



Mixed effects of an introduced ecosystem engineer on the foraging behavior and habitat selection of predators

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Abstract. Invasive ecosystem engineers both positively and negatively affect their recipient ecosystems by generating novel habitats. Many studies have focused on alterations to ecosystem properties and to native species diversity and abundance caused by invasive engineers. However, relatively few studies have documented the extent to which behaviors of native species are affected. The red seaweed *Gracilaria vermiculophylla* (Rhodophyta) invaded estuaries of the southeastern United States within the last few decades and now provides abundant aboveground vegetative cover on intertidal mudflats that were historically devoid of seaweeds. We hypothesized that *G. vermiculophylla* would affect the foraging behavior of native shorebirds positively for birds that target seaweed-associated invertebrates or negatively for birds that target prey on or within the sediment now covered with seaweed. Visual surveys of mudflats >1 ha in size revealed that more shorebirds occurred on mudflats with *G. vermiculophylla* relative to mudflats without *G. vermiculophylla*. This increased density was consistent across 7 of 8 species, with the one exception being the semipalmated plover *Charadrius semipalmatus*. A regression-based analysis indicated that while algal presence predicted shorebird density, densities of some bird species depended on sediment composition and infaunal invertebrate densities. At smaller spatial scales (200 m² and <1 m²), experimental removals and additions of *G. vermiculophylla* and focal observations showed strong variation in behavioral response to *G. vermiculophylla* among bird species. Birds preferentially foraged in bare mud (e.g., *C. semipalmatus*), in *G. vermiculophylla* (e.g., *Arenaria interpres*), or displayed no preference for either habitat (e.g., *Tringa semipalmata*). Thus, while the presence of the invasive ecosystem engineer on a mudflat appeared to attract greater numbers of these predators, shorebird species differed in their behavioral responses at the smaller spatial scales that affect their foraging. Our research illuminates the need to account for species identity, individual behavior, and scale when predicting the impacts of invasive species on native communities.

Key words: ecosystem engineers; estuaries; foraging behavior; foundation species; habitat-modifying species; niche; non-native species; novel ecosystems; shorebirds; soft sediment.

INTRODUCTION

Invasive species are one of the leading threats to global and local biodiversity (Vitousek et al. 1996); yet, their effects are often nuanced, affecting native species both negatively and positively by altering resource availability and quality, trophic interactions, and disturbance regimes (e.g., Straube et al. 2009, Byers et al. 2010, Simberloff 2011, Simberloff et al. 2013, Pintor and Byers 2015). Invasive species can have particularly far-reaching effects if they are ecosystem engineers, organisms that directly or indirectly regulate the availability of resources through physical state changes within an ecosystem (Jones et al. 1994, 1997, Crooks 2002). Their control of food and habitat resources makes invasive ecosystem engineers fundamental determinants of the diversity and abundances of native species (e.g., Di Tomaso 1998, Grosholz et al. 2009, Villamagna and Murphy 2010, DeVore and Maerz 2014).

Ecosystem engineers can disproportionately affect community structure, as these organisms influence both bottom-up and top-down controls. The effects of an invasive ecosystem engineer may be even more conspicuous because the invasive engineer may exert mixed effects through a variety of mechanisms that can ultimately transform whole ecosystems as they settle into new equilibria (Byers et al. 2010). Despite the potential for negative consequences of invasive ecosystem engineers during system transformation, they can positively affect native community members through the generation of habitat (e.g., Gribben et al. 2013, DeVore and Maerz 2014, Wright et al. 2014). Furthermore, the relative contribution of negative and positive effects is dependent on the context in which the ecosystem engineer is introduced (Guy-Haim et al. 2018). For example, in southeastern Appalachian forests, the invasion of herbaceous understory communities by Japanese stilt grass (*Microstegium vimineum*) has mixed effects on some native community members. The increased habitat complexity reduces arthropod density (Simoa et al. 2010) on the forest floor, but increases habitat availability for predatory spiders (DeVore and Maerz 2014). Both effects reduce populations of amphibians (DeVore and Maerz 2014). Thus, the studies of community-level

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interactions are important when identifying the potential mixed effects of invasive ecosystem engineers.

Positive effects of invasive ecosystem engineers can result when the habitats that they provision are different in kind from the structure that is naturally available (Crooks 2002). For instance, novel ecosystem engineers may provide new habitat structure that shifts prey distributions to areas with greater structural complexity (Tanner 2011). In fact, a review of facilitation of native species by invasive species identified habitat modification, specifically the creation of novel habitat, as the most frequently cited mechanism for these facilitative interactions (Rodriguez 2006). Furthermore, the introduction of structure by an invasive species could be more pronounced if structure is a limiting factor in the community. Such alterations in habitat quality and subsequent bolstering of native species may have cascading effects on an ecosystem's trophic structure. For instance, zebra mussels, *Dreissena polymorpha*, which provide novel structure and refuge in the benthic zones of freshwater lakes, house exponentially greater numbers of invertebrates than *D. polymorpha*-free substrate (Bially and MacIsaac 2000, Rodriguez 2006, Sousa et al. 2009). The greater abundance of food items in the invaded areas has led to increased growth rates of benthic consumers (Thayer et al. 1997, Rodriguez 2006). Not only can habitat modification lead to changes in overall prey abundance, it can also cause predators to change their preferences for foraging habitat. For example, the invasive tubeworm, *Ficopomatus enigmaticus*, creates reef structures that attract greater densities of invertebrates and increases shorebird foraging in the novel habitat (Schwindt et al. 2001, Bruschetti et al. 2009). Such positive interactions are not necessarily the norm, and these interactions and subsequent impacts are likely to be highly dependent on scale, history of invasion, and local community dynamics (Jones et al. 1997).

Another consideration when assessing how an ecosystem engineer may influence a recipient environment is how resident species distinctively respond to novel structure. For example, native species with different ecological niches may perceive the environmental modifications by invasive ecosystem engineers differently, suggesting the possibility of mixed effects across a community (e.g., Crooks 1998). Pronounced alterations of species behaviors can in turn lead to shifts in species interaction strengths for fundamental processes, like predation. Because predator identity and diversity are known to determine trophic structure by altering behavior and abundances of lower trophic levels (Bruno and O'Connor 2005, O'Connor et al. 2008), predator species reacting differently to an invasive ecosystem engineer could create effects that cascade through the food web. Thus, when assessing the effect of an invasive ecosystem engineer on native communities, it is important to recognize that species and individuals may respond distinctively. Additionally, determining the effects of invasive species on multiple predator species could reveal whether niche differentiation or behavioral differences produce divergent responses among a suite of predators that utilize the same prey resources. Here, we examine the responses of multiple native species within the same trophic level to a ubiquitous introduced ecosystem engineer. Such comparisons may elucidate the degree of variation in overall response by the native community and may help to predict responses of

individual species based on their foraging ecology and ecological roles within the community.

Research system and questions

A recent ecosystem engineer invasion in the southeastern United States provides an opportunity to investigate the roles these species play in recipient communities, specifically their roles in the foraging patterns of multiple predator species within the same trophic level. *Gracilaria vermiculophylla*, a red seaweed from the coast of Japan, has invaded many coastal habitats in Europe and North America (Thomsen et al. 2009, Kim et al. 2010, Krueger-Hadfield et al. 2017). Since the early 2000s, the invasive seaweed has considerably altered estuaries of Georgia by creating novel habitat on the previously bare mudflats (Byers et al. 2012). This system was largely devoid of macroalgae due to high turbidity and lack of hard substrate for algal attachment. The alga is anchored on mudflats due to an association with native tube-building polychaete worms, *Diopatra cuprea*, that attach the alga to their tubes (Thomsen and McGlathery 2005, Berke 2012, Byers et al. 2012, Kollars et al. 2016). Increased habitat structure and more amenable abiotic conditions (reduced surface temperatures and desiccation stress during low tide) created by *G. vermiculophylla* have increased abundance of epifaunal invertebrates and shifted many of their distributions from bare mudflats to those colonized by the invasive seaweed (Byers et al. 2012, Wright et al. 2014, Bishop and Byers 2015).

In these estuaries, migratory shorebirds are important predators and are pivotal in regulating macroinvertebrate abundances (Schneider and Harrington 1981, Steinmetz et al. 2003). Mudflat ecosystems provide shorebirds with high quality, often preferred, foraging habitat (Burger et al. 1977, Lourenço et al. 2015). Furthermore, the estuaries of the southeastern United States serve as important stopover and over-wintering sites for many shorebird species that migrate between the Arctic and the tropics using the Atlantic Flyway. The most common shorebird species found in the southeast during the peak migratory season (April–May) are dunlin (*Calidris alpina*), semipalmated plover (*Charadrius semipalmatus*), western sandpiper (*Calidris mauri*), least sandpiper (*Calidris minutilla*), semipalmated sandpiper (*Calidris pusilla*), ruddy turnstone (*Arenaria interpres*), willet (*Tringa semipalmata*), black-bellied plover (*Pluvialis squatarola*), and short-billed dowitcher (*Limnodromus griseus*) (Tomkins 1965, Stinson 1980, Harrington 2008, Rose and Nol 2010; L. Haram, *personal observation*). Shorebirds form dense aggregations of mixed species that forage on intertidal mudflats during low tide. Niche differentiation in these aggregations is achieved in part because each species has distinct foraging strategies (visual, tactile, or mixed) and feeding morphologies (body and bill size and shape) to catch epifaunal, epibenthic, and/or infaunal invertebrates in estuarine systems (Mouritsen 1994, Nettleship 2000, Jehl et al. 2001, Elner et al. 2005; Nebel et al. 2005, Thomas et al. 2006, Nebel and Cooper 2008, Hicklin and Gratto-Trevor 2010, Rose and Nol 2010, Lowther et al. 2001, Nol and Blanken 2014, Poole et al. 2016).

Shorebird species and community composition are non-randomly distributed within estuarine habitats. The abundance, biomass, and availability of prey are crucial predictors of shorebird communities on intertidal mudflats (Dugan et al. 2003, Spruzen et al. 2008, VanDusen et al. 2012), with shorebirds known to forage in areas with greater prey availability (Fraser et al. 2010). Across microhabitats and entire mudflats, prey availability is constrained directly by abiotic factors, such as sediment composition and tidal cycle (Burger et al. 1977, VanDusen et al. 2012). The presence of vegetation on mudflats also influences shorebird distributions due to its effects on macroinvertebrate abundance and shorebird foraging efficiency. Increased benthic structure provided by submerged macrophytes, such as seaweeds, seagrasses, and reef-forming fauna, can increase macroinvertebrate abundances (Spruzen et al. 2008, Bruschetti et al. 2009), possibly leading to greater densities of birds utilizing invaded mudflats. Macrophytic wrack subsidies to low productivity beaches can also increase availability of prey items for shorebirds, with positive relationships observed between standing crop of wrack and shorebird abundances (Dugan et al. 2003). However, dense macrophyte coverage on a mudflat may inhibit shorebird foraging, likely through interference with tactile and visual detection of prey, smothering of resources, and alteration of prey species composition (Spruzen et al. 2008). Given these scenarios, the effect of an invasive habitat modifier on shorebird foraging could be mixed. Furthermore, the impact of an ecosystem engineer may differ among predator species, causing divergent, species-specific responses in foraging behavior and habitat selection.

Shorebirds present an optimal target for investigating the effects of invasive ecosystem engineers like *G. vermiculophylla* on predator foraging because shorebirds adjust to local conditions, feed opportunistically, and shift their prey preferences with season and local prey availability (Dierschke et al. 1999; Nettleship 2000, Jehl et al. 2001, Lowther et al. 2001, Nebel and Cooper 2008, Hicklin and Gratto-Trevor 2010, Mathot et al. 2010, Rose and Nol 2010, Poole et al. 2016). Through two observational studies and two complementary manipulative experiments at various spatial scales, we assessed how the novel physical structure of an invasive ecosystem engineer alters shorebird foraging in essential stopover habitat. We hypothesized that the presence of *G. vermiculophylla* would have significant effects on the density of shorebirds, with shorebirds preferring mudflats inhabited by the invasive engineer due to greater prey availability. However, we also hypothesized that alterations in foraging behavior would be species-specific depending on each species' niche type. Despite the potential for mixed effects, we expected net positive relationships between the invasive ecosystem engineer and shorebird density and foraging effort, given the higher epifauna abundance associated with *G. vermiculophylla*, shorebirds' opportunistic foraging during migration, and the limited physical impediment we expected the alga would present. We intended our multi-species perspective to elucidate the degree of uniformity (or lack thereof) in the behavioral responses of higher trophic levels to invasive ecosystem engineers.

METHODS

Large scale habitat selection survey

To determine what habitat type (*Gracilaria*-colonized or bare mudflats) was more attractive to shorebirds, we conducted shorebird density surveys across twelve mudflats in Wassaw Sound, Savannah, Georgia (31°56'18.8" N, 80°56'53.7" W): six mudflats with *G. vermiculophylla* and six mudflats without *G. vermiculophylla* (Appendix S1: Table S1). We selected sites based on size (>1 ha), continuity of substrate, and observer access. During tides below 0 m mean lower low water (MLLW) in daylight hours, we surveyed 500 m transects parallel to the water line for shorebird abundance and species composition at each site. Along the transect, we surveyed the entire width of the intertidal mudflat from the low tide line to its highest elevation, which was visually determined based on water level predictions, time of day, and biological zonation of *Spartina* cord grass or oyster reef. The location of the 500 m transect was selected using low tide images on Google Earth, and clear landscape features were used as end points for the transect. Surveys were done by boat (and in one instance by foot due to logistical issues) ~50 m away. Care was taken to not flush the flocks, and no apparent disturbance of shorebird activity was detected across survey sites. A captain maintained a slow, consistent speed while a trained observer counted birds using 16x50 Nikon 7247 Action binoculars. A single observer identified and counted shorebirds across sites to eliminate observer differences and minimize potential error. Small sandpiper species (*Calidris* spp.) (approximately <17 cm in length) were counted collectively as "Peeps" because the distance from the mudflats, speed of surveys, and winter plumage was not conducive to further identification. To standardize conditions between sites, we conducted surveys on days when weather was fair, with no precipitation and wind speed < 20 knots. We surveyed each mudflat twice from April 2, 2015 to May 17, 2015 (excluding two sites, House Creek and Little Tybee, that we surveyed once) for a total of 22 surveys; surveys were averaged for each site to reduce the effect of sampling date. Spring movement begins in March for these species, with their peak migrations through the southeastern United States occurring in April to early May (see descriptions in Warnock and Gill 1996, Nettleship 2000, Jehl et al. 2001, Lowther et al. 2001, Nebel and Cooper 2008, Hicklin and Gratto-Trevor 2010, Nol and Blanken 2014, Poole et al. 2016). We attempted to standardize bird counts by recording them at their highest levels (i.e., during peak migration). We standardized the shorebird counts as densities by estimating the total area (hectares) of each mudflat spanned by the 500 m transect using the polygon tool on low tide images from Google Earth.

Because shorebirds are known to select foraging sites based on an array of conditions, we gathered additional data on environmental and biotic variables at each surveyed mudflat that may covary with *G. vermiculophylla* presence. Once we completed a shorebird survey, we established a 50 m transect in the middle of the 500 m transect at approximately 0 MLLW, along which we sampled *G. vermiculophylla* biomass density, epifaunal/epibenthic invertebrate density, infaunal invertebrate density, and sediment

composition every 5 m for a total of 10 sampling points per site. To quantify *G. vermiculophylla* biomass and its associated epifaunal (i.e., found on seaweed) and epibenthic (i.e., found on the sediment) invertebrates, we collected all *G. vermiculophylla* in a 0.25 m² quadrat and immediately placed it in Ziploc bags for transport back to the laboratory. We also recorded large epibenthic invertebrates (~1 cm and greater) in this same quadrat found on the sediment surface. Directly adjacent to each quadrat, we collected sediment cores (10 cm diameter, 10 cm deep) for abundance of infaunal and small epibenthic invertebrates (referred to collectively as infauna hereafter) and cores for sediment composition (3 cm diameter, 8 cm deep).

In the lab, we rinsed the *G. vermiculophylla* gathered from the quadrat samples, removed epifaunal and epibenthic invertebrates and preserved them in 10% buffered formalin. We then weighed the seaweed for wet biomass (g) and dried it at 60°C for a minimum of 2 d to attain dry biomass (g). For the infaunal abundance sediment cores, we sieved the cores using 250 µm mesh and filtered seawater. We immediately sorted visible infauna and preserved them in 10% buffered formalin. We preserved the remaining sample for sorting under a dissection scope. We later transferred all preserved samples to 80% ethanol. Due to high invertebrate abundances in the sediment cores, only the first four infauna sediment cores from each site were processed. We classified invertebrates based on their lowest identifiable taxonomy. After identification, we dried the organisms in our sediment core samples at 60°C for 3 d and weighed the organisms pooled by taxonomic unit for dry biomass (g). The ten sediment cores for sediment composition were combined by site and processed for percent composition of sand, silt, and clay by the Soil, Plant, and Water Laboratory at the University of Georgia.

To determine the relationship between shorebird density (shorebirds/ha), *G. vermiculophylla* presence, and other environmental variables, we performed a linear regression using the “stats” package in R 3.3.2 (R Core Team 2016). The predictor variables included algal presence (*Gracilaria* presence or absence), average infauna density (invertebrates/0.0079 m²), average epifaunal/epibenthic invertebrate density (invertebrates/0.25 m²) and the ratio of percent sand to percent silt. A site was designated as absent of *G. vermiculophylla*, or “bare”, if it (a) was largely denuded of *G. vermiculophylla* at the hectare level, and (b) averaged < 4.5 g dw/m² in our surveys at MLLW, an area of maximal *G. vermiculophylla* biomass (N.B., most bare sites had substantially less than this quantity - see Appendix S1: Table S1). All continuous variables were natural log-transformed to achieve normality based on visual inspection of distributions using the “qqnorm” function in “stats” package in R (R Core Team 2016). Independent variables were analyzed for correlation using the stepVIF function in the “pedometrics” package in R (Samuel-Rosa 2015). Epifaunal/epibenthic invertebrate density was correlated with algal presence in all bird species models, and thus was excluded from the final model. We determined the relationship between algal presence and shorebird density of all species pooled as well as for individual species. In addition, we constructed all possible models and ranked them for best fit using an AICc comparison in the “AICcmodavg” package in R (Mazerolle 2017). We completed this analysis again, replacing average

invertebrate densities with average invertebrate biomass densities. We included density and biomass predictors in separate models to reduce correlation effects. Although biomass measurements were completed for the infaunal core data, we did not measure biomass directly for the epifaunal/epibenthic quadrat data. Thus, we calculated the average per capita biomass of different invertebrate phyla/classes in the infaunal cores and multiplied the estimated per capita biomass by the total number of individuals of the corresponding taxon in the epifaunal/epibenthic quadrat data. Results for the analysis with infaunal and epibenthic/epifaunal biomass as predictor variables are presented in Appendix S1: Table S3.

To determine the effect of *G. vermiculophylla* presence on epifaunal/epibenthic and infaunal invertebrate densities, we constructed generalized linear mixed-effects models with negative binomial distributions and zero inflation in the “glmmADMB” package (Bolker et al. 2013) in R, with site as a random effect. We also determined the effect of *G. vermiculophylla* on epifaunal/epibenthic and infaunal invertebrate biomass densities, using linear mixed models with site, again, as a random effect. We evaluated the effect of algal presence on epifaunal/epibenthic invertebrates from the quadrat samples (total $n = 120$) and infaunal invertebrates from the sediment core samples (total $n = 48$) separately due to the different collection methods.

Intermediate scale habitat selection – experimental removal and addition of seaweed

Though abundance surveys provide essential information about shorebird habitat association at the large scale (>1 ha), we wanted to experimentally examine how *G. vermiculophylla* presence affects shorebirds’ habitat selection and foraging. Therefore, we conducted manipulative field experiments at an intermediate scale (200 m²) to determine if the birds foraged more in areas of *G. vermiculophylla* vs. adjacent bare treatments. We ran the first experiment over a 3-week period in April 2014, on three *G. vermiculophylla*-inhabited mudflats used in the habitat preference survey. We were unable to visit the three sites over successive days due to the need for two consecutive days of fair weather (<20 knot winds and no precipitation) and negative low tides (−0.5 to −1.0 MLLW) for each site. At each site, we haphazardly selected a location on the mudflat and established two 10 × 20 m² plots separated by 10 m. The proximity of the plots was meant to reduce variability in abiotic and biotic conditions between the plots and allowed for birds to encounter both plots in a short time period. We removed *G. vermiculophylla* from one plot and left *G. vermiculophylla* intact in the other. To remove *G. vermiculophylla* from the entire plot, while minimizing disturbance to the mud surface, we moved through the plot at low tide on flat flotation boards. We controlled for sediment disturbance by moving through the paired plots similarly and allowed the sediment to settle over a full tidal cycle before beginning our observations. Over the duration of a low tide (~3 h), 3-min focal bird observations were conducted for shorebirds that visited each treatment. We observed each bird for up to three minutes, or until it left the plot, recording number of pecks and overall time spent in the plot. We alternated observations between the removal vs. control plots. Observations were

made from the mudflat, at least 20 m away from the plots behind a mobile blind, using 16x50 binoculars. We standardized foraging effort by each observed bird by assessing foraging rates (pecks/minute). In these experiments, peck rate is the definitive response, as it depicts true foraging effort, while time spent in a plot may be a mixture of foraging and meandering.

From mid-April to mid-May 2015, we conducted a reciprocal experiment by adding *G. vermiculophylla* to experimental plots on three mudflats in Wassaw Sound where it was absent. The contrast in the effect of *G. vermiculophylla* between this addition experiment and the previous removal experiment should inform at least two factors. First, the contrast should allow us to examine whether the *G. vermiculophylla*'s presence or absence at a mudflat scale (i.e., the background context) influences bird foraging decisions on the smaller, experimental-plot scale. Second, the contrast suggests whether *G. vermiculophylla* addition immediately affects shorebird habitat preference or whether its influence accrues over time (e.g., through recruitment of invertebrates). For this experiment, we left one of the paired plots as natural bare mudflat and to the other we added a standard amount of *G. vermiculophylla* (~9 kg wet biomass). This amount was within the range of biomass that we removed from our high density *G. vermiculophylla* mudflats in the removal experiment. Using flat flotation boards, we added *G. vermiculophylla* to the plot in a haphazard manner, attempting to create a natural spread of the seaweed across the plot. *G. vermiculophylla* was secured in place through partial burial and garden pins. Both plots were similarly disturbed, and a similar number of garden pins were added to each plot. We harvested seaweed for the *G. vermiculophylla* addition treatment from a single site to ensure standard quality as well as epifauna within the *G. vermiculophylla*. We kept epifauna intact to mimic conditions on a high-density *G. vermiculophylla* mudflat. We used the same data collection methods and response variables as in the removal experiment.

We analyzed data for each experiment separately with a mixed-effects linear regression model in R, using the “lme4” package (Bates et al. 2015). For both experiments, the response variable, pecks/minute, was natural log-transformed to attain normality and assessed as a function of treatment (*G. vermiculophylla* vs. bare mud). We also analyzed the amount of time (seconds) spent foraging as a function of treatment using a generalized linear regression analysis with a negative binomial distribution. For analyses of both response variables, we treated site as a random effect. Due to the lack of uniform presence of all shorebird species across sites, we first examined foraging rates (pecks/minute) for all shorebirds pooled (removal: $n = 68$; addition: $n = 92$). We then performed species-specific analyses on the two most common species in our experimental plots, dunlin (removal: $n = 24$; addition: $n = 35$) and semipalmated plovers (removal: $n = 15$; addition: $n = 23$). Semipalmated plovers were only present at one site for each experiment, so for their analysis, we removed the random site factor and analyzed the data using regression analyses without mixed effects.

Patch scale foraging behavior study

To determine if shorebirds utilize *G. vermiculophylla* at the smallest scale (i.e., individual clumps of seaweed

attached to a *D. cuprea* worm tube, $<1 \text{ m}^2$), we conducted a study that assessed individual shorebird preference for foraging directly in *G. vermiculophylla* clumps vs. the bare mud interspersed between seaweed patches. This helped ascertain whether birds at the larger scales of our study are attracted to *G. vermiculophylla* specifically for foraging quality (e.g., because high densities of invertebrates are present in *G. vermiculophylla* patches) or are just associating generally with areas invaded by *G. vermiculophylla* due to a larger scale influence the seaweed has on the environment or another correlated characteristic. Thus, studying foraging behavior at this small scale ($<1 \text{ m}^2$) allowed us to determine if the shorebirds' habitat choices at the large scale ($>1 \text{ ha}$) are related to their actual foraging preferences.

In March 2015, on five mudflats colonized by *G. vermiculophylla* (and used in the Large Scale Habitat Selection Survey), we observed up to five individual shorebirds from each of the most common shorebird species [dunlin, semipalmated plover, least sandpiper, ruddy turnstone, willet short-billed dowitcher, least sandpiper, and “peeps” (as before, remaining sandpiper species were pooled together)]. We systematically visited one flat per sampling day, over the course of 17 d. Sampling days were not successive due to the need for fair weather and negative low tides. During low tide, we observed a single focal bird for up to three minutes (or until it flew away) using 16x50 binoculars. During that time, we recorded the number of pecks in natural *G. vermiculophylla* patches vs. the surrounding bare mudflat. To compare the frequency of pecks in *G. vermiculophylla* to the seaweed's frequency on the mudflat, we quantified *G. vermiculophylla* percent cover by photographing ten 0.25 m^2 quadrats during the Large Scale Habitat Selection Survey. From the photographs, we estimated the ratio of *G. vermiculophylla* to bare mud at each mudflat with the image analysis software ImageJ. We estimated the average percent cover of each patch type at each site and then averaged across all sites to obtain an overall average percent cover of *G. vermiculophylla* vs. bare mud. Photographs of one site (Priest Landing) were lost and not included in this average; however, its average *G. vermiculophylla* biomass (known from the Large Scale Habitat Selection Survey) was within the range of the other sites. We used the ratio of percent cover of *G. vermiculophylla* to bare mud (0.27:0.73) to determine if the observed distribution of pecks significantly differed from the availability of patches in nature.

We analyzed the data using a hierarchical Bayesian analysis, designed specifically for ecological count data, in the R 3.3.2 package “bayespref” (Fordyce et al. 2011). With this package, we estimated the strength of foraging preference for *G. vermiculophylla* patches vs. bare patches for each bird and each species. The “bayespref” package is preferred to other non-parametric methods because it directly estimates individual- and population-level preference, while allowing for non-normal distribution, dependent data, and uneven design (Fordyce et al. 2011). We ran models for 5,000 generations, with 10 generation burn-ins, setting prior distributions based on the expected distribution of pecks given the average proportion of percent cover of *G. vermiculophylla* patches to bare mud patches across sites. We visually assessed diagnostic plots of MCMC chain distributions to choose the most evenly mixed model. Once we generated

preference strengths for each species, we compared the credible intervals (evaluated at 95%) to the proportion of *G. vermiculophylla* cover to bare mud. If the credible intervals of a species did not overlap the expected patch type cover, the preference was considered significant.

RESULTS

Large scale habitat selection survey

We observed a significant, positive association of *G. vermiculophylla* presence and shorebird density (birds/ha) across all sites when shorebirds were pooled (LM: $F_{1,10} = 5.65$, $P = 0.04$, $R^2 = 0.30$) (Fig. 1a). This pattern was similar when assessed for individual species. Dunlin, black-bellied plovers, willets, and short-billed dowitchers showed positive relationships with *G. vermiculophylla* (LM: [dunlin – $F_{1,10} = 6.32$, $P = 0.03$, $R^2 = 0.33$]; [black-bellied plover – $F_{1,10} = 11.93$, $P < 0.01$, $R^2 = 0.50$]; [willet – $F_{1,10} = 15.23$, $P < 0.01$, $R^2 = 0.56$]; and [short-billed dowitcher – $F_{1,10} = 14.67$, $P < 0.01$, $R^2 = 0.55$]; Fig. 1b, e, g, h, respectively). Both peeps and ruddy turnstones demonstrated positive trends with *G. vermiculophylla* presence ([peeps – $F_{1,10} = 4.68$, $P = 0.06$, $R^2 = 0.25$] and [ruddy turnstone – $F_{1,10} = 4.07$, $P = 0.07$, $R^2 = 0.22$]; Fig. 1c, d). Semipalmated plover densities did not differ significantly (LM: $F_{1,10} = 0.14$, $P = 0.71$, $R^2 < 0.10$; Fig. 1f).

Algal presence yielded the best-fit model for all birds collectively and for some individual species in the AICc comparisons, including ruddy turnstones, black-bellied plovers and willet (see Appendix S1: Table S2 for AICc results). Semipalmated plover density was best fit by the null (intercept-only) model. Additionally, the null model was within two Δi for “all birds”, peeps and ruddy turnstones. However, for “all birds”, the algal presence model was over twice the Akaike weight of the null model. For ruddy turnstones and peeps, the algal presence-only model had 0.07 and 0.09

greater Akaike weights (respectively) than the null models. Other biotic and abiotic variables also accounted for variance in the top models for dunlin, peep, willet, and short-billed dowitcher densities. Dunlin densities were best fit by an additive model that included positive effects of the ratio of percent sand to silt ($P < 0.01$) and infauna density ($P = 0.04$). Peep densities were also best fit by an additive model of the ratio of percent sand to silt ($P < 0.01$) and infauna density ($P = 0.05$), both of which were positively related to peep density. For short-billed dowitchers, the best-fit model contained a significant negative interaction ($P < 0.01$) between algal presence ($P < 0.01$) and the ratio of percent sand to percent silt ($P = 0.11$).

Differences in the distributions of epibenthic/epifaunal and infaunal invertebrates were detected in response to *G. vermiculophylla* presence. When assessing epibenthic and epifaunal invertebrate abundances, we found that mudflats with *G. vermiculophylla* had greater epibenthos/epifauna densities (GLMM: $\chi^2_1 = 74.99$, $P < 0.01$, total $n = 120$; Appendix S1: Table S4) and biomass densities (LMM: $\chi^2_1 = 12.99$, $P < 0.01$; Appendix S1: Table S5). *Gammarus mucronatus* was the most abundant invertebrate within the quadrat samples (Appendix S1: Table S4), while gastropods accounted for the greatest biomass (Appendix S1: Table S5). However, when assessing infauna densities, we found no difference between *G. vermiculophylla* mudflats and bare mudflats (GLMM: $\chi^2_1 = 0.42$, $P = 0.50$, total $n = 48$; Appendix S1: Table S6). Similarly, we found no difference in infauna biomass between the two habitat types (LMM: $\chi^2_1 = 1.49$, $P = 0.22$; Appendix S1: Table S7). Marine annelids accounted for on average 63% of the infauna biomass in *G. vermiculophylla* mudflat sediment cores and 60% in bare mudflat cores (Appendix S1: Table S7). When assessing small epibenthic invertebrate biomass separately in the infaunal sediment cores, gastropods composed over 90% of the small epibenthos found in each habitat type (Appendix S1: Table S7).

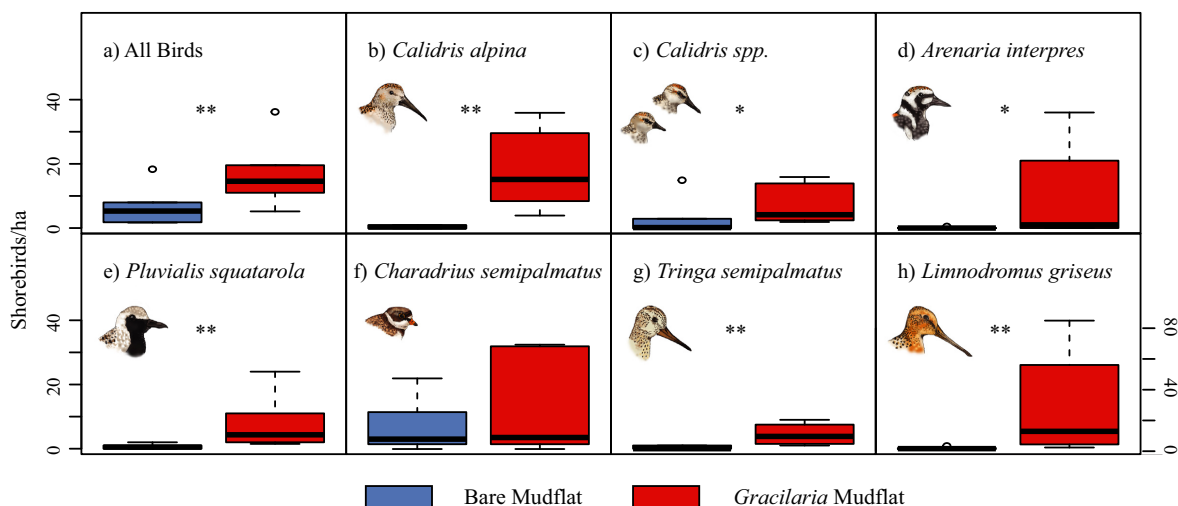


FIG. 1. Field surveys of shorebird density (shorebirds/ha) on twelve mudflats (six with *Gracilaria* and six with no *Gracilaria*, or “bare”) for (a) all birds and (b–h) individual species. Data were analyzed after natural log-transformation using linear regression in R (3.3.2). Figures depict raw densities from the algal presence-only model. * indicates a trend ($0.05 < P > 0.1$) and ** indicates significant difference ($P \leq 0.05$). Box and whisker plots represent the median with upper and lower quantiles. Species are presented as follows: (b) dunlin; (c) peep; (d) ruddy turnstone; (e) black-bellied plover; (f) semipalmated plover; (g) willet; and (h) short-billed dowitcher. Illustration credit: Rebecca Atkins.

Intermediate scale habitat selection – experimental removal and addition of seaweed

During the removal experiment, shorebirds on average foraged at a faster rate in 200 m² plots with *G. vermiculophylla* than in plots with *G. vermiculophylla* removed (LMM: $\chi_1^2 = 4.18$, $P = 0.04$, $n = 68$; Appendix S1: Fig. S1a). Yet shorebirds spent similar time (seconds) in each treatment (GLMM: $\chi_1^2 = 2.23$, $P = 0.14$). For the two most common birds, dunlin foraged at significantly faster rates where *G. vermiculophylla* was intact (LMM: $\chi_1^2 = 13.87$, $P < 0.01$, $n = 24$), while semipalmated plovers foraged at similar rates between treatments (LM: $F_{1,13} = 1.58$, $P = 0.23$, $n = 15$; Appendix S1: Fig. S2a). We found no difference in the amount of time spent in each treatment for either species (GLMM: $\chi_1^2 = 0.78$, $P = 0.38$; GLM: $\chi_1^2 = 2.58$, $P = 0.11$, respectively).

In the addition experiment, we did not detect a difference in foraging rate in 200 m² plots with or without *G. vermiculophylla* when all shorebirds were pooled (LMM: $\chi_1^2 < 0.01$, $P = 0.92$, $n = 92$; Appendix S1: Fig. S1b); however, pooled shorebirds tended to spend more time in *G. vermiculophylla* plots (GLMM: $\chi_1^2 = 3.07$, $P = 0.08$). Dunlin showed no difference in foraging rate between treatments (LMM: $\chi_1^2 = 0.9$, $P = 0.34$, $n = 35$; Appendix S1: Fig. S2b). Dunlin also spent similar amounts of time among treatments (GLMM: $\chi_1^2 = 0.09$, $P = 0.77$). Semipalmated plovers again did not forage at different rates in bare mud vs. *G. vermiculophylla* addition plots (LM: $F_{1,21} = 2.02$, $P = 0.17$, $n = 23$; Appendix S1: Fig. S2b); yet, they spent more time in *G. vermiculophylla* plots (GLM: $\chi_1^2 = 18.10$, $P < 0.01$).

Patch scale foraging behavior study

At the small scale (<1 m²), shorebird species differed in their foraging responses to *G. vermiculophylla* patches. Dunlin ($n = 24$) weakly preferred *G. vermiculophylla* patches at the population level, though individual preference varied (Fig. 2a; Appendix S1: Table S8). Least sandpipers (a species that was pooled with other peeps at the large scale, $n = 15$) and ruddy turnstones ($n = 5$) showed strong preferences for foraging in *G. vermiculophylla* patches at both the individual and population level (Fig. 2b, d; Appendix S1: Table S8). In contrast, the remaining peeps ($n = 7$) and semipalmated plovers ($n = 19$) avoided *G. vermiculophylla* patches (Fig. 2c, e; Appendix S1: Table S8). Both willets ($n = 6$) and short-billed dowitchers ($n = 9$) showed no overall preference for pecking in bare mud vs. in *G. vermiculophylla* patches (Fig. 2f, g, respectively; Appendix S1: Table S8). However, individuals of both species varied, with some individuals preferring to forage in bare mud or *G. vermiculophylla*.

DISCUSSION

Shorebirds demonstrated varied preferences for foraging habitat type across species and spatial scales, suggesting complex mixed responses to the invasive ecosystem engineer, *G. vermiculophylla* (see Table 1 for summary). Shorebird species were more abundant on large (>1 ha) mudflats with *G. vermiculophylla* relative to those without

G. vermiculophylla, though the strength of this presence effect was clearly species dependent (Fig. 1; Appendix S1: Table S2). At smaller spatial scales, the responses of birds to local patches of *G. vermiculophylla* depended on species-specific foraging strategies (Fig. 2). Given that introduced ecosystem engineers can have both positive and negative effects on communities (e.g., Boughton and Boughton 2014), the varied responses of these community members suggest that behavioral mechanisms may help to explain mixed effects of engineering, specifically in the context of novel habitat generation.

For ruddy turnstones, preference for mudflats with *G. vermiculophylla* at large spatial scales (>1 ha) generally reflected foraging preferences at the small, patch-level scale (<1 m²) and existing literature on their tendency to forage near structure. Ruddy turnstones typically use structure to their advantage, turning over shell, stones and vegetation to reveal sheltering marine invertebrates and eggs in dense aggregations (Fleischer 1983, Sullivan 1986, Nettleship 2000). This behavior may pre-adapt the birds to readily utilize novel structure, such as that provided by *G. vermiculophylla*. In Wassaw Sound, we often observed ruddy turnstones traveling from patch to patch of *G. vermiculophylla*, flipping the seaweed over with their heads or beaks and picking out epifaunal prey, including amphipods and crabs. Black-bellied plovers, a similarly sized species that also forages visually and targets large epifaunal/epibenthic prey (Poole et al. 2016), showed similar habitat selection at the large scale (>1 ha). Because of low densities, we could not statistically assess their behavioral responses at smaller spatial scales (<1 m²).

Willetts, short-billed dowitchers, and dunlin had greater densities on mudflats with *G. vermiculophylla*, with varying effects of sediment composition and infauna densities on bird densities (Appendix S1: Table S2). However, these species did not differ in foraging preferences between bare mud and *G. vermiculophylla* patches at the smallest spatial scale (<1 m²), although preference for *G. vermiculophylla* patches was statistically marginal for dunlin. These are larger shorebirds, with long beaks used for tactile foraging, that often probe deep into the substrate to capture infaunal prey, though willets and dunlin also use visual detection (Stenzel et al. 1976, Rojas et al. 1999, Castillo-Guerrero et al. 2009, Novcic 2016). Given that these shorebirds forage below the sediment surface, the presence of *G. vermiculophylla* may not hinder prey detection, leading to their observed largely random foraging across patch types. This is further supported by the lack of significant difference in infaunal prey densities and biomasses between sites in the habitat preference survey (Appendix S1: Tables S4–S7).

Semipalmated plovers and two peep species (western sandpipers and semipalmated sandpipers) notably avoided foraging in *G. vermiculophylla* patches at the small scale (<1 m²), but they either weakly preferred or had no preference for *G. vermiculophylla*-dominated mudflats at the large scale (>1 ha). Avoidance of *G. vermiculophylla* patches by semipalmated plovers emphasizes constraints of their foraging behaviors as this species relies heavily on visual detection of infaunal polychaetes and other small epifaunal invertebrates (i.e., ostracods, amphipods and small gastropods) (Rose et al. 2016). Such behavior suggests that

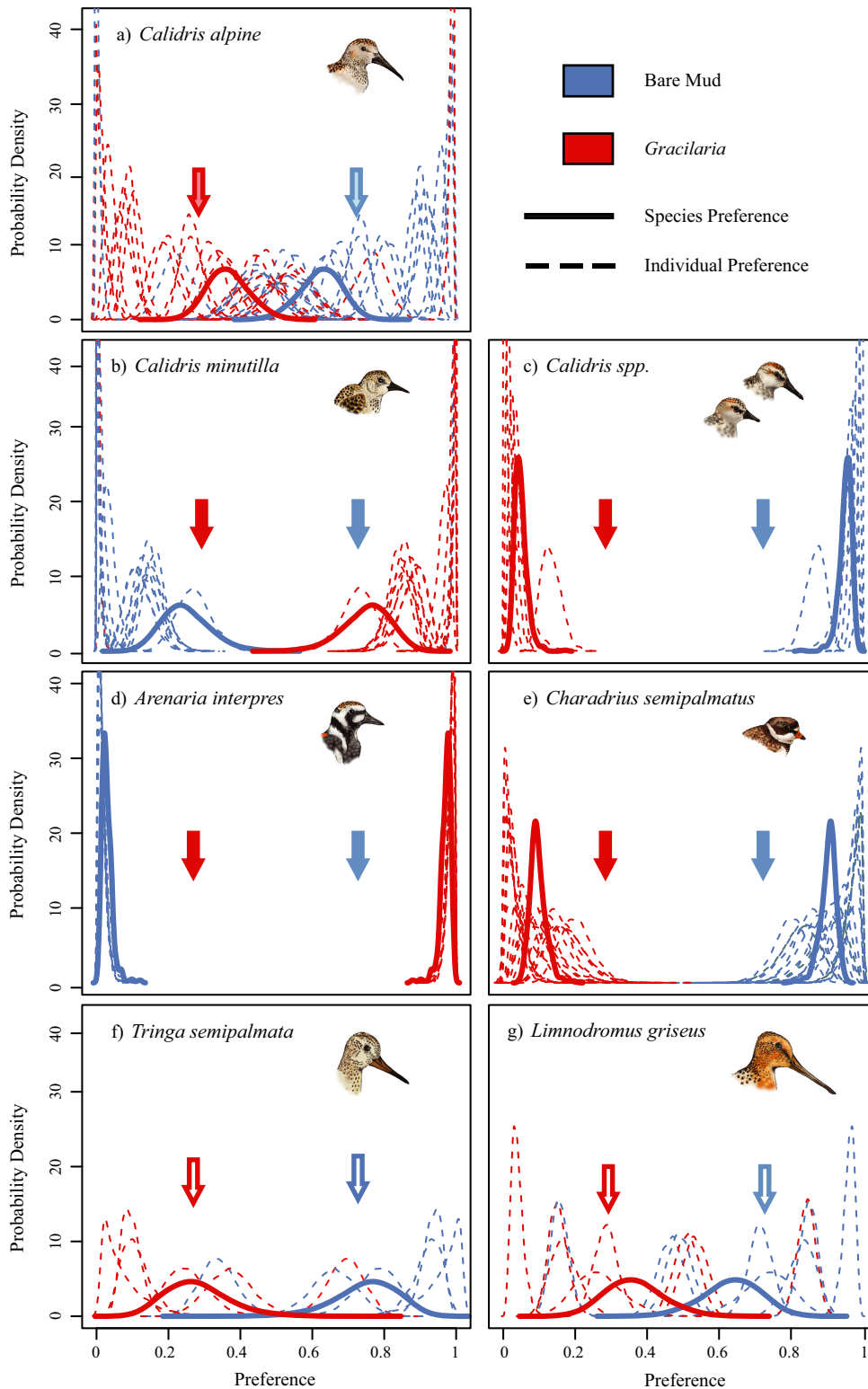


FIG. 2. Foraging-habitat patch preferences for shorebirds during the 2015 spring migration season. We analyzed all species for individual-level (dotted lines) and population-level (solid lines) preferences using a hierarchical Bayesian analysis in R (3.3.2). Preference curves for *G. vermiculophylla* patches are illustrated in red and for bare mud in blue. Arrows denote where the preference curves should peak for each patch type if the birds foraged randomly, given the average percent cover of each habitat patch type. Filled arrows indicate that birds foraged differently from the random distribution, while unfilled arrows indicate that birds foraged randomly. Lightly filled arrows in panel a) indicate a marginal difference from random foraging (credible intervals slightly overlap with patch type cover). Species are presented as follows: (a) dunlin ($n = 24$); (b) least sandpiper ($n = 15$); (c) peep ($n = 7$); (d) ruddy turnstone ($n = 5$); (e) semipalmated plover ($n = 19$); (f) willet ($n = 6$); (g) short-billed dowitcher ($n = 9$). Illustration credit: Rebecca Atkins.

TABLE 1. Summary of habitat associations and preferences determined from surveys, experiments, and behavioral studies for the common shorebird species examined.

Shorebird species	Foraging ecology (visual, tactile, or mixed)	Habitat selection surveys (>1 ha)	<i>Gracilaria</i> removal foraging (200 m ²)	<i>Gracilaria</i> addition foraging (200 m ²)	Patch foraging preference (<1 m ²)
Dunlin (<i>Calidris alpina</i>)	Tactile (Mixed)	++	++	=	+
Western Sandpiper (<i>Calidris mauri</i>)	Mixed	+	—	—	B
Semipalmated Sandpiper (<i>Calidris pusilla</i>)	Mixed	+	—	—	B
Least Sandpiper (<i>Calidris minutilla</i>)	Visual (Mixed)	+	—	—	++
Ruddy Turnstone (<i>Arenaria interpres</i>)	Visual	+	—	—	++
Black-Bellied Plover (<i>Pluvialis squatarola</i>)	Visual	++	—	—	—
Semipalmated Plover (<i>Charadrius semipalmatus</i>)	Visual	=	=	=	B
Willet (<i>Tringa semipalmata</i>)	Tactile (Mixed)	++	—	—	=
Short-Billed Dowitcher (<i>Limnodromus griseus</i>)	Tactile	++	—	—	=

Notes: Two plus signs (++) indicate a statistically significant positive relationship between *G. vermiculophylla* presence and bird density or foraging, while one (+) indicates a positive trend ($0.05 < P < 0.1$). An equal sign (=) indicates no difference between treatments. B indicates a significant preference for bare mudflat. Foraging ecology was determined from literature reviews, with individual species reviews from *The Birds of North America* (Rodewald 2015) as important sources. We merged three peep species for the Large Scale Habitat Selection Survey due to identification limitations; during the Patch Foraging Preference study, least sandpipers were identifiable, while western and semipalmated sandpipers were pooled. Dashes indicate no analysis due to species absence.

G. vermiculophylla presence may impede the plovers' prey detection, although they did not avoid *G. vermiculophylla* mudflats at the large (>1 ha) or intermediate (200 m²) scales. Western and semipalmated sandpipers predominantly rely on tactile detection of infaunal polychaetes and on slurping of biofilm and small planktonic invertebrates (Nebel et al. 2005, Hicklin and Gratto-Trevor 2010, Mathot et al. 2010). Thus, their greater densities on *G. vermiculophylla* mudflats, but the avoidance of small seaweed patches, may point to these birds cuing into other key factors at the large scale, such as sediment composition (Appendix S1: Tables S2 and S3). Notably, the third peep species, least sandpipers, strongly preferred foraging in *G. vermiculophylla* patches at the small scale – a pattern distinct from the other peeps species. Indeed, least sandpipers are known to utilize heavily vegetated microhabitats for foraging (Novic 2016) and feed primarily on amphipods (Nebel and Cooper 2008). Thus, peeps and semipalmated plovers provide notable examples of how species identity (particularly morphology, behavior, and ecological niche) can alter the overall response of a community to an invasive ecosystem engineer.

The results of the manipulative field experiments demonstrate the complexity of *G. vermiculophylla*'s role in the observed mixed effects between the large and the small scale studies. For instance, semipalmated plovers showed no difference in peck rate between treatments in either experiment (Appendix S1: Fig. S2). The lack of response in foraging effort by semipalmated plovers between treatments was expected given their lack of response to algal presence in the Large Scale Habitat Selection Survey (>1 ha). Their indifference also indicates that the presence of *G. vermiculophylla* may not negatively affect semipalmated plover foraging

effort, despite their avoidance of *G. vermiculophylla* patches at the small scale (<1 m²). On the other hand, dunlin showed a mostly positive response to the alga. At the large scale (>1 ha), dunlin densities were greater on *G. vermiculophylla* mudflats. Additionally, at the small scale (<1 m²), dunlin showed a slight preference for foraging in *G. vermiculophylla* patches, with great variability in foraging response between individuals. In the experiments, dunlin pecked at faster rates where *G. vermiculophylla* was left intact; however, *G. vermiculophylla* had no effect on dunlin foraging in the experiments where it was newly added to mudflats. Therefore, lower peck rate in response to *G. vermiculophylla* removal may be the result of a covarying factor (i.e., prey density or sediment characteristics) that is not expressed immediately upon the addition of *G. vermiculophylla*. Despite the contrasting results between species, it is notable that across all the experiments, observations and species, birds rarely preferred the native bare habitat relative to *G. vermiculophylla* (Table 1). Thus, *G. vermiculophylla* seems to generate either no or a positive response by shorebirds, though the mechanism is likely different for each species examined.

The presence of contrasting preferences at the large scale (>1 ha) and small scale (<1 m²) may indicate the importance of other habitat variables that may simultaneously affect shorebird densities and *G. vermiculophylla* presence. For dunlin, short-billed dowitchers, willets and peeps, some variation in densities depended on sediment composition and/or infaunal densities in the Large Scale Habitat Selection Survey. Additionally, *G. vermiculophylla* presence on southeastern mudflats is tightly correlated with the density of native tubeworms, *D. cuprea*, which attaches the seaweed to its

tube (Byers et al. 2012, Kollars et al. 2016). *D. cuprea* densities are dependent on abiotic conditions, such as salinity, sediment type, and inundation (Berke 2012, Kollars et al. 2016), and thus restrict *G. vermiculophylla* distributions to the lower estuary even though *G. vermiculophylla* can tolerate the lower salinities of the upper estuaries (Weinberger et al. 2008, Sotka et al. 2018). Beyond habitat characteristics, the mixed effects of *G. vermiculophylla* on shorebird habitat selection and foraging behavior across spatial scales could be partially attributable to flocking behavior, whereby birds following the cues of other species or individuals may be led to less preferred foraging habitat.

Although shorebirds generally responded positively to the invasive ecosystem engineer's presence at the large scale (>1 ha), their responses at the small scale (<1 m²) were mixed, despite the increased epifaunal prey availability within *G. vermiculophylla* patches (Byers et al. 2012, Wright et al. 2014). The divergent bird responses demonstrate that even polyphagous predators within the same trophic assemblage experience effects of biological invasions differently. Though our methods cannot address the invasive engineer's impact on shorebird fitness, our results do indicate that invasive ecosystem engineers that provision additional complex habitat and boost associated prey abundance do not positively affect all native species, even those that utilize similar prey resources. Rather, predators utilize these new habitats differently across spatial scales based on inherent foraging behaviors. Thus, as invasive ecosystem engineers become more prevalent globally, the direction of their local effects may depend in part on species-specific behaviors.

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