortality avoidance (Dahlgren & Eggleston 2000, Halpin 2000, Johnston & Lipcius 2012), so preference for a specific habitat should reflect its structural complexity and value as a refuge, especially in the presence of predation risk (Schofield 2003, van Montfrans et al. 2003, Brooker et al. 2013). Recruit habitat preference was consistently stronger in the presence of predator cues, suggesting that habitat is selected for refuge. The only clear habitat preference emerged for *Spartina* in the fall, though low statistical power in preference trials means that failure to reject the null of no difference between vegetation types should be interpreted cautiously. The origin of seasonal variation is unknown, but it may relate to grass emergence in spring and senescence in fall. This hypothesis is supported in part by crab preference for *Spartina* wrack and detritus as structural refuge (Smith et al. 2016).

Although juvenile portunid crabs are voracious and effective predators on conspecific megalopae, in the preference study, juvenile cues could have been perceived as either conspecific or predator cues (Hines & Ruiz 1995, Smith 1995, Moksnes et al. 1997, Aumann et al. 2006). Conspecific cues enhance

settlement and metamorphosis (Forward et al. 2001, Diele & Simith 2007), while predator cues generally reduce metamorphosis or accentuate habitat choices (Moksnes et al. 1997, Welch et al. 1997). If the juvenile cue treatment was perceived as conspecifics, we would have expected settler distributions to remain even among habitat types. If anything, conspecific cues should increase the rate of metamorphosis, resulting in more first instar juveniles (J1s) recovered from megalopae trials with the cue treatment. Instead, differences in habitat use became stronger and recovery of metamorphosed J1s was reduced by more than half in the presence of juvenile cues (1.2 compared to 3.6 average J1 recovered per habitat). Both results indicate that juveniles were perceived as predators rather than conspecific settlement cues. Thus, consistently stronger preferences in the presence of predation risk suggests that preferred habitats are likely of higher quality and should confer higher probability of survival.

Survival

In studies that compare vegetated (i.e. seagrass and salt marsh) habitat to mud and sand areas, the vegetated habitats often enhance survival of juvenile fish and invertebrates (Heck et al. 2001, Minello et al. 2003, but see Horinouchi et al. 2009). Vegetation also enhanced survival of settlers in this study. The variation in survival probability among vegetation types suggests that (1) survival depends on the refuges provided by vegetation structures and that (2) not all vegetation structure provides equally beneficial habitat. In particular, survival was highest in *Spartina* vegetation. Differences in survival likely originate from differences in refuge quality, particularly size-scaling and influences of vegetation structure on relative predator and prey mobility (Bartholomew et al. 2000). *Spartina*'s thin but high-density branched architecture (i.e. long leaves diverging from stems) may provide the most effective size-scaling between vegetation structures and small settling crabs. Similarly, *Callinectes sapidus* survive better in finely branching macroalgae than in structurally simpler seagrass in Chesapeake Bay (Johnston & Lipcius 2012).

Notably, the influences of habitat on survival may change with vegetation density if survival thresholds exist for structural features (Gotceitas & Colgan 1989, Hovel & Lipcius 2001, Scheinin et al. 2012). In this study, we used relatively low vegetation densities compared to mean natural densities of *Spartina*, *Rhizophora*, and *Avicennia*; further studies are needed to assess the relationship between survival in mangrove and marsh vegetation across a broader range of densities to determine if and where survival thresholds may exist, and how they differ among vegetation types. Nonetheless, our results provide initial evidence that marsh vegetation more strongly enhances recruit survival compared to mangrove vegetation, indicating that differences in ecotone vegetation use corresponds to differences in refuge quality, based in part on their structural forms.

Implications of mangrove expansion

This study demonstrates that the replacement of saltmarsh by mangroves is changing wetland habitat for *Callinectes*. Recruiting *Callinectes* selectively settled among mangrove and marsh vegetation types based on both structural and non-structural habitat attributes. The preferred *Spartina* shoots provided the highest probabilities of survival in laboratory experiments, suggesting that settlers can distinguish among ecotone vegetation types and that their choices correspond to habitat quality. Stronger preference in the presence of predation risk further supports the inference that selective settlement into *Spartina* is driven at least in part by mortality avoidance.

Based on these findings, *Avicennia* intrusion into saltmarsh represents effective habitat loss for *Callinectes* that may be partially alleviated with the subsequent emergence of *Rhizophora*. In both mangrove types, however, there is either low recruitment or low post-recruitment persistence. Recruits preferentially colonized *Rhizophora* habitat, but no evidence for preference or enhanced survival in the laboratory and poor recruit persistence in the field suggest that *Rhizophora* could represent an ecological trap or population sink (Battin 2004, Patten & Kelly 2010). Thus, high recruit arrival there should not necessarily be interpreted as an indicator of good habitat quality. Given (1) the potential for survival to vary with habitat density (and our test of only low densities in the laboratory) and (2) the potential influence of arrival alone on population dynamics, additional tests of survival thresholds across vegetation densities and examination of habitat occupancy by older stages would help to clarify *Rhizophora* habitat quality for *Callinectes*.

Prior studies have reported contradictory evidence about the importance of structural and non-structural cues in *Callinectes* selection of habitat (Forward et al. 1996, Welch et al. 1997, Diaz et al. 1999). Here, *Calli-*

nectes responded to both structural and non-structural cues when sorting among patchy, co-occurring wetland habitats. Our preliminary analyses suggest the potential importance of vegetation structural attributes, particularly the presence of branching, in mediating patterns of habitat use (see the Supplement). Additional studies will be needed to more explicitly determine (1) the non-structural attributes that shape habitat use and (2) differences in food availability and recruit growth rates among habitats. These studies would help identify the habitat attributes that stimulate high *Callinectes* settlement in suboptimal *Rhizophora* habitat, as differences in use could not be ascribed to the influence of structure alone. Many fish and invertebrates recruit to habitat with well-developed epifaunal communities, which suggests that non-structural cues, such as chemical odors associated with food, may attract *Callinectes* to *Rhizophora* prop roots (Laegdsgaard & Johnson 2001, Verweij et al. 2006). Epifaunal prey communities may be more developed on prop roots than grass shoots that senesce annually, thus potentially contributing to higher *Callinectes* recruitment to *Rhizophora* in the field (Bishop et al. 2013).

With this study, mangroves and saltmarshes join the suite of habitats that *Callinectes* distinguish among during settlement. Even though *Spartina* wetlands often provide poorer habitat quality than co-occurring seagrass for nursery-stage marine fauna (Minello et al. 2003, Bloomfield & Gillanders 2005), here we found that *Spartina* is superior habitat to tropical mangrove vegetation. As such, mangrove expansion is likely to have a negative impact on *Callinectes* populations. *Callinectes* are highly connected species within estuarine food webs (McCann et al. 2017); thus, diminished habitat quality for *Callinectes* with climate-driven wetland shifts is likely representative of changing conditions and cascading impacts for the broader estuarine macrofauna community (Scheffel et al. 2017). Beyond this system, these findings shed light on the habitat attributes that shape *Callinectes* habitat use. Their response to physical structure in the field, and corresponding results in the laboratory (see the Supplement), indicates that shifts between habitats with differing structural attributes should be safely considered a change in habitat quality, especially in terms of survival. Thus, the displacement of one foundation species by another can alter habitat quality and availability without a net loss of structured habitat. Such shifts should be evaluated so that differences in quality can be taken into consideration when characterizing habitat availability and developing fisheries management plans.

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