Engineering or food? mechanisms of facilitation by a habitat-forming invasive seaweed

Jeffrey T. Wright,[1,4] James E. Byers,[2] Jayna L. DeVore,[2,5] and Erik E. Sotka[3]

[1]*National Centre for Marine Conservation and Resource Sustainability, Australian Maritime College, University of Tasmania, P.O. Box 986, Launceston 7250 Australia*
[2]*Odum School of Ecology, University of Georgia, Athens, Georgia 30602 USA*
[3]*Grice Marine Laboratory and Department of Biology, College of Charleston, 205 Fort Johnson Road, Charleston, South Carolina 29412 USA*

Abstract. Nonnative species that form novel habitats strongly affect ecosystem processes. The effects of these ecosystem engineers can be both positive and negative but the mechanisms behind their effects are not well described. In this study we determined the relative importance of three main mechanisms by which invasive ecosystem engineers can facilitate native fauna. The engineer may provide new physical structure that reduces harsh abiotic conditions or gives refuge from predation (both engineering mechanisms), or provide a new profitable food resource (a trophic mechanism). The invasive seaweed *Gracilaria vermiculophylla* is a novel addition to estuarine intertidal mudflats of the southeastern United States. The epifaunal amphipod *Gammarus mucronatus* is up to 100 times more abundant on *Gracilaria*-invaded mudflats compared to uninvaded mudflats. Feeding assays, a survivorship experiment and stable isotope analysis demonstrated that *Gammarus* consumes little *Gracilaria* and cannot survive on *Gracilaria* alone. However, the structural engineering effects of *Gracilaria* greatly enhanced the survivorship of *Gammarus* in the presence of predators during high tide and when exposed to harsh abiotic conditions during low tide. Our results demonstrate that invasive ecosystem engineers can dramatically affect the distribution and abundance of native species by providing a novel protective structure.

Key words: *amphipods; ecosystem engineering; facilitation; feeding;* Gammarus mucronatus; Gracilaria vermiculophylla; *nonnative species;* Spartina alterniflora.

Introduction

Invasive species that form novel habitat often have large effects on ecosystems (Parker et al. 1999, Crooks 2002). These ecosystem engineers add physical structure, alter the abiotic environment, and change food webs (Jones et al. 1997, Hastings et al. 2007) and often these changes negatively affect native species (Crooks 2002, Levine et al. 2003). However, where the invasive species adds novel structure to ecosystems, positive effects on native species are frequently observed (Crooks 2002). In particular, invasive marine ecosystem engineers that colonize substrata with little aboveground structure, such as bare rock or sediment, often contain diverse epifaunal assemblages (Castilla et al. 2004, Byers et al. 2012), but there is little known about the relative importance of mechanisms that determine the facilitation.

Invasive ecosystem engineers can facilitate associated fauna via alterations to resource availability or by modifying abiotic conditions. Changes in resource availability occur when the invasive species provides a new food source for native species (Parker et al. 2006) including detritivores (Levin et al. 2006, Bradford et al. 2012). In the case of invasive seaweeds, small marine herbivores (mesograzers) are frequently a large component of invertebrate assemblages (Wikström and Kautsky 2004, Byers et al. 2012), but often consume less of the invasive species compared to native algae (Gollan and Wright 2006, Hammann et al. 2013). Although there are several engineering mechanisms by which invasive ecosystem engineers can facilitate native consumers (Crooks 2002), two are likely to be particularly important in the marine intertidal. First, the structure provided by native intertidal engineers reduces abiotic stresses for associated species (disturbance by waves, air temperature, and evaporation rates), which facilitates plant (Bruno 2000) and animal (Bertness et al. 1999) communities. Second, engineered structure provides a refuge from predation for small marine invertebrates, such as amphipods (Stoner 1982, Duffy and Hay 1994). Invasive marine ecosystem engineers have similar effects (Gribben and Wright 2006, Neira et al. 2006). Overall, although a number of studies have identified trophic and engineering mechanisms by which invasive ecosystem engineers facilitate native fauna, few have explicitly

Reports

distinguished between the different mechanisms in either marine or terrestrial systems.

The invasive Japanese seaweed *Gracilaria vermiculophylla* (hereafter *Gracilaria*), has established on both coasts of North America and northern Europe (Nyberg et al. 2009, Thomsen et al. 2009, Byers et al. 2012). In the southeastern United States (South Carolina and Georgia), *Gracilaria* is a novel addition to estuaries where the vegetation has historically been dominated by the salt marsh angiosperm *Spartina alterniflora* (hereafter *Spartina*) and its detrital input. With high turbidity and little substrate for seaweed attachment, these estuaries were mostly devoid of macroalgae prior to the invasion of *Gracilaria*. On mudflats in these estuaries, *Gracilaria* is now commonly found attached to the tube-building worm, *Diopatra cuprea* (Polychaeta: Diopatridae), and as drift, and its biomass reaches up to 1 kg/m^2 (Byers et al. 2012). Prior to the *Gracilaria* invasion, the microphytobenthos was the only source of primary productivity on the mudflat.

The addition of this large amount of algal tissue to these homogenous mudflats appears to be having dramatic effects on the community. Small invertebrates including amphipods, gastropods, shrimp, and crabs are abundant on *Gracilaria* (Nyberg et al. 2009, Thomsen et al. 2009, Byers et al. 2012) but it remains unclear whether these invertebrates are responding to *Gracilaria* as a source of food, protective structure or an abiotic ameliorator. In Europe, mesograzers generally eat only small amounts of invasive *Gracilaria* (Nejrup et al. 2012, Hammann et al. 2013).

Our overall aim was to determine the relative importance of three main mechanisms by which an invasive ecosystem engineer facilitates its associated faunal community. Initially, we surveyed amphipods on *Gracilaria* vs. other benthic macrophytes on mudflats and in the salt marsh. Next we determined habitat selection by the numerically dominant mesograzer in the system (the omnivorous amphipod *Gammarus mucronatus*, family Gammaridae; hereafter *Gammarus*) for live *Gracilaria* vs. bare mudflat during high and low tide (submersion and emersion, respectively). Then, to understand the mechanisms promoting the high association of *Gammarus* with *Gracilaria* that we observed, we determined (1) the use of *Gracilaria* as a food source by *Gammarus* using laboratory feeding and survivorship experiments and a stable isotope survey, and (2) structural engineering effects of *Gracilaria* on amphipod survivorship at low tide via desiccation-resistance effects and at high tide via predation-refuge effects.

MATERIALS AND METHODS

Species and study system

Our study was done in the Wilmington River and Wassaw Sound near Savannah, Georgia, USA, in summer 2012. Like much of the Atlantic coast of the southern United States, this estuary is dominated by the salt marsh grass *Spartina alterniflora*, *Crassostrea virgi-*

nica oyster reefs, and mudflats on which *Gracilaria* is becoming increasingly common (Byers et al. 2012; see Plate 1). Air temperatures on these intertidal mudflats in summer can reach >40°C while summer water temperatures reach >30°C. *Gammarus* is an abundant, mobile omnivore in this region (Cruz-Rivera and Hay 2000, Parker et al. 2001).

Distribution patterns and habitat selection by Gammarus

Patterns of amphipod abundance in the mudflat and saltmarsh were determined at low tide at three locations. Quadrats (0.5 × 0.5 m) were randomly placed in both habitats and all live algae and *Spartina* detritus was collected and weighed, and amphipod abundance on different hosts determined. Habitat selection by *Gammarus* for invaded and uninvaded patches on mudflats was determined by measuring immigration into experimentally out-planted *Gracilaria* or bare sediment at both high and low tide. Distribution patterns and habitat selection were both analyzed with generalized linear models (GLMs) in an analysis of deviance framework, followed by multiple comparisons tests. Significance was tested against an *F* distribution (Crawley 2007). We used R 2.12.1 (R Development Core Team 2009) for all analyses. See Appendix A for full detail of these methods.

The use of Gracilaria as a food resource by Gammarus

Previously *Gammarus* has been shown to consume filamentous red and green algae including *Enteromorpha* (now *Ulva*), seagrass detritus, and animal matter (Zimmerman et al. 1979, Duffy and Hay 1994, Cruz-Rivera and Hay 2000). To determine whether *Gammarus* was using *Gracilaria* as a food resource, we fed *Gammarus* the two abundant mudflat macrophytes (live *Gracilaria* and *Spartina* detritus) in choice (feeding preference) and no-choice (feeding rate) experiments in the lab. Each experiment ran for 72 hours and feeding preference and feeding rates were determined relative to autogenic controls following Peterson and Renaud (1989). See Appendix B for additional methodological detail.

We used stable isotope analysis to determine whether field-collected *Gammarus* derived trophic resources from *Gracilaria*. *Gammarus* and potential resources were sampled from Tybee Cut in January 2013. We haphazardly collected replicate pieces of live *Gracilaria*, *Spartina* detritus, and scrapings of the surface sediment (to ~3 mm) from the mudflat at spatial intervals >5 m, as well as live *Spartina* plants (<20 cm height, clipped at base) from the adjacent marsh. Sediment values only indirectly represent the isotopic ratios of potential trophic resources available on the mudflat surface (Gratton and Denno 2006), because benthic microalgae, bacteria, phytoplankton, and decaying plant material are all likely to be represented in the microphytobenthos on the surface sediment, and consumers may select between them. *Spartina* and *Gracilaria* samples were

Reports

PLATE 1.   Mudflat with extensive cover of *Gracilaria vermiculophylla* near Savannah, Georgia, USA. Photo credit: J. E. Byers.

rinsed prior to processing. *Gammarus* were collected from *Gracilaria* at the same time and held in seawater for 48 h to allow for gut evacuation prior to freezing at −20°C. Samples were processed and analyzed for carbon and nitrogen isotope ratios as outlined in Appendix B.

The survivorship of *Gammarus* was compared on four diets: live *Gracilaria*, *Spartina* detritus, sediment, and no food over 28 days. This experiment was done in 45 mm diameter × 10 mm high petri dishes with one *Gammarus* per replicate ($N = 20$ per treatment). *Gammarus* survivorship in each treatment was recorded every three to four days and survivorship analyzed using log rank tests (Hutchings et al. 1991). See Appendix B for full details.

Structural engineering effects of Gracilaria *on amphipod survivorship*

To test whether *Gracilaria* increased amphipod survivorship while exposed at low tide on the mudflat, we placed amphipods into petri dishes containing mudflat sediment in the presence and absence of *Gracilaria* (8 g wet mass) and transplanted the petri dishes onto the mudflat for 1 and 3 hours ($N = 5$ amphipods per petri dish and $N = 5$ petri dishes per treatment for each time period). After each time period, petri dishes were collected and amphipod survivorship determined. Differences in amphipod survivorship between *Gracilaria* (presence/absence) and time (1 and 3 hours) were determined using a GLM in an analysis-

of-deviance framework (Crawley 2007). Loss of water from the sediment in petri dishes was measured and differences between treatments determined with a two-factor ANOVA (*Gracilaria* × time). Temperature of the mudflat surface with and without *Gracilaria* ($N = 8$ of each) was measured nearby (to avoid disturbing the sediment and amphipods in the petri dishes) and differences determined with a *t* test. Detailed methods for this experiment are in Appendix C.

We determined the protective role of *Gracilaria* in reducing predation on amphipods by two common predators in this system, shrimp *Palaemonetes vulgaris* and Panopeid mud crabs, predominately *Europanopeus depressus*, but including a few *Panopeus herbstii* and *Dyspanopeus sayi*. Separate experiments for each predator used the same design: predator presence/absence crossed with *Gracilaria* presence/absence with experiments done in closed 6.15-L tubs ($N = 5$ per treatment) that were placed into large (~1000 L) outdoor flow-through tanks. Experiments ran for 72 hours, after which we used GLMs to determine differences in survivorship between *Gracilaria* (presence/absence) and predator (presence/absence). Following the GLMs, we used multiple comparison tests done within the *Gracilaria* x predator interaction using the multcomp package in R 2.12.1 (Hothorn et al. 2008) to determine whether survivorship of amphipods differed between treatments with and without *Gracilaria* when predators were present. See Appendix C for detailed methods.
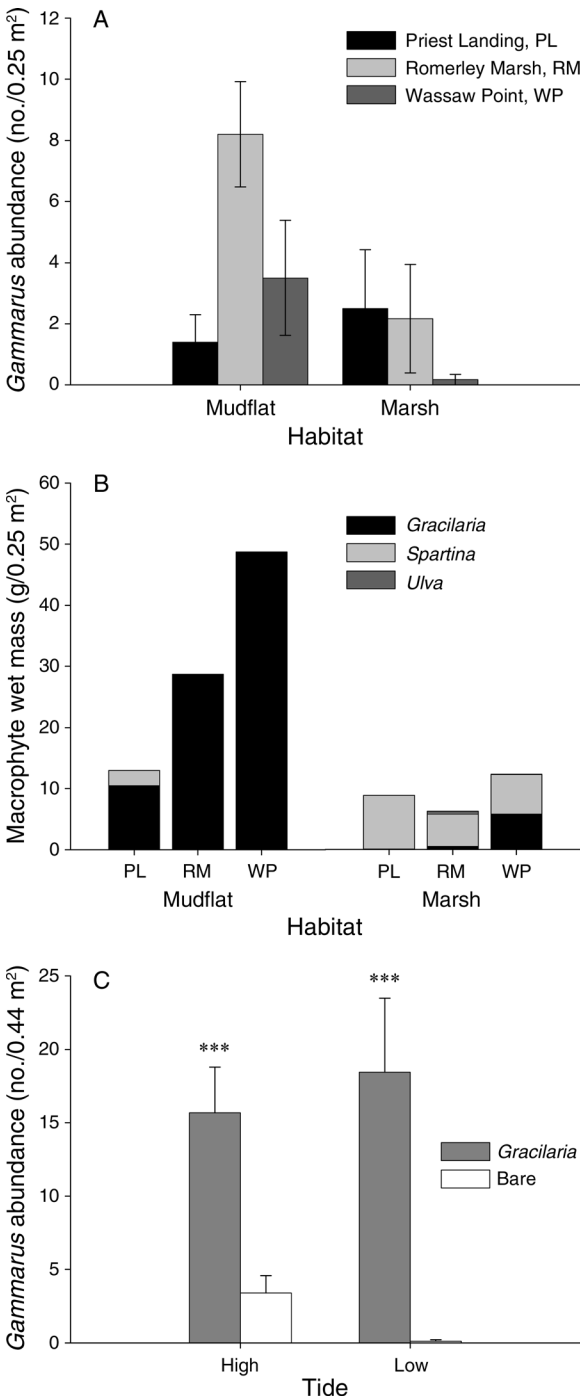
Reports

FIG. 1. (A) Abundance (mean ± SE) of *Gammarus* at low tide on the mudflat (*N* = 10 quadrats) and in the marsh (*N* = 6 quadrats), pooled across available macrophyte habitats in each quadrat at three sites. Results of multiple comparisons tests (Tukey's α < 0.05) for habitat, mudflat > marsh; for site, Romerley Marsh > Wassaw Pt. = Priest Landing. (B) Biomass (mean only, SE not shown for clarity) of available macrophyte habitats for *Gammarus* at low tide on the mudflat (*N* = 10 quadrats) and in the marsh (*N* = 6 quadrats) at three sites. (C) Habitat selection (mean ± SE) of *Gammarus* on the mudflat in the presence and absence of experimentally deployed *Gracilaria* at high and low tide (*N* = 18 plots, pooled across four sites).

RESULTS

Distribution patterns and habitat selection by Gammarus

Gammarus was significantly more abundant on the mudflat, where *Gracilaria* made up 97% of macrophyte biomass (pooled across locations) than on the marsh, where *Spartina* and *Gracilaria* made up 73% and 25% of the biomass, respectively ($F_{1,44}$ = 6.470, P = 0.015; Fig. 1A and B). On the mudflat, *Gammarus* showed a strong habitat preference for *Gracilaria* over bare mud when surveyed at both high ($F_{1,31}$ = 39.706, P < 0.001) and low ($F_{1,31}$ = 76.446, P < 0.001) tide (Fig. 1C). *Gammarus* abundance also differed among locations at both high tide ($F_{3,32}$ = 12.077, P < 0.001) and low tide ($F_{3,32}$ = 12.201, P < 0.001; Appendix A: Table A1).

The use of Gracilaria *as a food resource by* Gammarus

In the no-choice experiment, *Gammarus* consumed more *Spartina* detritus than live *Gracilaria* but there was no significant difference in feeding rate (the diet × amphipod presence/absence interaction was marginally nonsignificant, $F_{1,40}$ = 3.202, P = 0.081, Fig. 2A). In the choice experiment, *Gammarus* consumed significantly more *Spartina* detritus than live *Gracilaria* (t = −2.034, df = 34, P = 0.049).

Carbon and nitrogen isotope ratios indicated *Gammarus* does not utilize *Gracilaria* as a trophic resource (Fig. 2B). Trophic fractionation of ^{13}C is generally minimal (~0.4% [Post 2002]) and closely approximates the difference between *Spartina* and *Gammarus* (0.34%), whereas the difference between *Gammarus* and *Gracilaria* (4.66%) greatly exceeds this value, precluding *Gracilaria* as a major trophic resource. Additionally, δ^{15}N values of *Gammarus* were indistinguishable from those of *Gracilaria*, making *Spartina* (3.14% enrichment) or sediment (2.18% enrichment) more likely resources for *Gammarus*.

Survivorship of *Gammarus* was lower on *Gracilaria* than on *Spartina* detritus or sediment by day 8 (χ^2 = 17.86, df = 3, P < 0.001) and, by day 14, all *Gammarus* fed *Gracilaria* were dead (Fig. 2C). All *Gammarus* with no food were dead by day 8. In contrast, 40% of *Gammarus* with sediment and 20% of *Gammarus* fed *Spartina* detritus survived to day 28 and there was no significant difference in survivorship between those two food sources (Fig. 2C; χ^2 = 3.43, df = 1, P = 0.064). Survivorship of *Gammarus* on *Gracilaria* was only higher than the no-food controls on day 5 (χ^2 = 17.030, df = 1, P < 0.001).

Structural engineering effects of Gracilaria *on amphipod survivorship*

Amphipod survivorship at low tide was greater with *Gracilaria* than on bare mudflat ($F_{1,18}$ = 42.205, P <

←

Asterisks indicate P values from GLMs comparing between *Gracilaria* and bare mudflat at each tide: *** P < 0.001.

0.001; Appendix C: Table C1). After 1 hour exposure, amphipod survivorship in the presence of *Gracilaria* was 84.0% ± 7.5% (mean ± SE) compared to 24.0% ± 11.7% with no *Gracilaria*. After 3 hours exposure, amphipod survivorship in the presence of *Gracilaria* was 88.0% ± 8.0% compared to 4.0% ± 4.0% with no *Gracilaria*. There was no difference in amphipod survivorship between 1 and 3 hours exposure in the presence of *Gracilaria* ($F_{1,17} = 0.985$, $P = 0.336$; Appendix C: Table C1). During the experiment, amphipods on bare mudflats were exposed to sediments with less water and higher temperatures than amphipods with *Gracilaria*. After 1 hour, there was no difference in water loss from the sediment with *Gracilaria* (19.2% ± 1.3%) vs. without *Gracilaria* (18.3% ± 1.1%) but, after 3 hours, there was significantly greater loss of water without *Gracilaria* (37.2% ± 1.1%) vs. with *Gracilaria* (30.0% ± 2.0%; significant *Gracilaria* presence/absence × time interaction, $F_{1,16} = 8.315$, $P = 0.011$, Tukey's α < 0.05). Sediment temperature was slightly lower beneath *Gracilaria* (33.6° ± 0.2°C) compared to adjacent areas without *Gracilaria* (34.2° ± 0.4°C, $N = 8$, $t = 3.416$, $P = 0.011$, paired *t* test).

Gracilaria increased the survivorship of amphipods in the presence of the predatory shrimp *Palaemonetes* and Panopeid mud crabs. For *Palaemonetes*, there was a significant interaction between *Gracilaria* and predator presence ($F_{1,14} = 9.789$, $P = 0.007$; Appendix C: Table C1); after 72 hours there were no amphipods alive in tubs with *Palaemonetes* lacking *Gracilaria* compared to 53.8% ± 10.2% survivorship in tubs with *Palaemonetes* and *Gracilaria* (Tukey's α < 0.05). For Panopeid mud crabs, this interaction was marginally nonsignificant ($F_{1,16} = 4.049$, $P = 0.061$), although amphipod survivorship in the presence of Panopeid mud crabs was more than three times higher in the tubs with *Gracilaria* (52.4% ± 5.4%) compared to tubs lacking *Gracilaria* (14.0% ± 1.9%, Tukey's α < 0.05). In both experiments, the positive effect of *Gracilaria* only occurred when predators were present, such that there was no effect of *Gracilaria* on amphipod survival during submersion in the absence of predators (Tukey's α > 0.05, *Palaemonetes* experiment, with *Gracilaria*, 91.0% ± 4.6% vs. without *Gracilaria*, 85.0% ± 9.1%; Panopeid mud crab experiment, with *Gracilaria*, 76.0% ± 8.3% vs. without *Gracilaria*, 62.0% ± 6.4%).

DISCUSSION

Although invasive ecosystem engineers often facilitate native species, the relative importance of mechanisms underpinning that facilitation is not well understood. In particular, small consumers could switch to invasive hosts because they are a novel food source; the host protects them from predators and harsh abiotic conditions, or both. We have shown that one of the most abundant benthic amphipods in the southeastern United States, *Gammarus mucronatus*, is facilitated by the invasive *Gracilaria*, with densities 5–100 times higher
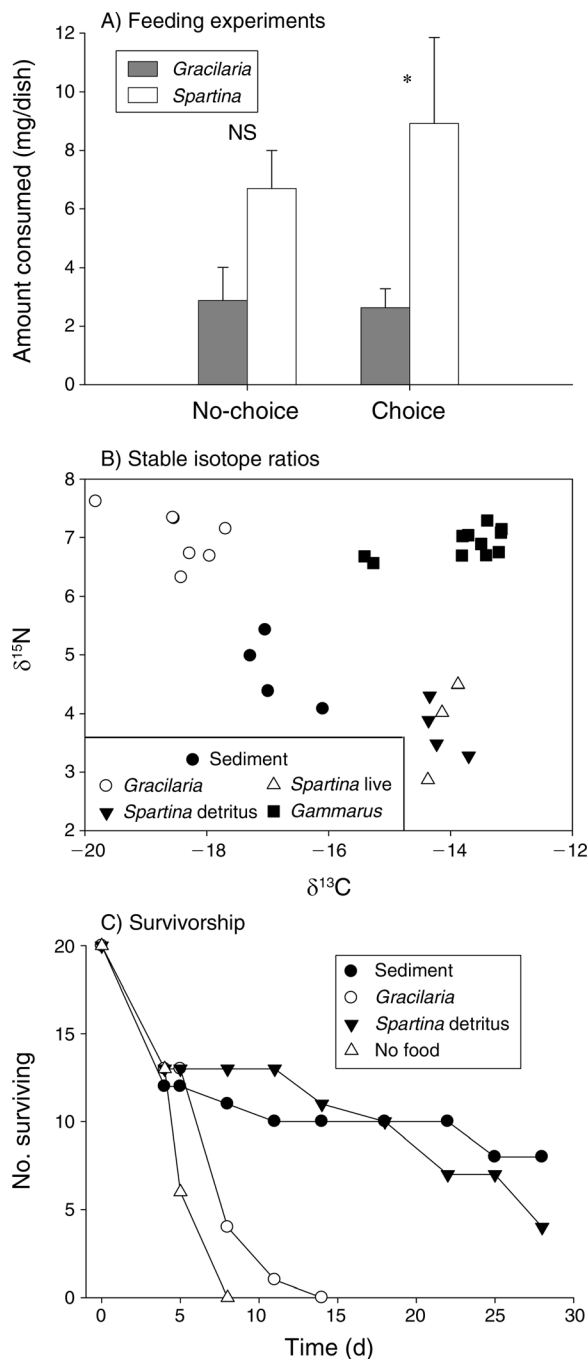

FIG. 2. (A) No-choice ($N = 11$), and choice ($N = 20$) feeding experiments for *Gammarus* on live *Gracilaria* and *Spartina* detritus. Plots show the mean (±SE) of wet mass loss over 72 h after adjustment for autogenic changes in food in treatments without amphipods. Asterisks indicate *P* values from *t* tests following Peterson and Renaud (1989): * $P < 0.05$; NS, not significant. (B) Carbon and nitrogen isotope ratios of *Gammarus*, live *Gracilaria*, *Spartina* detritus, live *Spartina*, and sediment from the mudflat surface. (C) Survivorship of *Gammarus* on *Gracilaria*, *Spartina* detritus, sediment from the mudflat surface, and a no-food control.

Reports

on mudflats with *Gracilaria* compared to uninvaded mudflats. Although *Gracilaria* potentially represents a novel food resource to native consumers, it is not an important food for *Gammarus*. Indeed, amphipods recruit to structural mimics of *Gracilaria* that have no nutritional value, albeit at lower levels than they recruit to *Gracilaria* itself (Byers et al. 2012). Instead, the high abundance of *Gammarus* on *Gracilaria*-dominated mudflats is likely maintained by reductions in predation mortality during high tide and abiotic stress during low tide.

Habitat structure is an important mediator of predator–prey interactions (Grabowski 2004) and the lower predation on *Gammarus* in the presence of *Gracilaria* is likely due to *Gracilaria* structure reducing predator–prey encounter rates or predator foraging efficiency. In the laboratory, we observed both *Palaemonetes* and Panopeid mud crabs actively pursuing and consuming *Gammarus*, particularly when *Gracilaria* was absent. Native habitat-forming seaweed and seagrass reduce predation by fish on herbivorous amphipods, particularly mobile species like *Gammarus*, which are at a higher risk of predation than more sedentary nest-building species (Van Dolah 1978, Stoner 1982, Duffy and Hay 1994). Moreover, *Gracilaria*'s chemical defenses (Nylund et al. 2011) may deter omnivorous predators such as fish and reduce predation on amphipods in *Gracilaria* (Duffy and Hay 1994). In fact, lower predation rates on epifauna within the structure of chemically defended invasive seaweed are known across multiple taxa, including bivalve recruits and herbivorous isopods (Gribben and Wright 2006, Enge et al. 2013).

The role of canopy-forming seaweed in ameliorating harsh abiotic conditions and facilitating understory invertebrates on rocky shores is well established (Bertness et al. 1999). On the mudflats of coastal Georgia, temperatures regularly exceed 35°C and the *Gracilaria* canopy massively reduced mortality of *Gammarus* when exposed at low tide. Thus, in addition to the predator refuge effect at high tide, *Gracilaria* likely reduces desiccation and heat stress for amphipods at low tide, demonstrating a second mechanism of facilitation by this invasive seaweed that occurs at a different time in the tidal cycle. Although *Gracilaria* is typically only exposed for ~3–4 hours at low tide, the strong survivorship benefit of *Gracilaria* after 3 hours exposure suggests survivorship over longer tidal periods is likely.

Given these survivorship results and that *Gammarus* were virtually absent from bare mudflat at low tide, it is likely they seek out structural refugia on the mudflat to avoid the harsh abiotic conditions. The low value of *Gracilaria* as a food emphasizes its importance as a structural, protective habitat for *Gammarus*. Indeed, *Gracilaria* provides virtually all aboveground habitat available for colonization by *Gammarus* on the mudflats with virtually no vegetative structure on these mudflats prior to *Gracilaria* invasion. Only small

amounts of *Spartina* detritus occur on the mudflat because most *Spartina* wrack is deposited at the high-tide mark (where *Spartina* habitat occurs). *Ulva* is found in small quantities on the mudflat only during winter and few amphipods are present on *Diopatra* tubes themselves.

Previous feeding experiments showed *Gammarus mucronatus* consumed *Ulva* at higher rates compared to other seaweeds, including the native *Gracilaria tikvahiae* (Duffy and Hay 1994, Cruz-Rivera and Hay 2003), and consumed more seagrass detritus and epiphytic filamentous algae compared to other seaweeds (Zimmerman et al. 1979). Similarly, in northern Europe, *Gammarus locusta* eats relatively little invasive *Gracilaria* compared to native seaweeds, particularly *Ulva* (Nejrup et al. 2012). Our experiments indicate that *Gammarus* will eat some *Gracilaria*, but cannot survive when isolated with it. Consistent with this, our isotope data show that natural populations of *Gammarus* consume little *Gracilaria*, but instead favor a combination of *Spartina* detritus, microalgae, or periphyton on the sediment surface or on *Gracilaria*. The low feeding of *Gammarus* on *Gracilaria* could reflect the alga's chemical defenses (Nylund et al. 2011). Our survivorship experiment showed that a diet comprised of either *Spartina* detritus or sediment alone increased survivorship relative to *Gracilaria*. At first glance, the low fitness on *Gracilaria* was surprising given that *Spartina* detritus is nutritionally poorer than *Gracilaria*, but combining *Spartina* detritus and microalgae in its diet may enhance fitness for *Gammarus* (Cruz-Rivera and Hay 2000, Parker et al. 2008). Moreover, fungi and bacteria may colonize *Spartina* detritus (Buchan et al. 2003) potentially enhancing its nutritional value for *Gammarus*. As *Gammarus* is relatively mobile (Duffy and Hay 1994), it will frequently come into contact with food of variable quality and it can maintain fitness as long as it consumes an adequate amount of high-quality food (Cruz-Rivera and Hay 2000).

The generally higher density of *Gammarus* on the mudflat compared to the saltmarsh and the near absence of *Gammarus* on bare mud compared to *Gracilaria*, suggests that *Gracilaria*'s invasion onto mudflats may have allowed *Gammarus* to move out of the low marsh to utilize the mudflat. *Gammarus* was found in the marsh on *Spartina* wrack and *Ulva*, suggesting it occurred there prior to *Gracilaria* invasion although, we have no information on *Gammarus* abundance on these mudflats or in the saltmarsh before *Gracilaria* invasion. The substantially lower tidal elevation of the mudflat compared to the marsh may be advantageous for *Gammarus* by reducing the amount of time they are exposed to harsh abiotic conditions at low tide. In addition to structural effects, *Gracilaria* provides a massive increase in primary productivity on these mudflats. However, the lack of feeding on *Gracilaria* by the most abundant grazing epifaunal species associated with it suggests that secondary productivity is

enhanced indirectly via structural provisioning. Our experiments indicate *Gracilaria* reduces *Gammarus* mortality from predation and harsh abiotic conditions but it is also possible that *Gracilaria* facilitates microalgae (either on the sediment or on *Gracilaria* itself), which *Gammarus* then feeds on.

Ecosystem engineers that create habitat are increasingly being considered as influential in determining community organization (Crooks 2002, Hastings et al. 2007). *Gracilaria* is making major changes to estuarine mudflats in southeastern USA that were historically devoid of macroalgae by providing a novel habitat that attracts and protects native epifauna. Although the abiotic changes caused by invasive ecosystem engineers can negatively impact associated species, in structurally depauperate systems, abiotic changes caused by the addition of novel structure may dampen harsh environment conditions allowing community wide facilitation and enhancing overall productivity.

Literature Cited

Bertness, M. D., G. H. Leonard, J. M. Levine, P. R. Schmidt, and A. O. Ingraham. 1999. Testing the relative contribution of positive and negative interactions in rocky intertidal communities. Ecology 80:2711–2726.

Bradford, M. A., M. S. Strickland, J. L. DeVore, and J. C. Maerz. 2012. Root carbon flow from an invasive plant to belowground foodwebs. Plant and Soil 359:233–244.

Bruno, J. F. 2000. Facilitation of cobble beach plant communities through habitat modification by *Spartina alterniflora*. Ecology 81:1179–1192.

Buchan, A., S. Y. Newell, M. Butler, E. J. Biers, and M. A. Moran. 2003. Dynamics of bacterial and fungal communities on decaying salt marsh grass. Applied and Environmental Microbiology 69:6676–6687.

Byers, J. E., P. E. Gribben, C. Yeager, and E. E. Sotka. 2012. Impacts of an abundant introduced ecosystem engineer within mudflats of the southeastern US coast. Biological Invasions 14:2587–2600.

Castilla, J. C., N. A. Lagos, and M. Cerda. 2004. Marine ecosystem engineering by the alien ascidian *Pyura praeputialis* on a mid-intertidal rocky shore. Marine Ecology Progress Series 268:119–130.

Crawley, M. J. 2007. The R book. First edition. John Wiley, Chichester, UK.

Crooks, J. A. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97:153–166.

Cruz-Rivera, E., and M. E. Hay. 2000. The effects of diet mixing on consumer fitness: macroalgae, epiphytes, and animal matter as food for marine amphipods. Oecologia 123:252–264.

Cruz-Rivera, E., and M. E. Hay. 2003. Prey nutritional quality interacts with chemical defenses to affect consumer feeding and fitness. Ecological Monographs 73:483–506.

Duffy, J. E., and M. E. Hay. 1994. Herbivore resistance to seaweed chemical defense: the roles of mobility and predation risk. Ecology 75:1304–1319.

Enge, S., G. M. Nylund, and H. Pavia. 2013. Native generalist herbivores promote invasion of a chemically defended seaweed via refuge-mediated apparent competition. Ecology Letters 16:487–492.

Gollan, J. R., and J. T. Wright. 2006. Limited grazing pressure by native herbivores on the invasive seaweed *Caulerpa taxifolia* in a temperate Australian estuary. Marine and Freshwater Research 57:685–694.

Grabowski, J. H. 2004. Habitat complexity disrupts predator–prey interactions but not the trophic cascade on oyster reefs. Ecology 85:995–1004.

Gratton, C., and R. F. Denno. 2006. Arthropod food web restoration following removal of an invasive wetland plant. Ecological Applications 16:622–631.

Gribben, P. E., and J. T. Wright. 2006. Invasive seaweed enhances recruitment of a native bivalve: roles of refuge from predation and the habitat choice of recruits. Marine Ecology Progress Series 318:177–185.

Hammann, M., G. Wang, E. Rickert, S. M. Boo, and F. Weinberger. 2013. Invasion success of the seaweed *Gracilaria vermiculophylla* correlates with low palatability. Marine Ecology Progress Series 486:93–103.

Hastings, A., J. E. Byers, J. A. Crooks, K. Cuddington, C. G. Jones, J. G. Lambrinos, T. S. Talley, and W. G. Wilson. 2007. Ecosystem engineering in space and time. Ecology Letters 10:153–164.

Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models. Biometrical Journal 50:346–363.

Hutchings, M. J., K. D. Booth, and S. Waite. 1991. Comparison of survivorship by the logrank test: criticisms and alternatives. Ecology 72:2290–2293.

Jones, C. G., J. H. Lawton, and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946–1957.

Levin, L. A., C. Neira, and E. D. Grosholz. 2006. Invasive cordgrass modifies wetland trophic function. Ecology 87:419–432.

Levine, J. M., M. Vila, C. M. Antonio, J. S. Dukes, K. Grigulis, and S. Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society of London B 270:775–781.

Neira, C., E. D. Grosholz, L. A. Levin, and R. Blake. 2006. Mechanisms generating modification of benthos following tidal flat invasion by a *Spartina* hybrid. Ecological Applications 16:1391–1404.

Nejrup, L. B., M. F. Pedersen, and J. Vinzent. 2012. Grazer avoidance may explain the invasiveness of the red alga *Gracilaria vermiculophylla* in Scandinavian waters. Marine Biology 159:1703–1712.

Nyberg, C. D., M. S. Thomsen, and I. Wallentinus. 2009. Flora and fauna associated with the introduced red alga *Gracilaria vermiculophylla*. European Journal of Phycology 44:395–403.

Nylund, G. M., F. Weinberger, M. Rempt, and G. Pohnert. 2011. Metabolomic assessment of induced and activated chemical defence in the invasive red alga *Gracilaria vermiculophylla*. PLoS ONE 6:e29359.

Parker, I. M., D. Simberloff, W. Lonsdale, K. Goodell, M. Wonham, P. Kareiva, M. Williamson, B. Von Holle, P. Moyle, and J. Byers. 1999. Impact: toward a framework for understanding the ecological effects of invaders. Biological Invasions 1:3–19.

Parker, J. D., D. E. Burkepile, and M. E. Hay. 2006. Opposing effects of native and exotic herbivores on plant invasions. Science 311:1459–1461.

Parker, J. D., J. E. Duffy, and R. J. Orth. 2001. Plant species diversity and composition: experimental effects on marine

Reports

epifaunal assemblages. Marine Ecology Progress Series 224: 55–67.

Parker, J. D., J. P. Montoya, and M. E. Hay. 2008. A specialist detritivore links *Spartina alterniflora* to salt marsh food webs. Marine Ecology Progress Series 364:87–95.

Peterson, C. H., and P. E. Renaud. 1989. Analysis of feeding preference experiments. Oecologia 80:82–86.

Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83: 703–718.

R Development Core Team. 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org

Stoner, A. W. 1982. The influence of benthic macrophytes on the foraging behavior of pinfish, *Lagodon rhomboides*

(Linnaeus). Journal of Experimental Marine Biology and Ecology 58:271–284.

Thomsen, M. S., K. McGlathery, A. Schwarzschild, and B. Silliman. 2009. Distribution and ecological role of the non-native macroalga *Gracilaria vermiculophylla* in Virginia salt marshes. Biological Invasions 11:2303–2316.

Van Dolah, R. F. 1978. Factors regulating the distribution and population dynamics of the amphipod *Gammarus palustris* in an intertidal salt marsh community. Ecological Monographs 48:191–217.

Wikström, S. A., and L. Kautsky. 2004. Invasion of a habitat-forming seaweed: effects on associated biota. Biological Invasions 6:141–150.

Zimmerman, R., R. Gibson, and J. Harrington. 1979. Herbivory and detritivory among gammaridean amphipods from a Florida seagrass community. Marine Biology 54:41–47.

SUPPLEMENTARY MATERIAL

Appendix A

Methods and generalized linear models (GLM) results for amphipod distribution and habitat selection (*Ecological Archives* E095-235-A1).

Appendix B

Detailed methods for the use of *Gracilaria* as a food resource by *Gammarus* (*Ecological Archives* E095-235-A2).

Appendix C

Detailed methods and GLM results for structural engineering effects of *Gracilaria* on amphipod survivorship (*Ecological Archives* E095-235-A3).

Reports