

Research Article

Biogeographic patterns of community diversity associated with an introduced alga

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Abstract

Non-native foundation species may alter physical environments and provide habitat, thereby impacting recipient communities. Along the US east coast, we assessed biogeographic patterns of free-living and parasitic community diversity associated with the non-native red alga *Gracilaria vermiculophylla*, which is characterized by fixed (with holdfast) or free-floating thalli depending on the availability of hard substratum. In summer 2019, we surveyed 17 sites across 3 biogeographic regions. We used a random quadrat design to collect *G. vermiculophylla* and associated mobile macroinvertebrates per site, and we took abiotic measurements. We also haphazardly collected 100 *Ilyanassa obsoleta* snails per site to assess trematode diversity. In the lab, macroinvertebrates were removed from thalli and identified to lowest taxonomic level, and snails were dissected to determine trematode prevalence and diversity. Biotic and abiotic variables were analyzed for the best sets of predictors for species richness, abundance, and diversity of macroinvertebrates and trematodes across bioregions. *Gracilaria vermiculophylla* biomass was used as an offset in free-living analyses. Across all our US east coast sites, we detected 10,113 free-living (mobile) macroinvertebrates across 39 taxa. Three Gammaridean amphipods (*Gammarus mucronatus*, *Ampithoe longimana*, and *Gammarus lawrencianus*) comprised >50% of all detected organisms. We found biogeographic region to be a key predictor of macroinvertebrate abundance and richness. Trematode prevalence and richness were best explained by *G. vermiculophylla* biomass, while biogeographic region best explained diversity. As a widespread invader, our study provides evidence for associations that have formed as this foundation species has become established outside its native range. Over time, the presence and spread of *G. vermiculophylla* could continue to impact macroinvertebrate structure and diversity, and future work should directly compare macroinvertebrate communities with *G. vermiculophylla* to other foundation species along coastlines it is now common.

Key words: Amphipod, ecosystem engineer, foundation species, *Gracilaria vermiculophylla*, *Ilyanassa obsoleta*, invasion, trematode

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Introduction

Over the last several decades, biological invasions have become recognized as a major environmental and management concern due to their significant impacts on biodiversity, human health, and global economies (Pimentel et al. 2001). However, for many invasive species that do not have an immediate and direct effect on human food production, infrastructure, or health, their presence may go unnoticed or unstudied for extensive periods of time. This lag time can hinder our understanding of the potential for environmental impact, as well as the roles these species may assume within recipient communities (Crooks 2005). Even among highly abundant and widespread invaders, there is often insufficient baseline information of their ecological effects in the invasive range, including novel associations they may form with native species and habitats. This hinders our ability to effectively manage species invasions in terms of mitigating impacts of established species on native communities and in preventing future invasions (Epanchin-Niell and Liebhold 2015).

During an invasion, a species' ecological role and its consequences on the invaded community could be considerable, especially if the species is habitat-forming or significantly alters the structure of existing habitats (Hastings et al. 2007). These species are often termed “ecosystem engineers,” and their introductions to novel communities may be expected to have far-reaching influences. This is because these species can alter the structural complexity and abiotic environment within an ecosystem, which may enhance habitat heterogeneity and resource availability and thereby facilitate the abundance and diversity of numerous species (Dangerfield et al. 1998; Crooks 2002). Given the intricate network of interacting species within communities, it is vital that we closely investigate organisms that play such pivotal roles on community structure and function, as changes to their population abundance can ripple through and across ecosystems, especially for broadly distributed or range expanding species (Ellison et al. 2005; Osland et al. 2013).

Some ecosystem engineers, particularly plants and some algae, are referred to as “foundation species” because they provide foundational support in terms of food, shelter, and nursery grounds to associated organisms (Dayton 1972; Ellison et al. 2005; Sorte et al. 2017; Metzger et al. 2019). In aquatic systems, foundation species, like macroalgae, serve a vital role as both food and shelter to associated macroinvertebrate species, which occupy multiple trophic levels in aquatic food webs and represent pivotal components of aquatic energy flows (Umanzor et al. 2017). When changes occur to the composition and biomass of foundation species in aquatic communities, such as with species invasions, macroinvertebrate densities and diversities may also change, greatly influencing the community structure and function of invaded ecosystems (Benke 2001; Runck 2007).

In recent decades, multiple anthropogenic activities (e.g., shipping, aquaculture, food, aquaria/pets) have led to the intentional and unintentional introductions of numerous biota, including foundation species like macroalgae (Williams and Smith 2007; Andreakis and Schaffelke 2012; Grosholz et al. 2015). Some introduction vectors, like shipping and aquaculture, can move associated organisms vast distances to locations where they have no prior evolutionary history, thus imposing novel species interactions on invaded communities (Strauss et al. 2006). Specifically, the introductions of habitat-forming macroalgae around the world has led to significant changes in community structure and function in invaded regions due to resultant alterations in an ecosystem's structural complexity (Wernberg et al. 2004). The Northern Hemisphere, in particular, has been subject to multiple introductions of macroalgae via several introduction mechanisms over the last

century (Williams and Smith 2007; Provan et al. 2008; Andreakis and Schaffelke 2012; Minchin and Nunn 2014), with a prominent example being the East Asian red macroalga *Gracilaria vermiculophylla* (Ohmi) Papenfuss (Krueger-Hadfield et al. 2017, 2018). This structurally complex foundation species has been introduced to almost every temperate coastline in the Northern Hemisphere (Kim et al. 2010; Krueger-Hadfield et al. 2017). On the U.S. East Coast, *G. vermiculophylla* was introduced from Japan to the mid-Atlantic USA in the mid 20th century (Fredrico et al. 2004; Kim et al. 2010; Krueger-Hadfield et al. 2017), likely through the importation of oysters, followed by secondary vectors, such as fishing and/or boating activities (Krueger-Hadfield et al. 2017). Over the last several decades, the alga was observed to spread into multiple populations up and down the east coast with records from New Hampshire to Georgia (Krueger-Hadfield et al. 2017). In some locations, particularly the Southeast U.S., *G. vermiculophylla* has vastly transformed soft-sediment habitats by increasing structural complexity (Byers et al. 2012). In sites with abundant hard substratum, such as boulders, rocks, and large cobbles, thalli are ‘fixed’ (*sensu* Krueger-Hadfield et al. 2018) by holdfasts to hard structures, indicating sporic recruitment (see also Krueger-Hadfield et al. 2023). In sites without abundant hard substratum, especially in the southeastern U.S., thalli drift (i.e., are ‘free-floating’) and are often incorporated into the tube caps of the polychaete worm *Diopatra cuprea*, thereby stabilizing drifting thalli in these systems (Thomsen and McGlathery 2005; Kollars et al. 2016; Krueger-Hadfield et al. 2016; Mott et al. 2022). Prior localized studies have also noted increases in macroinvertebrate densities of some taxonomic groups, like crustaceans, gastropods, and bivalves, in response to *G. vermiculophylla* establishment (Thomsen et al. 2007; Nyberg et al. 2009; Thomsen et al. 2013). This is presumably because the alga provides novel refuge, shelter, and structural complexity to these communities (Nyberg et al. 2009). On the other hand, *G. vermiculophylla* thalli may be a less preferred alga for herbivorous macroinvertebrates compared to native algae, such as *Ulva* spp. (Nejrup et al. 2012), indicating that some grazers may use *G. vermiculophylla* more for its habitat-forming structure than for consumption.

The present-day range of *G. vermiculophylla* on the U.S. East Coast crosses two major geographic barriers – Cape Cod and Cape Hatteras – which have been shown in past surveys to delineate macroinvertebrate assemblages (Engle and Summers 1999; Spalding et al. 2007; Hale 2010; Pappalardo et al. 2015). However, to date, there are no published studies in this region that have investigated biogeographic patterns of community composition and structure of associated organisms with *G. vermiculophylla*. Moreover, nothing is yet known of the alga’s potential impact on communities that are not free-living (i.e., parasite communities). Many parasites have multi-host life cycles that form numerous links across community members (Luque et al. 2004; Santoro et al. 2020), and trophically transmitted parasites can be a key structuring force of aquatic communities (Wood et al. 2007; Lafferty et al. 2008; Dunne et al. 2013). Co-occurring with *G. vermiculophylla* throughout much of its range is the eastern mudsnail *Ilyanassa obsoleta* (= *Tritia obsoleta*), a highly abundant gastropod in coastal marshes that is frequently infected by several digenean trematode species that predominantly use fish or birds as definitive hosts (Curtis and Hurd 1983; Blakeslee et al. 2012; Phelan et al. 2016; Blakeslee et al. 2020b). Recent work has suggested that the presence of *G. vermiculophylla* may attract resident and migratory birds presumably due to the alga’s association with diverse macroinvertebrate prey assemblages (Haram et al. 2018). Because many of these birds also serve as definitive hosts to digenean trematodes (Fredensborg et al. 2006; Phelan et al. 2016; Besterman et al. 2020), a greater abundance of birds at a site due to a greater biomass of *G. vermiculophylla*

could result in a heightened exposure of the first-intermediate host, *I. obsoleta*, to digenean trematode eggs from the feces of definitive bird hosts (Byers et al. 2008).

In our study, we aimed to characterize and establish the community composition, abundance, richness, and diversity of mobile macroinvertebrate communities (free-living and parasitic) associated with the non-native alga, *G. vermiculophylla*, throughout much of its U.S. East coast range. To do so, we surveyed 17 sites within three biogeographic regions across two biogeographic breaks for free-living macroinvertebrates associated with fixed and free-floating *G. vermiculophylla*, as well as trematode parasites infecting the abundant co-occurring gastropod *I. obsoleta*. We predicted that (1) *G. vermiculophylla* would support a diverse assemblage of macroinvertebrates throughout the study region and (2) biogeographic region would strongly influence the community composition of free-living and trematode species along the U.S. East Coast. Altogether, our work provides an important baseline of mobile, macroinvertebrate communities that associate with this foundation species throughout its non-native range, furthering our general understanding of the influence that introduced foundation species may have on community composition and structure in coastal soft-sediment ecosystems.

Methods

Study system

The red macroalga *Gracilaria vermiculophylla* (Figure 1a) is tolerant to variable temperatures and salinities (Rueness 2005; Phooprong et al. 2008; Sotka et al. 2018) and has colonized coastal habitats across a wide range of latitudes (Krueger-Hadfield et al. 2017). Due to its haploid-diploid life cycle, “fixed sites” include all three phases of the alga’s life cycle, including haploid male and female gametophytes and diploid tetrasporophytes, but “free-floating sites” are overwhelmingly dominated by tetrasporophytes (Krueger-Hadfield et al. 2016; see also Krueger-Hadfield et al. 2023 for a description of terminology). Past work has noted associations of macroinvertebrates with non-native populations of *G. vermiculophylla* (e.g., Thomsen 2010; Byers et al. 2012; Wright et al. 2014; Wood and Lipcius 2022), but our study represents the first broad-scale biogeographic examination of associated organisms, like amphipods (Figure 1b), with the non-native red alga throughout its U.S. East Coast range.

The eastern mudsnail *Ilyanassa obsoleta* (= *Tritia obsoleta*) (Figure 1c) is a highly abundant gastropod found in coastal habitats throughout eastern North America from the Gulf of Saint Lawrence, Canada to Northern Florida, forming densities as high as 8,000 individuals/m² (Dimon 1902; Abbott 1974; Curtis and Hurd 1983; Harmon and Allen 2018), and adult sizes range from 11–30 mm (Scheltema 1964; Blakeslee et al. 2012; Fofonoff et al. 2018). These gastropods primarily live on soft-sediment habitats and have wide thermal and salinity tolerances, contributing to their ecological and evolutionary success (Scheltema 1965; DeLorenzo et al. 2017; Fofonoff et al. 2018). In habitats with *G. vermiculophylla*, *I. obsoleta* may co-occur with the non-native macroalga, and have been shown to lay egg capsules on its algal fronds (Guidone et al. 2014). *Ilyanassa obsoleta* serves as a first intermediate host to nine species of digenean trematodes (Blakeslee et al. 2012; Phelan et al. 2016; Figure 1d). The life cycles of these parasites typically require two to three hosts and begin when *I. obsoleta* grazes on feces of definitive hosts that contain trematode eggs (Combes et al. 1994; Rohde 2005). An infected *I. obsoleta* is castrated and parasitized for life (Curtis 1995). Downstream second-intermediate hosts include a wide range of molluscs, crustaceans, polychaetes, and fish, and definitive hosts include fish, birds, and terrapins (Blakeslee et al. 2012; Phelan et al. 2016).

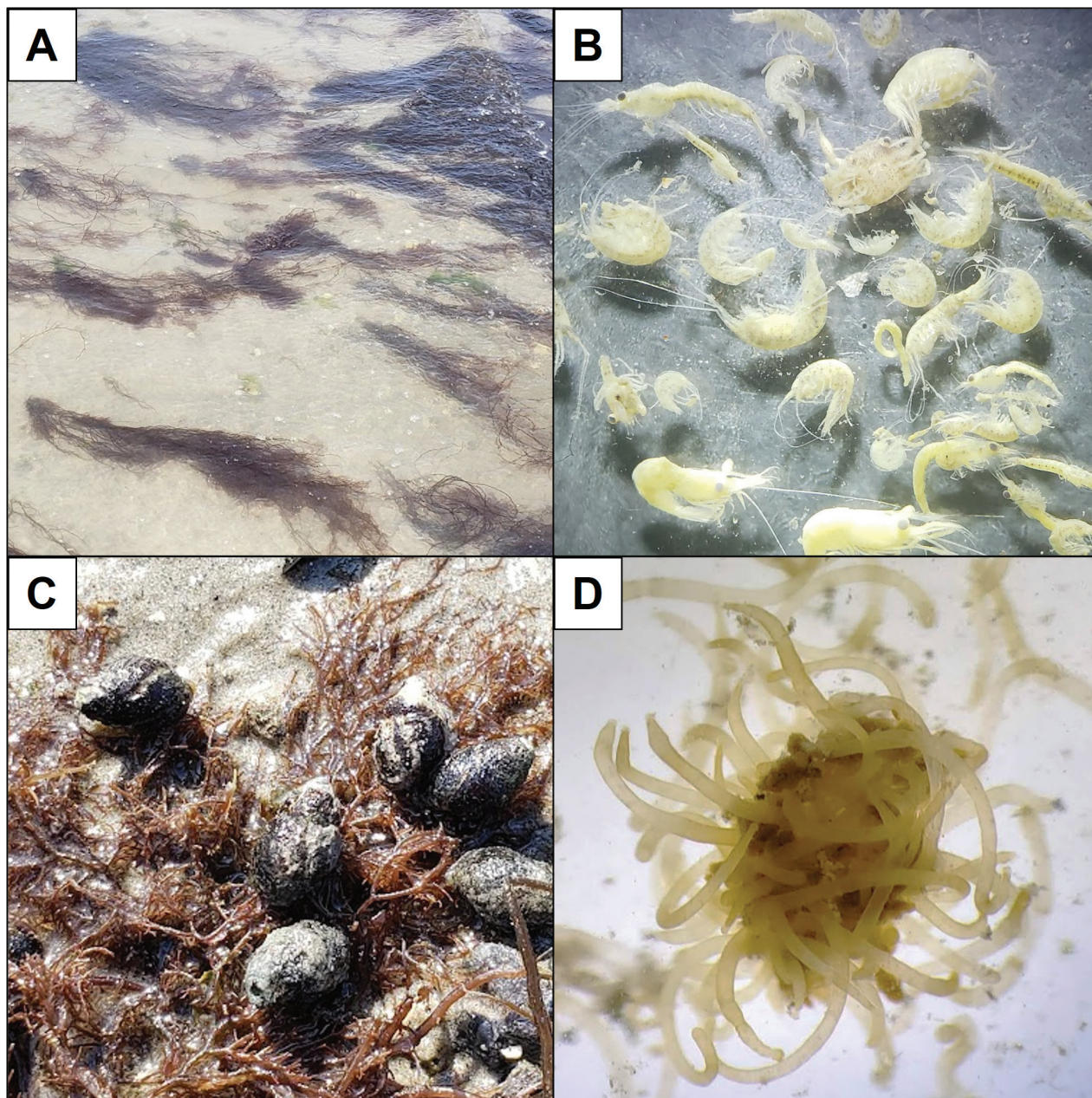


Figure 1. Images of **A.** *Gracilaria vermiculophylla* in the field; **B.** Preserved macroinvertebrates found within a sample of *G. vermiculophylla* thalli; **C.** *Ilyanassa obsoleta* co-occurring with *G. vermiculophylla*; and **D.** Sporocysts / cercariae of *Diplostomum nassa* found within gonad tissues of *I. obsoleta*. PC's: Timothy S. Lee.

Study sites

We identified sample sites with verified *G. vermiculophylla* presence from previous studies (Nettleton et al. 2013; Krueger-Hadfield et al. 2017). In summer 2019, we sampled 17 U.S. East Coast sites, capturing much of the species' introduced range and encompassing two major geographic barriers at Cape Hatteras and Cape Cod (Engle and Summers 1999; Spalding et al. 2007; Hale 2010) (Figure 2). Since summer temperatures are lagged in northern versus southern latitudes, southern sites were sampled earlier than northern sites (Suppl. material 1: table S1): South of Cape Hatteras (henceforth, SCH) was sampled May 21 – June 22 (n = 6, avg = 29.9 °C); Virginian Province (between Cape Hatteras and Cape Cod: henceforth, VP) was sampled June 25 – Aug 3 (n = 8, avg = 26.7 °C); and North of Cape Cod (henceforth NCC) was sampled Aug

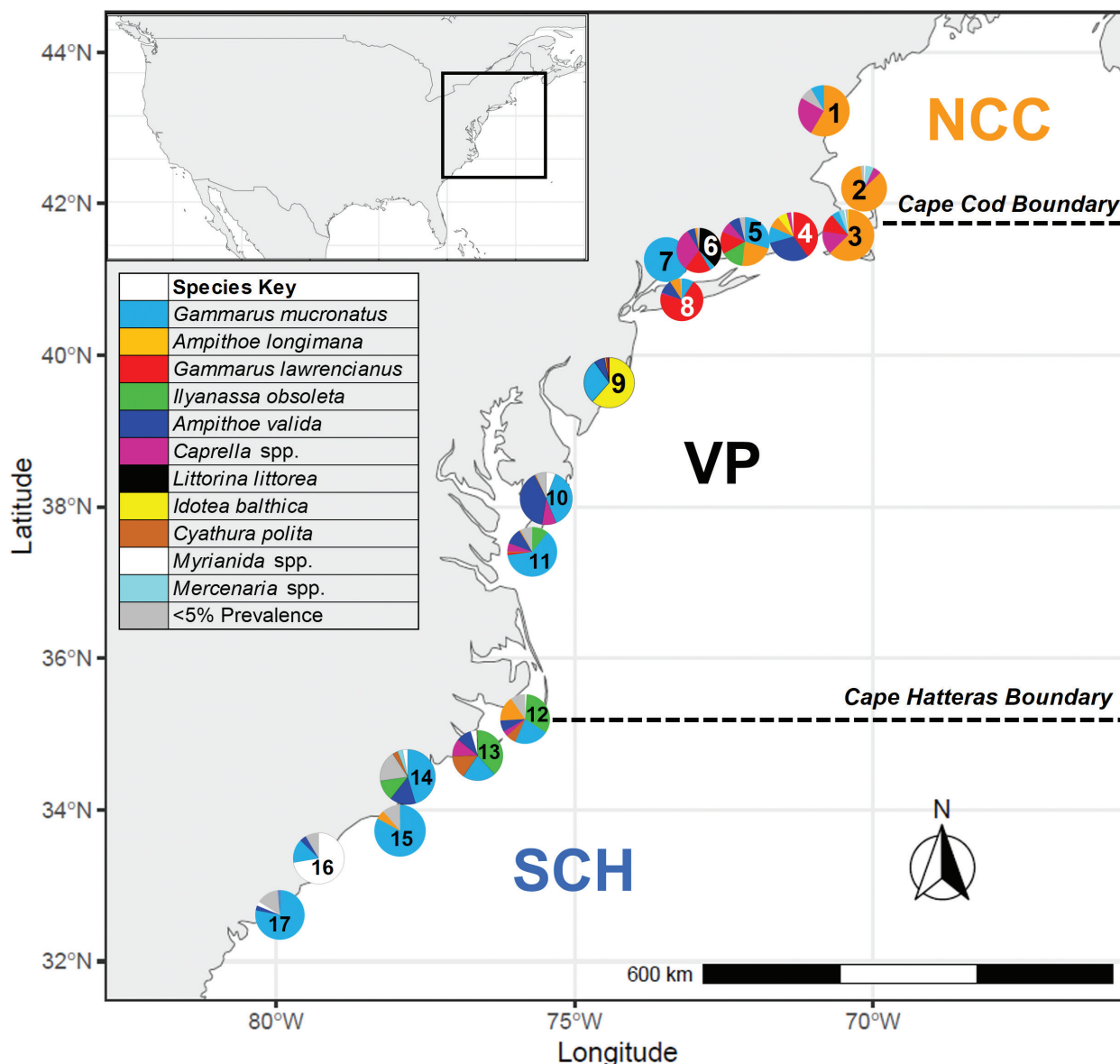


Figure 2. Map of sampled sites for May–August 2019 with ecoregion boundaries (Cape Cod and Cape Hatteras) and ecoregion labels: 1 = Durham, NH; 2 = Provincetown, MA; 3 = Millway Beach, MA; 4 = Sandy Point, RI; 5 = Warwick, RI; 6 = New Haven, CT; 7 = Bridgeport, CT; 8 = Northport, NY; 9 = Tuckerton, NJ; 10 = Chincoteague, VA; 11 = Quinby, VA; 12 = Ocracoke Island, NC; 13 = Harkers Island, NC; 14 = Wilmington, NC; 15 = Fort Fisher, NC; 16 = Georgetown, SC; 17 = Fort Johnson, SC. The pie pieces represent composition of free-living macroinvertebrates for each site (see species key). NCC = North of Cape Cod; VP = Virginian Province; SCH = South of Cape Hatteras. For the complete list of sampled sites and details, see Suppl. material 1: table S1.

4–9 ($n = 3$, avg = 23.5 °C). Water temperatures were taken in the shallow intertidal zone just before low tide (see below). For this study, since we were specifically interested in conducting a biogeographic study of macroinvertebrates along the temperate coastline of the U.S. east coast, and given the large swath of sites within VP vs. other biogeographic regions as well as the availability of sites with verified *G. vermiculophylla* presence/accessibility, the number of study sites per biogeographic region was uneven.

Sampling of associated free-living macroinvertebrates

We sampled each site for *G. vermiculophylla* in the shallow intertidal zone while thalli were still submerged before low tide. At each site, we established a 30-meter transect tape along the water-land interface, selected five random numbers (1–30) using a

random number generator (each number representing a meter marker on the 30-meter transect), and collected all *G. vermiculophylla* clumps from those five randomly selected 0.25 m² quadrats along the transect. We sampled environmental parameters (water temperature, salinity) using a handheld YSI Pro-1030 (Yellow Springs, OH).

We placed sealed bags of algae and water immediately into coolers and then transported them to the lab for processing. In the lab, we soaked the *G. vermiculophylla* from each replicate in a large bin filled with fresh tap water to induce osmotic shock in the associated mobile macroinvertebrates (e.g., Blakeslee et al. 2016; Fowler et al. 2016). We then used a Fisher Scientific™ 250 micron sieve to separate macroinvertebrates from macroalgae; upon separation, we preserved macroinvertebrates in Pharmaco™ 200 proof Ethyl Alcohol. After shaking off excess water, we weighed the thalli to obtain wet weights (g).

Following field surveys at all sites, macroinvertebrates were dyed with Rose Bengal (Gbogbo et al. 2020) and identified to the lowest possible taxonomic level using guidebooks and keys (Bousfield 1973; Johnson and Allen. 2012). Organisms were observed using a Zeiss MS Series Fixed Magnification Stereo Microscope (6×) and/or a Neatfi Elite XL HD Magnifying Lamp (5×). Gammaridean amphipods, which comprised up to 75% of the total macroinvertebrates at sites (see Results), can be difficult to identify to species level using morphology alone. We therefore classified amphipods into morphotypes and then later barcoded those morphotypes using standard DNA protocols (e.g., Blakeslee et al. 2020a). This allowed us to identify amphipods to species level by BLASTing our resultant sequence data for each morphotype using the NCBI database (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>).

Sampling of trematode parasites

We collected all *I. obsoleta* at the same sites as described above, except for Provincetown, MA, where *I. obsoleta* was not found (parasite data = 16 sites). We used the same 30-meter transect tape and 0.25 m² quadrats as above to collect snails; however, *G. vermiculophylla* and *I. obsoleta* were placed into separate bags. We counted all *I. obsoleta* per quadrat, and then randomly selected 100 snails across the five quadrats to dissect. Because birds are common final hosts for trematode parasites, we also counted the total number of birds by species (waders, seabirds, and dabblers) at each site using a point-count method, while standing stationary for 10 minutes (Byers et al. 2008). In the lab, we measured each live gastropod using digital calipers and then dissected gonad tissues under a Zeiss™ MS Series Fixed Magnification Stereo Microscope at 6× magnification. If infected, we identified the digenean trematode to species level based on its rediae/sporocyst and cercarial morphology using published images and keys and prior knowledge within the lab (Curtis and Hurd 1983; Curtis 1985; Esch et al. 2001; Blakeslee et al. 2012). At the snail stage, trematodes asexually produce hundreds to thousands of clones on a continual basis (i.e., the “reproductive firepower” of digenean trematodes; Rohde 2005); thus we did not count cercariae, rediae, or sporocysts within infected snails, as these do not represent genetically-distinct individuals (e.g., Blakeslee and Byers 2008).

Statistical analyses

To explore which factors best explained the patterns in the communities we observed, we used Generalized Linear Mixed Models (GLMM) in R 4.2.2 (package `glmmTMB`) for free-living macroinvertebrates (using site as a random effect, families = Gaussian for all response variables) and Generalized Linear Model (GLM) for parasites (families: prevalence = Binomial, richness = Poisson, diversity =

Gaussian). For parasite analyses, we used GLM models that included fixed effects only, because at each site, there were no replicates of response variables, since $n = 100$ snails were selected to be dissected randomly across all replicates. Due to the unevenness in detecting fixed versus free-floating *G. vermiculophylla* across sites, we did not have the number of replicates to analyze algal type (fixed or free-floating) as a predictor in our statistical models; as a result, we separately analyzed the abundance, richness, and diversity of macroinvertebrates associated with fixed and free-floating *G. vermiculophylla* thalli using two-tailed t-tests across all sites.

For free-living macroinvertebrates, we identified a strong positive and significant relationship between invertebrate raw counts, richness (number of species), and diversity index (Shannon-Wiener Diversity Index) with *G. vermiculophylla* biomass (Figure 3). To prevent overparameterization and to standardize the response variables, we adjusted our response variables with *G. vermiculophylla* biomass as an offset [abundance: square root(raw count/*G. vermiculophylla* biomass); richness: log(number of species/*G. vermiculophylla* biomass + 1); diversity: square root(Shannon-Wiener Diversity Index)]. We applied these transformations for these response variables to avoid zero variance problems in our models. For parasites, since we dissected an equal number of snails per site ($n = 100$) and all three response variables were obtained from those individuals, we did not need to standardize by *G. vermiculophylla* biomass. For parasites, prevalence was the proportion of infected *I. obsoleta* out of 100 randomly dissected snails per site; richness was the number of digenean species; and diversity was the Shannon-Weiner Diversity Index.

We selected biologically-relevant predictors for our models after testing for autocorrelations. For free-living organisms, these predictors were water temperature ($^{\circ}\text{C}$), salinity (PPT), and biogeographic region, with site as a random effect. Since our response variables were standardized by biomass of *G. vermiculophylla*, the biomass of the seaweed was not included as a predictor in these models to reduce overparameterization. We constructed rarefaction and extrapolation curves to determine the expected number of species per biogeographic region across accumulated individuals using EstimateS (v 9.1.0). For parasites, the predictors were *G. vermiculophylla* biomass (g), water temperature ($^{\circ}\text{C}$), salinity (PPT), average snail count, seabird and wading bird count, and biogeographic region (Suppl. material 1: tables S3–S5, S14–S16).

For both free-living and parasitic communities, we used the corrected Akaike's Information Criterion (AIC_c) to determine which model, or sets of environmental variables, best explained the dependent variables of free-living macroinvertebrates and parasites (package AICcmodavg). AIC_c compares multiple models with different combinations of independent variables (Anderson and Burnham 2002). We used ΔAIC_c of ≤ 2.0 as a cutoff value to determine the top models. Based on our AIC_c results and their selected predictors in top performing models, we conducted a series of univariate analyses to observe how response variables change for both free-living macroinvertebrates and parasites with key predictors.

For free-living macroinvertebrates, we used a Nonmetric Multidimensional Scaling (nMDS) plot to create a two-dimensional ordination plane to visually evaluate community composition among sites (Clarke and Warwick 2001). Per recommendations by Cao et al. (2001), we removed species that occurred $<5\%$ in nMDS analyses, and we used square-root transformation and Bray-Curtis Similarity (Clarke and Warwick 2001). For free-living and parasite organisms, we also conducted Similarity of Percentage (SIMPER) analyses to determine the percent each species contributed to the differences observed between biogeographic regions (Clarke 1993; Clarke and Warwick 2001). For free-living macroinvertebrates, we used abundance standardized by *G. vermiculophylla* biomass. These latter analyses and figures were created using PRIMER-e (v.7).

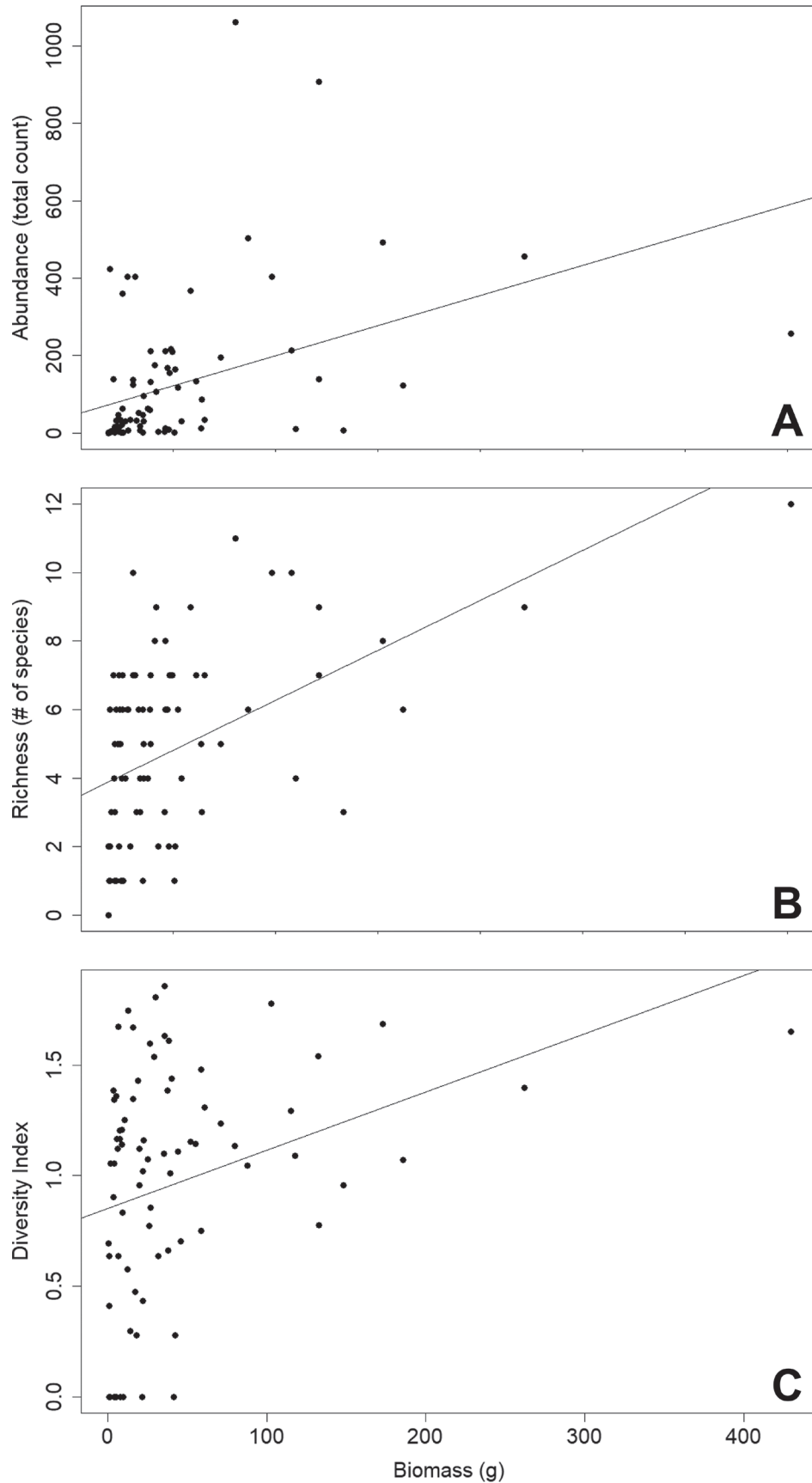


Figure 3. Relationships of *G. vermiculophylla* biomass with response variables of free-living macroinvertebrates: **A.** Abundance, or raw count ($R^2 = 0.407$, $p < 0.001$), **B.** Taxa richness, or number of species ($R^2 = 0.505$, $p < 0.001$), and **C.** Diversity, or Shannon-Wiener Diversity Index ($R^2 = 0.319$, $p = 0.004$).

Raw data, statistical analyses, and the supporting information file can be found as a Dryad dataset: <https://doi.org/10.5061/dryad.tht76hf4b>.

Results

Free-living organisms

Across all sampled sites, we found 39 free-living taxa ($N = 10,113$). Three Gammaridean amphipods (*Gammarus mucronatus*, *Ampithoe longimana*, and *Gammarus lawrencianus*) comprised >50% of all the free-living macroinvertebrates. When examining free-living diversity by bioregion, we found 13 NCC taxa ($N = 2,009$), 28 VP taxa ($N = 5,550$), and 20 SCH taxa ($N = 2,554$). Two amphipod species, *G. lawrencianus* and *G. mucronatus*, comprised >50% of the regional abundance in VP, while in NCC, the amphipod *A. longimana* comprised >80% of the total abundance, and in SCH, *Ilyanassa obsoleta* and *G. mucronatus* comprised >50% of the abundance (Figure 2; Suppl. material 1: table S2). Rarefaction and extrapolation curves of free-living mobile macroinvertebrates demonstrated a greater expected species richness in VP compared to NCC and SCH (Suppl. material 1: fig. S1), whereby the number of macroinvertebrate species associated with *G. vermiculophylla* in VP was expected to be 31 compared to the 28 species we observed. NCC was second highest at 25 expected species versus 13 observed, while SCH reached 23 expected species versus 20 observed. Thus, greater sampling effort is predicted to reveal 5 more species in VP, 12 in NCC, and 3 in SCH. Although we were able to sample VP more extensively than the other two regions, rarefaction analyses continued to show greater expected richness in VP.

In GLMM analyses of free-living macrofauna associated with *G. vermiculophylla* thalli across our sample sites, standardized by *G. vermiculophylla* biomass and transformed appropriately (see “Statistical Analysis”), we found that for abundance, the highest performing models were the model with 1) water temperature and biogeographic region as fixed effects ($\Delta\text{AICc} = 0$) and 2) the model with region only ($\Delta\text{AICc} = 1.64$) (Suppl. material 1: tables S3–S5). For richness, the top performing model had just biogeographic region as a fixed effect ($\Delta\text{AICc} = 0$) (Suppl. material 1: tables S6, S7). For diversity, the top performing model was the null model ($\Delta\text{AICc} = 0$) (Suppl. material 1: tables S8, S9). Based on the results from AICc, we created boxplots of abundance, richness, and diversity among biogeographic regions and conducted Kruskal-Wallis tests with pairwise comparisons of response variables (Figure 4). We found that abundance was significant between NCC and SCH ($p = 0.002$) and between NCC and VP ($p = 0.001$) (Figure 4A). Richness was significant between NCC and VP ($p < 0.001$) and between NCC and SCH ($p < 0.001$) (Figure 4B). Diversity was marginally significant only between NCC and VP ($p = 0.055$). Since water temperature was a fixed effect predictor in the top performing model for abundance, we also ran a regression between abundance and water temperature, and found that abundance had a negative relationship ($R^2 = -0.443$, $p < 0.001$) with increasing temperature (Figure 5). We also used a two-tailed t-test to compare the abundance, richness, and diversity of free-living macroinvertebrates between *G. vermiculophylla* types (fixed and free-floating). None of the response variables were significantly different between fixed and free-floating *G. vermiculophylla* ($p > 0.05$) (Suppl. material 1: fig. S2).

Finally, in nMDS plots, we found some separation of free-living macroinvertebrate assemblages with biogeographic region (Figure 6). In particular, NCC sites were relatively distinct in their communities from SCH, while VP overlapped more with the other biogeographic regions, especially SCH. In part, this could

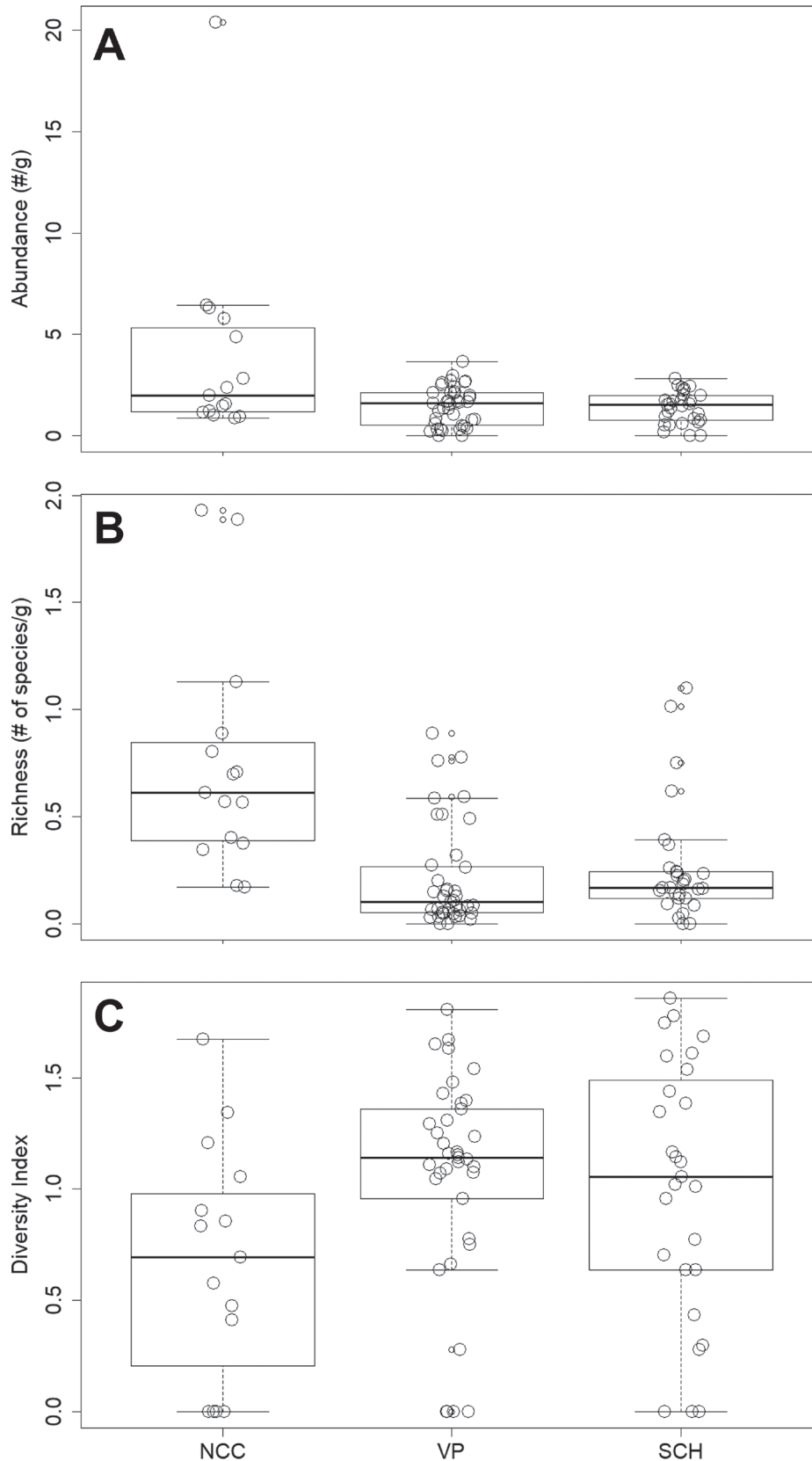


Figure 4. Boxplots of free-living **A.** Abundance, or count/grams of *G. vermiculophylla* square-root transformed (significant pairs between NCC and SCH: $p = 0.002$, NCC and VP: $p = 0.001$), **B.** Richness, or number of species/grams of *G. vermiculophylla* $\log(x+1)$ transformed (significant pairs between NCC and VP: $p < 0.001$, NCC and SCH: $p < 0.001$), and **C.** Diversity, or Shannon-Wiener Diversity Index square-root transformed (marginally significant pair between NCC and VP: $p = 0.055$) across biogeographic regions. NCC = North of Cape Cod, VP = Virginian Province, SCH = South of Cape Hatteras. Black circles represent each replicate (jittered).

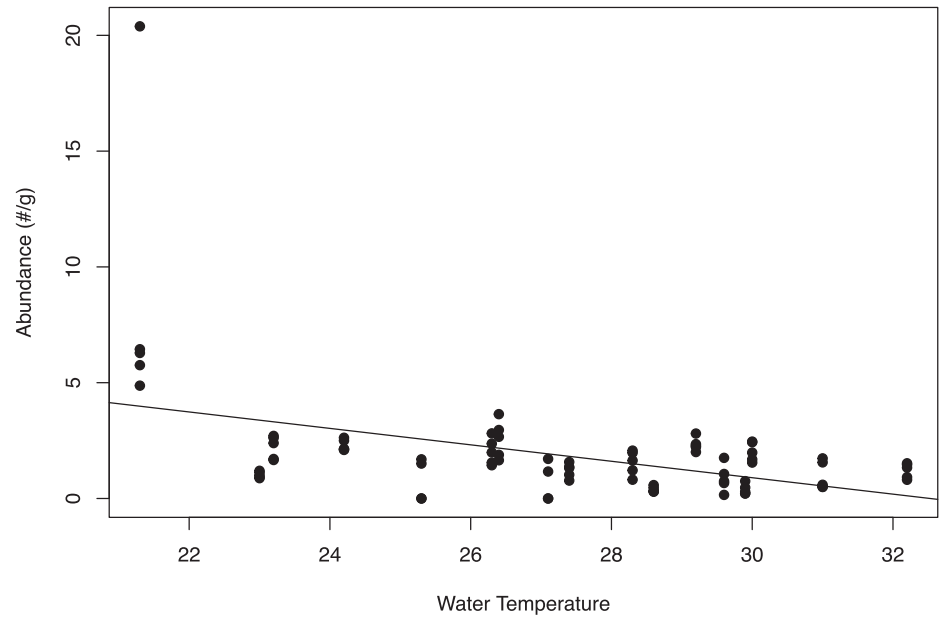


Figure 5. Relationship between water temperature (degrees Celsius) and abundance, or raw counts/ biomass of *G. vermiculophylla* square-root transformed ($R^2 = -0.443$, $p < 0.001$).

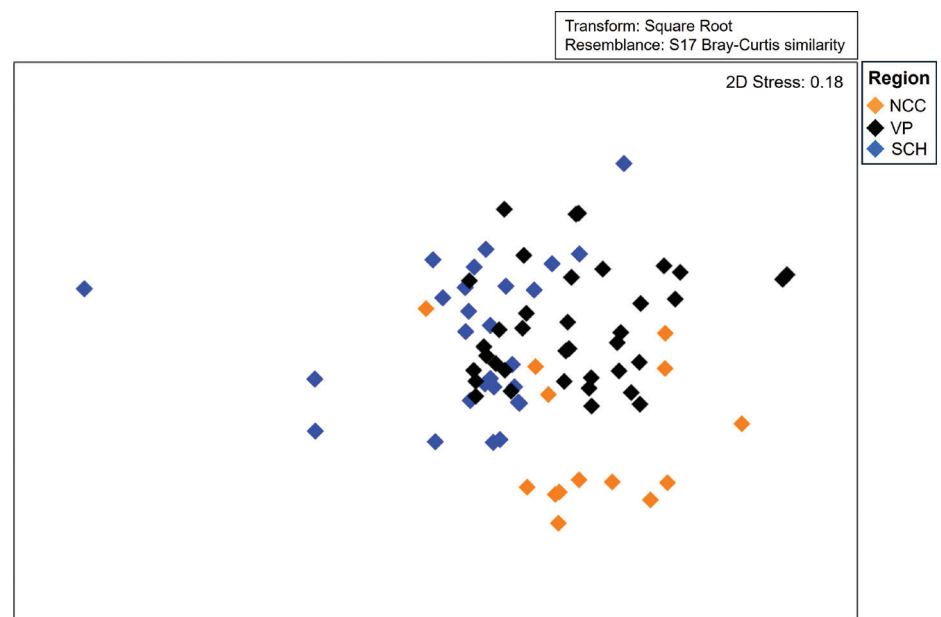


Figure 6. Non-metric multidimensional scaling plot of free-living macroinvertebrate abundances/grams of *G. vermiculophylla* by biogeographic region. Samples that are closer to each other are more similar in terms of species composition and evenness. Species with <5% occurrence have been removed.

be attributed to differences in key community members. For example, in NCC, the amphipod *A. longimana* contributed to >80% of abundance, and in VP, the two amphipods *G. mucronatus* and *G. lawrencianus* contributed to >50% of abundance, while in SCH, *I. obsoleta* and *G. mucronatus* contributed >50% of abundance (Suppl. material 1: table S2). Moreover, some replicate assemblages in SCH differed from other replicates within the same biogeographic zone because they were comprised of only one or two individuals (e.g., one count of *Myrianida* spp.), a combination that was not found in other replicates. When comparing macroinvertebrate assemblages between biogeographic regions using SIMPER, three spe-

cies of Gammaridean amphipods - *G. mucronatus*, *G. lawrencianus*, and *A. valida*, and the snail *I. obsoleta* - together contributed to the greatest dissimilarity (>50%) of macroinvertebrate assemblages between SCH and VP (Suppl. material 1: table S10). When comparing between SCH and NCC, and between VP and NCC, two species of Gammaridean amphipods - *A. longimana* and *G. mucronatus*, and the skeleton amphipod *Caprella* spp. together contributed to the greatest dissimilarity (>50%) between the biogeographic regions (Suppl. material 1: tables S11, S12).

Trematode parasites

Across all sample sites, we found nine digenean trematode taxa (N = 183 infected *I. obsoleta* out of 1,600 dissected), with *Lepocreadium setiferoides* and *Gynaecotyla adunca* comprising >50% of the infected snails (Suppl. material 1: table S13). In NCC, *Zoogonus lasius* and *Himasthla quissetensis* comprised >50% of the infected snails, while *L. setiferoides* and *Z. lasius* comprised >50% in VP. Finally, >70% of the infected snails were parasitized by *G. adunca* in SCH (Suppl. material 1: table S13).

In GLM analyses, the model with *G. vermiculophylla* biomass best predicted ($\Delta\text{AICc} = 0$) trematode prevalence and richness; however, biomass was not significant in either model (Suppl. material 1: tables S14–S17). The second-best model ($\Delta\text{AICc} = 1.39$) for trematode richness included biogeographic region, and this was a significant predictor, demonstrating declining richness from NCC to VP to SCH (Suppl. material 1: table S18). The model with biogeographic region best predicted ($\Delta\text{AICc} = 0$) trematode diversity (Suppl. material 1: table S19) and was significant (Suppl. material 1: table S20). In a graphical examination of diversity across biogeographic regions, there was a trend for trematode diversity declines from north to south (Figure 5). The second-best model ($\Delta\text{AICc} = 0.93$) for trematode diversity included *G. vermiculophylla* biomass only, but this was not significant (Suppl. material 1: table S21). In addition, in linear regression analyses, we found trematode prevalence, richness, and diversity all demonstrated trends for declines with increasing *G. vermiculophylla* biomass; however, these trends were not significant (Suppl. material 1: fig. S3).

In SIMPER analyses, we found that between SCH and VP, *L. setiferoides*, *G. adunca*, and *Z. lasius* were the greatest contributors to dissimilarity, with *L. setiferoides* and *Z. lasius* having higher prevalence in VP, and *G. adunca* having higher prevalence in SCH. When comparing SCH and NCC, we found that *H. quissetensis*, *Z. lasius*, and *G. adunca* were the greatest contributors to the dissimilarity between these two regions, with *H. quissetensis* and *Z. lasius* having higher prevalence in NCC, and *G. adunca* having higher prevalence in SCH. Finally, when comparing NCC and VP, we found that *H. quissetensis*, *L. setiferoides*, and *Z. lasius* were the greatest contributors to the dissimilarity between these two regions, with *L. setiferoides* having higher prevalence in VP, and *H. quissetensis* and *Z. lasius* having higher prevalence in NCC (Suppl. material 1: tables S22–S24).

Discussion

Foundation species can influence ecosystem structure and function by accommodating communities of associated fauna, creating microclimates, and reducing negative impacts of severe environmental events (Ellison et al. 2005; Franssen et al. 2011; Schob et al. 2012). Non-native foundational species can also greatly impact biodiversity and community structure in novel communities by influencing the diversity of associated organisms, like macroinvertebrates in aquatic systems (Dijkstra et al. 2017). Past work has shown the invasive alga *G. vermiculophylla* can provide

structured habitat for a diverse array of macroinvertebrates, and in some cases, may even harbor a greater abundance of associated organisms than some native macroalgae (Thomsen et al. 2009, 2013). In addition, more localized studies, such as from the Chesapeake Bay, have indicated that *G. vermiculophylla* may serve as nursery habitat for commercially important species, like blue crabs, as the density of some foundation species have declined (Johnston and Lipcius 2012; Wood and Lipcius 2022). Yet, though this alga is widespread and has been established in some U.S. East Coast locations for decades, prior to our study, there were no published community surveys of associated organisms at the broader biogeographic scale. This incomplete understanding highlights the substantial lag times that may exist in some investigations of non-native species even among widespread and perceptible species invasions (Crooks 2005). Altogether our results can help advance understanding of community response to foundation species introductions in this era of rapid global change.

Associated macroinvertebrates with *Gracilaria vermiculophylla*

Gracilaria vermiculophylla provides three-dimensional structure that can offer niche space for numerous macroinvertebrate species (Thomsen et al. 2013), as we detected in our study along the U.S. East Coast (Figure 2). Indeed, other studies have found *G. vermiculophylla* can serve as habitat for a number of macroinvertebrate species (Thomsen et al. 2007; Thomsen 2010; Thomsen et al. 2013), including native blue crabs (Johnson and Lipcius 2012), Gammaridean amphipods (Wright et al. 2014), and several other native estuarine and marsh macroinvertebrates, with the classes Malacostraca and Gastropoda most common (Nyberg et al. 2009). There is also evidence for preferential egg deposition by the eastern mudsnail, *I. obsoleta*, on *G. vermiculophylla* (Guidone et al. 2014).

Prior to the introduction of *G. vermiculophylla*, the coastlines of South Carolina and Georgia had been historically low in consistent biomass of structurally complex macroalgae and seagrass species (Sandifer 1980). Post-introduction, *G. vermiculophylla* has not only dramatically transformed the appearance of these systems, but has provided novel habitat for crustaceans and gastropods (Byers et al. 2012). In fact, the native tube-building polychaete (*Diopatra cuprea*) may be a contributor to this transformation of habitat complexity in what otherwise would be soft-sediment habitats with relatively low macroalgal biomass (Byers et al. 2012; Kollars et al. 2016). These polychaetes incorporate and then anchor drifting *G. vermiculophylla* thalli to their tubes, with a recent study suggesting that this incorporation may be preferential over other offered macrophytes (Mott et al. 2022). Thus, through this relationship, where the worm stabilizes free-living *G. vermiculophylla* thalli to the benthos, algal biomass in some systems has become enhanced (Thomsen et al. 2009; Byers et al. 2012; Kollars et al. 2016; Berke 2022; Mott et al. 2022).

Of the associated free-living species we detected in our study, the most dominant taxa across all biogeographic regions were Gammaridean amphipods (Figure 2, Suppl. material 1: table S2). Within the Gammarideans, two species were most prominent: *Ampithoe longimana*, which is a grazer, and *Gammarus mucronatus*, which is a generalist (Fredette and Diaz 1986; Duffy et al. 1994, 2001). While macroinvertebrate grazers and generalists are commonly found associated with *G. vermiculophylla*, past work has suggested many associated species are using this alga as habitat rather than a direct food source (Nejrup and Pedersen 2012; Wright et al. 2014). For example, in experimental trials, Weinberger et al. (2008) found that native macroinvertebrates preferred to graze on native macroalgae over *G. vermiculophylla*; however, their field surveys showed that macroinvertebrates preferred *G. vermiculophylla* as refuge over native macroalga in winter months. Alternatively,

other studies have suggested that *G. vermiculophylla* could lower abundance and diversity of associated organisms (Berke 2022). For example, Keller et al. (2019) observed that during super-blooms of *G. vermiculophylla*, the tube-forming polychaete *Diopatra cuprea* declined in abundance, possibly due to the alga limiting oxygen flow and thereby increasing anoxic conditions.

The influence of biogeographic region

Across the northwest Atlantic coastline, there are four major biogeographic provinces: 1) Boreal Province, which ranges from Nova Scotia to Cape Cod, 2) Virginian Province, which ranges from Cape Cod to Cape Hatteras, 3) Carolinian Province, which ranges from Cape Hatteras to Cape Canaveral, and 4) Caribbean Province, which ranges from Cape Canaveral to the Caribbean Islands (Johnson 1934). In our study, *G. vermiculophylla* crosses two biogeographic breaks at Cape Cod and Cape Hatteras; thus we analyzed diversity patterns north of Cape Cod (to New Hampshire), between Cape Cod and Cape Hatteras (i.e., Virginian Province), and south of Cape Hatteras (to South Carolina). Past work has demonstrated provinces to be characterized by differing species assemblages. For example, Cerase-Vivas and Gray (1966) found significantly different macroinvertebrate assemblages when comparing North Carolina sites north and south of Cape Hatteras, while Coomans et al. (1962) found significantly different mollusk compositions between the Virginian Province and the Carolinian Province. Moreover, an extensive macroinvertebrate survey by Engle and Summers (1999, 2000) found Cape Cod and Cape Hatteras acted as major dispersal barriers, with macroinvertebrate composition differing significantly north and south of these geographic boundaries. Cape Cod is widely recognized as the northernmost defining ecoregion boundary of the eastern U.S., since it is the northernmost limit for many species that occur within the Virginian Province (Hale 2010). Cape Cod also acts as the southernmost limit for arctic and boreal species, particularly mollusks (Franz and Merrill 1980). Further south, Cape Hatteras has been found to reduce intraspecific gene flow, since parcels of water from the Gulf Stream traveling northward along the eastern U.S. are deflected northeast, thereby preventing homogeneity of climate across this boundary and creating different microclimates (Boehm et al. 2015).

In our investigation, we similarly found biogeographic region to influence associated macroinvertebrates with *G. vermiculophylla* (when accounting for algal biomass), with the greatest abundance and richness of macroinvertebrates in NCC and the greatest diversity in VP (Figure 4). Rarefaction and extrapolation curves indicated the highest predicted richness of associated macroinvertebrate diversity to be VP, followed by NCC, and lastly SCH (Suppl. material 1: fig. S1). Non-metric multidimensional scaling plots also demonstrated shifting communities with biogeographic region (Figure 6), suggesting that Cape Hatteras and Cape Cod also differentiate invertebrate communities associated with *G. vermiculophylla*. The Virginian Province had the largest representation in our dataset given that *G. vermiculophylla* is found throughout this entire province, while it only presently exists up to New Hampshire within the Boreal Province. For the Carolinian Province, we captured its range to South Carolina (it exists as far south as Georgia; Krueger-Hadfield et al. 2017). Thus, we likely better captured associated diversity with *G. vermiculophylla* in the VP, given its predominance in this region. It may be that VP is better climactically for this temperate algal species (i.e., SCH may become too warm in the summer and NCC too cold in the winter).

The physical environment also changes across these biogeographic regions, with greater hard substratum in the northern portion of the alga's range, which may

have influenced the abundance and richness of associated macroinvertebrates. In nature, the presence or absence of hard substratum leads to differences in whether thalli are fixed by holdfasts versus drifting/free-living following detachment from the hard substratum. When there is abundant hard substratum, gametophytes and tetrasporophytes are common (Krueger-Hadfield et al. 2016; Krueger-Hadfield 2018; Krueger-Hadfield unpublished data). By contrast, when found in soft sediment habitats, the tetrasporophytes consistently dominate in both the native and non-native range (Krueger-Hadfield et al. 2017). It is possible that the fixed type provides more stability for associated organisms than free-floating, as it is more stationary and may prevent organisms from getting dislodged as opposed to the free-floating type. Furthermore, fixed thalli have been shown to possess greater genotypic diversity than free-living thalli (see Krueger-Hadfield et al. 2016, 2017 for genotypic data at some of the same sites sampled here), which has been predicted by Krueger-Hadfield et al. (2019) to promote greater abundance and richness of associated faunal communities (i.e., genetic diversity promotes taxonomic diversity). Our examinations of diversity between fixed and free-floating *G. vermiculophylla* did not yield major differences; however, experimental work is needed to investigate community assembly and diversity depending on the substratum type in a more explicit way, particularly in large, expansive mudflats where *G. vermiculophylla* biomass can be substantial (Krueger-Hadfield and Ross 2022).

Trematode diversity in a co-occurring snail host

Digenean trematodes have complex, multi-host life cycles that typically include two to three different hosts and alternate between trophically transmitted parasitic and free-living environmental stages (Rohde 2005). Trematodes are therefore influenced by multiple abiotic and biotic forces during their environmental stages, as well as influences upon and by their hosts during their parasitic stages. Thus, drivers of trematode diversity in systems are likely to come from multiple sources. In our investigation of trematode communities infecting *I. obsoleta* (an abundant gastropod that co-occurs with *G. vermiculophylla* throughout our study region), we found *G. vermiculophylla* biomass to be the best predictor of trematode prevalence and richness, and second-best predictor of trematode diversity. Interestingly, the relationship between *G. vermiculophylla* and trematodes was negative (albeit these linear trends were not significant; prevalence was marginal at $p = 0.0865$; Suppl. material 1: fig. S3). We had initially predicted the opposite trend: a positive association between *G. vermiculophylla* and trematodes given past work demonstrating *G. vermiculophylla* can enhance the presence of vertebrate species that act as final hosts for trematodes, like wading birds (Haram et al. 2018). Indeed, prior studies examining driving factors of trematode prevalence in snails have identified final hosts to be a key predictor. For example, in the marine snail *Littorina littorea*, Byers et al. (2008) found prevalence of infection to be primarily influenced by average snail size and bird count. In this *Littorina* trematode system, nearly all parasite species infecting *L. littorea* use birds as final hosts (Blakeslee and Byers 2008); whereas, in our system, *I. obsoleta* is infected by trematodes that use birds, fish, and diamondback terrapins as final hosts (Blakeslee et al. 2012, 2020b; Phelan et al. 2016). While we counted definitive bird hosts (waders, seabirds, and dabblers) at each site, we did not collect information on fish abundance and diversity. As a result, our understanding of the influence of host abundance on parasite diversity was limited. In addition, because we targeted sites to collect faunal data associated with *G. vermiculophylla*, we did not sample sites without *G. vermiculophylla*, instead using *G. vermiculophylla* biomass to investigate the potential effect on trem-

atode diversity. Future work examining sites with and without *G. vermiculophylla* could be designed with an explicit goal of determining how the presence and biomass of *G. vermiculophylla* influences parasitic diversity and parasite transmission across multiple host species.

Our analyses also found biogeographic region was the top predictor of trematode diversity (Figure 7) and second-best predictor of trematode prevalence and richness, with significant differences identified between the northern-most (NCC) and southern-most (SCH) biogeographic regions (Figure 5). Overall, our southern sites were dominated by just a few trematode species that predominantly use fish as final hosts, while trematode diversity was more evenly spread out across the northern sites with trematode species using both fish and birds as final hosts. This observation is similar to a past biogeographic study of trematode parasites in *I. obsoleta* along the U.S. East Coast, where trematode infections in southern sites were dominated by trematode species that predominantly use fish as definitive hosts (Blakeslee et al. 2012, 2020b). Though often cryptic, parasites can be strong drivers of community structure and function, as well as the evolutionary ecology of their hosts. While most studies involving community structure have focused on connections among free-living organisms, recent studies have demonstrated that parasites are pivotal and integral components of communities and food webs (Huxham et al. 1995; Lafferty et al. 2008; Moore et al. 2023). Future work in this system could help elucidate the influence that species invasions and global change are having on foundational species and how those changes affect the community composition and diversity of parasites along the U.S. East Coast.

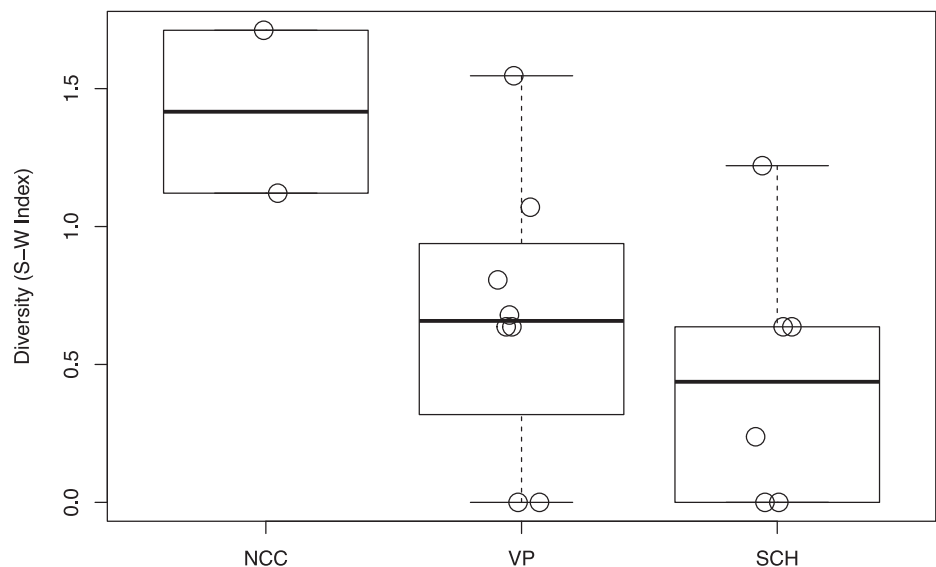


Figure 7. Boxplot of trematode diversity (Chi-sq = 4.36, $p = 0.113$). NCC = North of Cape Cod; VP = Virginian Province; SCH = South of Cape Hatteras; S-W Index = Shannon-Wiener Diversity Index. Black circles represent each replicate (jittered).

Conclusions

Though *G. vermiculophylla* has been present along the U.S. East Coast for decades, our study represents the first large-scale biogeographic examination of mobile macroinvertebrate communities associated with *G. vermiculophylla* in its non-native range along the U.S. Atlantic Coast. We found *G. vermiculophylla* to provide structure and habitat for a diverse assemblage of associated macroinvertebrates, which are essential species in food webs and critical for sustaining

healthy ecosystems (Luczkovich et al. 2002; Alfaro 2006; Chaplin and Valentine 2009; Medina-Contreras et al. 2020). Specifically, biogeographic region was the main predictor driving observed patterns of abundance, richness, and diversity in free-living macroinvertebrates associated with the non-native macroalga. However, the long-term effects of *G. vermiculophylla* presence in these communities requires further monitoring and investigation. This study, while biogeographic in scale, represents a single snapshot in time; thus future sampling across multiple years and seasons is needed to assess how free-living macroinvertebrates are shaped by *G. vermiculophylla* spatially and temporally. Moreover, sampling native macrophytes would also allow us to determine how much overlap there may be between macroinvertebrate communities associated with native foundational species and *G. vermiculophylla* in these systems. Targeted sampling of parasite communities with and without *G. vermiculophylla* would also allow us to determine the influence of *G. vermiculophylla* on parasite diversity metrics. Overall, with continued investigation, it may be possible to generate a more comprehensive understanding of community associations with *G. vermiculophylla* that integrates both free-living and parasitic organisms.

Author Contributions

Research conceptualization: TSL, AEF, SAKH, AMHB; sample design and methodology: TSL, AEF, SAKH, AMHB; investigation and data collection: TSL, AEF, SAKH, CG, AMHB; data analysis and interpretation: TSL, AEF, SAKH, AMHB; ethics approval: TSL, AMHB; funding provision: TSL, AMHB; roles/writing - original draft: TSL, AMHB; writing - review & editing: TSL, AEF, SAKH, CG, AMHB.

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Ethics and Permits

Field collections were authorized by the North Carolina Division of Marine Fisheries (Scientific or Educational Permit #706671). Animal husbandry protocols were approved by East Carolina University's (ECU) Institutional Animal Care and Use Committee (Animal Use Protocol #D346).

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Supplementary material 1

Supporting information

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