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ORIGINAL PAPER

Non-uniform consumption of a novel, non-native seaweed by native consumers

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Abstract Introduced seaweeds can alter the structure and productivity of marine food webs, especially when they lack top-down control by native herbivores. However, relatively little is known about the role of consumption of introduced seaweeds by native herbivores, and the potential role of seaweed nutrient content to mediate local herbivore consumption. In southeastern USA estuaries, the introduced red seaweed, *Gracilaria vermiculophylla*, has transformed unvegetated intertidal mudflats into a patchwork of non-native seaweed beds. We used a series of laboratory feeding assays to assess how invertebrate and fish species on the Georgia coast utilize *G. vermiculophylla* as a novel food resource. Because *G. vermiculophylla* readily absorbs nutrients, we also tested the role of nutrient enrichment on its consumption. We found that *G. vermiculophylla* was not significantly consumed by the mud snail *Ilyanassa obsoleta* nor the mud crab *Eurypanopeus despressus*, but it was rapidly eaten and even preferred over the native seaweed *Ulva lactuca* by adult pinfish *Lagodon rhomboides*. Nutrient enrichment of *G. vermiculophylla* did not affect consumption rates by the amphipod *Ampithoe valida*, but did double consumption rates by pinfish over unenriched seaweed. The differential responses of native consumers highlight the importance of evaluating multiple species when investigating introduced species' impacts on recipient communities. Given that consumer identity and nutrient content of the seaweed mediated the consumption of the non-native seaweed, site-specific patterns of consumer populations and environmental conditions could lead to patchy abundance and impacts of the non-native seaweed.

Keywords Diet breadth · Enemy escape · Herbivory · Marine algae · Novel prey · Secondary metabolites

Introduction

Across ecosystem types, one of the proposed causes for rapid expansion of introduced primary producers is the enemy escape hypothesis that can stem from the lack of top-down control by native herbivores (Keane and Crawley 2002; Callaway and Ridenour 2004; Thomsen et al. 2016). While some non-native seaweeds appear to fit this pattern of escape from native herbivore control (e.g., Gollan and Wright 2006; Monteiro et al. 2009; Nejrup et al. 2012; Wright et al. 2014), many marine generalists consume a wide range of resources, including non-native seaweeds (e.g., Pedersen et al. 2005; Pedersen et al.

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2016; Sumi and Scheibling 2005; Cummings and Williamson 2008; Britton-Simmons 2004; Thomsen et al. 2016). The incorporation of non-native seaweeds into native grazer diets can reduce competition among grazers, alleviate stress from dwindling native resources, and provide more nutrient-rich resources for native consumers (Nejrup et al. 2012). In nearshore regions where native macroalgal production is low, non-native macroalgae may benefit native consumers by increasing the diversity and abundance of basal resources (Rodriguez et al. 2006). However, if native herbivores do not consume non-native seaweeds, introduced seaweeds left unchecked can outcompete native primary producers and further reduce food availability. Thus, understanding the foraging preferences of native grazers is necessary to determine the effects of non-native seaweeds on recipient ecosystems' trophic structures.

Herbivore food preferences are dictated by resource traits, including morphology, chemical defenses, nutritional quality, and availability (Nicotri 1980; Hay 1991, 1996; Duarte et al. 2010. 2011; Jiménez et al. 2015). Seaweeds are particularly plastic in their responses to biotic and abiotic conditions (Pelletreau and Targett 2008), and a single population can express an array of chemical, nutritional, and structural traits. For example, despite their ubiquity in marine systems, chemical defenses can vary within a single seaweed population based on genetic variation, environmental conditions, and herbivore pressure (Hay 1996; Hay and Fenical 1996; Van Alstyne et al. 2007; Jormalainen and Honkanen 2008). Furthermore, the chemical defenses and nutritional quality of macroalgae can be linked because nutrient availability can drive tradeoffs in growth and generation of secondary compounds in seaweeds (Stefels 2000; Pavia and Toth 2008). Though seaweed traits exist on a continuum in nature, few studies have investigated how variability in non-native seaweed traits, such as C:N content, affect herbivory by native grazers.

The responses of native herbivores to an introduced primary producer can vary. Commonly, marine invertebrate grazers are the focus of invasive seaweed-herbivore interaction studies, yet herbivorous fish (and sometimes turtles) can shape seaweed communities (e.g., Ojeda and Munoz 1999). Despite fundamental differences in size, mobility, and nutrient requirements between herbivorous invertebrates and fish, few studies have simultaneously tested the feeding preferences of diverse species with non-native seaweeds (Enge et al. 2017). Our current understanding of native and non-native plant–herbivore interactions may underestimate the incorporation of non-native primary producers into marine trophic structures.

The recent invasion of the South Atlantic Bight, USA by *Gracilaria vermiculophylla,* a rhodophyte native to Asia, provides an opportunity to investigate the role of a novel, non-native basal resource in native herbivore diets across different trophic levels. *Gracilaria vermiculophylla* was first documented on the east coast of North America in North Carolina in the early 2000s (Freshwater et al. 2006) and was likely cryptically introduced to Georgia around that time; though, the first record of the non-native seaweed in Georgia did not occur until nearly a decade later (Byers et al. 2012). Its rapid spread, tolerance to harsh environmental conditions, lack of competition, and mutualistic relationship with the native tubeworm *Diopatra cuprea* have led to its current dominance on intertidal mudflats throughout the southeastern USA (Thomsen and McGlathery 2007; Byers et al. 2012; Kollars et al. 2016). In much of *G. vermiculophylla*'s non-native range, native submerged aquatic vegetation, such as seaweeds and seagrasses, are diverse and abundant. However, the estuaries and coast of Georgia have low production and diversity of native seaweeds, likely due to high turbidity, high sedimentation of soft sediments, and a general scarcity of hard substrate needed for attachment. For example, *G. vermiculophylla* represented 90–100% of macroalgal biomass at sites surveyed along the coasts of South Carolina and Georgia, with the native *Ulva* spp. representing the remaining biomass (Byers et al. 2012). In this area, *G. vermiculophylla*'s novel structure is an important habitat resource for epifaunal invertebrates, harboring greater densities than the previously unvegetated mudflat (Byers et al. 2012; Wright et al. 2014). Despite the prevalence of *G. vermiculophylla* in southeastern estuaries and its role as preferred habitat for many herbivorous species, little is known about the seaweed's role as a novel food source for native, generalist consumers (Wright et al. 2014).

Prior to the introduction of *G. vermiculophylla*, primary productivity in southeastern estuaries originated from the detritus of *Spartina alterniflora* stands (Teal 1962) and from benthic and planktonic microalgae (Mann 1988). Because seaweeds can provide more readily digestible and more nutrient rich primary production than co-occurring marine vascular plants (Mann 1988; Hay and Steinberg 1992; Duarte et al. 2010; Haram et al. 2020), the novel, non-native seaweed may be an attractive resource for generalist consumers in these ecosystems. In fact, *G. vermiculophylla* is known for its fast absorption of nitrogen, making *G. vermiculophylla* a potentially nutritious resource (Abreu et al. 2011a,b; Pedersen and Johnsen 2017). However, previous work suggests that high levels of chemical defenses in *G. vermiculophylla* tissue deter invertebrate grazers in the seaweed's introduced range (Nylund et al. 2011; Rempt et al. 2012; Hammann et al. 2016), though some species consume *G. vermiculophylla* despite the presence of inhibitory compounds (Weinberger et al. 2008). Furthermore, the strength of herbivory can be nuanced, with seasonality and diversity of native resources affecting consumption of the non-native seaweed (Weinberger et al. 2008; Nejrup et al. 2012).

To investigate how *G. vermiculophylla* is utilized by common, generalist consumers in southeastern estuaries, we conducted laboratory feeding assays across diverse potential consumers. For the epifaunal invertebrates, we tested the mud crab *Eurypanopeus depressus*, the mud snail *Ilyanassa obsoleta*, and the amphipod *Ampithoe valida*. These macroinvertebrates are commonly associated with *G. vermiculophylla* on intertidal mudflats in Georgia, USA (Byers et al. 2012; Bishop and Byers 2015; Haram et al. 2018, 2020) and are known to consume algae and other plant material (MacDonald 1982; Cruz-Rivera and Hay 2000; Lohrer et al. 2000; Giannotti and McGlathery 2001; Douglass et al. 2011; Reynolds et al. 2012). We also selected the native pinfish *Lagodon rhomboides*. This species is one of the most abundant bait fish in estuarine waters of the southeastern USA (Stoner 1980). They also undergo an ontogenetic dietary shift as they mature, with older fish consuming more macrophytes (Stoner 1980; Winemiller et al. 2007). Due to their high abundance and their mixed diets, *L. rhomboides* are responsible for shaping epifaunal communities and organic matter cycling through substantial consumption of plant material and epifaunal invertebrates during peak seasonal abundances in the spring and summer (Adams 1976; Nelson 1979; Stoner 1980), making them a possible pathway for *G. vermiculophylla* entering into the estuarine trophic structure. Given that our selected consumers are generalists, we hypothesized that the native grazers would eat *G. vermiculophylla* in both choice and no-choice assays.

We also assessed how nutrient enrichment of the seaweed affects its consumption, again using laboratory feeding assays. We hypothesized that higher nutrient content would make the non-native resource more attractive to native grazers, thus increasing consumption by generalist grazers across experiments. Our experimental assays demonstrate how *G. vermiculophylla* may be integrated into southeastern estuarine food webs, including what native species consume it and possibly limit its abundance.

Methods

Site description

All feeding experiments were conducted in a flow-through seawater system at the Skidaway Institute of Oceanography in Savannah, Georgia. Invertebrates and seaweed were collected from a single site at Priest Landing, Savannah, Georgia (31°57′43.88"N, 81° 0′46.00"W) to reduce variability in consumer condition and seaweed quality. However, *Ulva lactuca*, the native, low-abundance seaweed was collected from one site at the Grice Marine Laboratory in Charleston, South Carolina (32°45′3.93"N, 79°54′5.85"W) in 2014 due to very low abundances in Savannah, Georgia. All seaweeds were defaunated prior to use by rinsing the tissue with filtered seawater and removing any remaining invertebrates and eggs by hand.

Native versus non-native feeding assays

Epifaunal Invertebrate Consumers To test if the selected generalists consume the non-native seaweed when native food resources are not available, we conducted a no-choice feeding assay. We paired this with a choice assay to determine if consumption of the non-native seaweed was consistent when multiple resources were available. Using the mud crab *Eurypanopeus depressus* and the mud snail *Ilyanassa obsoleta*, we conducted the epifaunal invertebrate choice and no-choice feeding assays in July 2014. For each assay, we collected all invertebrates from the mid-intertidal region. We haphazardly collected large *I. obsoleta* individuals (10–18 mm) from the mudflat. Snails were not sexed due to the difficulty of non-destructively distinguishing between sexes. We collected *E. depressus* by extracting oyster clumps, which are its habitat, and removing the crabs from the oysters. We kept only *E. depressus* (9–11 mm) with both claws intact for the experiment. Snails and crabs were housed separately in plastic containers with mesh sides in the flow-through seawater system prior to the assays.

We conducted *E. depressus* and *I. obsoleta* assays simultaneously with ten replicates of each treatment level. A single invertebrate was housed in an individual tubular PVC container (3.81 cm diameter x ~ 12 cm depth) with 0.5 mm mesh secured to the openings that allowed for seawater circulation. For the no-choice assays, we placed ~ 0.5 g wet mass (wm) of either *G. vermiculophylla* or *U. lactuca* in each container. All macroalgae were spun in a salad spinner for 30 s before weighing to remove excess water and standardize wet mass measurements. For the choice assays, ~ 0.5 g wm of both *G. vermiculophylla* and *U. lactuca* were placed simultaneously into the container of each *I. obsoleta* and *E. depressus*. We included paired autogenic controls (n = 10 for each seaweed) of the same quantity of each seaweed species, held in consumer-free containers, to account for natural variability in macroalgal biomass due to photosynthesis and decomposition of the macroalgae during the experiment (Sotka and Hay 2002). The assays ran for seven days, at which point the remaining macroalgae in each container were removed, spun and weighed to measure the remaining wet biomass (g wm).

Fish Consumer For the fish, we assayed *L. rhomboides* in August 2012. We collected *L. rhomboides* (9–12 cm) from the Skidaway River estuary using baited traps that were checked every 24 h. During the feeding assays, one *L. rhomboides* was placed in a plastic container (0.7 m × 0.4 m × 0.3 m depth) within a flow-through seawater system. We divided each container in half with plastic Vexar® mesh (1 mm), and on both halves of each container we placed one of three treatment levels: *G. vermiculophylla* (no choice), *U. lactuca* (no-choice), or *G. vermiculophylla* and *U. lactuca* (choice). On the treatment half of the container, we placed one fish; on the opposite half we did not place a fish so that side served as an autogenic control. The position of the fish and autogenic controls were systematically alternated across the replicates. For all replicates, we threaded the seaweed through 9 cm of twisted nylon rope and attached it to a weight to keep the seaweed in place. While in holding, the fish were fed shrimp pellets *ad libidum*. Prior to the initiation of the experiment, we withheld food for 24 h. We conducted the no-choice assay first, offering each fish ~ 1.0 g of either *U. lactuca* or *G. vermiculophylla* ($n = 4$ per treatment level). We ran the assays for 48 h, at which point we removed the seaweed, spun it for 30 s to remove excess water, and weighed the remaining wet biomass (g). We used the same fish for the choice assays. For the choice assay, we offered each fish ($n = 8$) a total of ~ 2.0 g of seaweed (~ 1.0 g of each seaweed species). The seaweed treatment levels were kept separate by attaching the different treatment levels to separate ropes. Otherwise, the choice assay followed the methods of the no-choice assay.

Data Analysis In all assays, the response variable, consumed biomass (g wm), was calculated for each seaweed species using the following equation: $T_i (C_f / C_i)—T_f$, where T_i and T_f represent the initial (i) and final (f) biomass of seaweed offered to consumers and C_i and C_f represent that of the paired autogenic control (Sotka and Hay 2002). For all data presented in this study, we determined data normality, and therefore the appropriateness of parametric analyses, by visually assessing our distributions with the 'qqnorm' function (package 'stats') and by running Shapiro–Wilk tests ($\alpha = 0.05$) with the 'shapiro.test' function (package 'stats'). All data were analyzed in R 3.4.0 (R Core Team 2017).

For the epifaunal invertebrate experiment, the response variable, consumed biomass (g wm), was not normally distributed for both the choice and no-choice assays. Therefore, we used non-parametric analyses, which do not assume normal distributions or equal variances. We analyzed the choice assays using Wilcoxon Signed Rank tests due to the paired nature of the data. However, we analyzed the no-choice invertebrate feeding assays with Wilcoxon Rank Sum tests because independent consumers were used for each replicate and therefore were not paired. For the fish consumer experiment, the distribution of consumed biomass (g wm) met parametric assumptions. Thus, we analyzed our fish consumer choice assay using a paired *t*-test and our no-choice assay with a Welch's two sample t-test due to dissimilarity of variances (package 'stats').

Nutrient enrichment assays

Fish Consumer We collected adult *L. rhomboides* (9 – 12.5 cm) from the Wilmington River estuary, Georgia in August 2014 using baited traps that were checked every 24 h. In the laboratory, prior to the start of the experiment, individuals were housed together (up to 3 per container) in ~ 28 L filtered aquaria. In addition to a recirculating filter, each aquarium was aerated, and seawater salinity was maintained at ~ 35 psu. Nutrient quality in the aquaria was monitored daily using an API® Saltwater Master Test Kit. The fish were fed shrimp pellets daily ad libitum and a 25% water change was completed every other day.

During the feeding assays, each *L. rhomboides* was placed in a plastic container (0.7 m × 0.4 m × 0.3 m depth) within a flow-through seawater system. As described above in *Native versus Non-Native Feeding Assays 'Fish Consumer',* each container was divided in half with mesh and designed to hold a fish treatment level on one half and an autogenic control on the other. After allowing 24 h for the fish to acclimate, each container received one of three treatment levels [enriched *G. vermiculophylla* (no-choice), non-enriched *G. vermiculophylla* (no-choice), or enriched and non-enriched *G. vermiculophylla* (choice)]. A fish was added to one side, and the other side was the autogenic control that received no fish.

Fish were offered ~ 1.0 g of seaweed in the no-choice assay and a total of ~ 2.0 g of seaweed (1 g of each treatment level) in the choice assay. For all replicates, the seaweed was threaded through 9 cm of twisted nylon rope and attached to a weight to keep the seaweed in place (Fig. 1). Each trial ran for three days, when the seaweed was removed, spun for 30 s, and weighed for final biomass (g wm). In this experiment, we allowed the fish to eat for three days rather than two days (as in *Native vs. Non-Native Feeding Assay 'Fish Consumer')* because this experiment was conducted late in the fall when seawater temperatures were lower and fish consumption rates were depressed. Due to constraints in the number of flow-through containers available, we were only able to run up to two replicates of each treatment level simultaneously. Unlike the previous *L. rhomboides* *f*eeding trials, each fish was cycled through to receive all treatments over the course of the experiment. The sequence of treatment levels was randomized per fish, and food was withheld for 24 h before each trial. The experiment was completed from November to December 2014 with a total of ten replicates of each treatment level per assay.

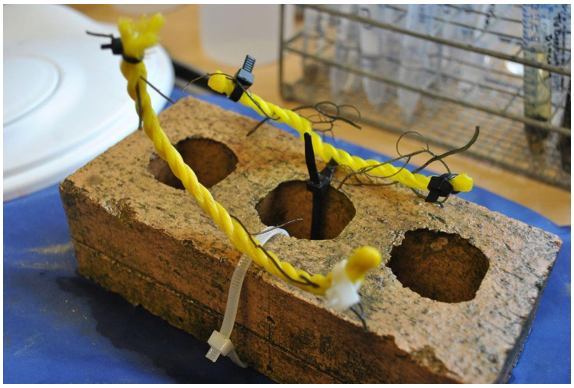

Fig. 1 Enriched (forefront) and non-enriched (back) *Gracilaria vermiculophylla* paired in a replicate of the nutrient enrichment, *Lagodon rhomboides* choice experiment. The seaweed is threaded through rope for attachment and shows more consumption of enriched *G. vermiculophylla* than the non-enriched

For the enriched and non-enriched treatment levels, ~ 200 g wm of *G. vermiculophylla* were collected from the field, rinsed in filtered seawater, and manually defaunated. We placed ~ 100 g of *G. vermiculophylla* in two clear, plastic Sterilite® bins (42.5 cm × 30 cm × 17.8 cm depth), with 14 L of aerated, filtered seawater. The seaweed was grown under Phillips® T8 32-W daylight deluxe bulbs 6500 K set to a 16:8 h light:dark cycle to mimic natural summer conditions for ten days before initiation of the feeding trials. Deionized water was added to each bin daily to maintain consistent salinity (~ 31 psu). For the nutrient-enriched treatment level, one bin of *G. vermiculophylla* was treated with a solution of 1.0 g of NH4Cl, 1.5 g of NaNO3, and 0.15 g of Na2HPO4 six times over the course of the growth period. The combined use of ammonium, nitrate, and phosphorus was adapted from methods in Abreu et al. (2011b) and previous pilot studies.

To assess effectiveness of our nitrogen enrichment method, halfway through the enrichment process, we took five *G. vermiculophylla* tissue samples (~ 1 g) from five different thalli within each treatment level bin (nitrogen-enriched and non-enriched). We pooled the samples per treatment level, rinsed them with deionized water, and dried them at 55 °C in a drying oven for 48 h. Once dried, we ground each pooled sample using a mortar and pestle and placed it in a glass scintillation vial. We dried the ground samples again at 55 °C in a drying oven overnight to remove moisture that may have accumulated during the grinding process. The samples were homogenized and ~ 25 mg of each sample was placed in individual foil packets. The samples were analyzed with a CHN analyzer at the Skidaway Institute of Oceanography for percent nitrogen content and C:N. Our nutrient-enriched method increased nitrogen content from ~ 2% N (C:N ~ 14) to ~ 6% N (C:N ~ 5), which mimics levels of percent nitrogen found in *G. vermiculophylla* in highly urbanized estuaries (e.g., Gorman et al. 2017).

Epifaunal Invertebrate Consumer To investigate the role of nutrient content on consumption by invertebrates, we conducted a no-choice assay to test consumption of *G. vermiculophylla* by a known consumer across three nutrient absorption regimes. We used the native amphipod *Ampithoe valida*, which co-occurs with *G. vermiculophylla* in southeastern USA estuaries (Haram et al. 2020) and are known to readily consume *G. vermiculophylla* (Bippus et al. 2018) and congeneric seaweed species (Reynolds et al. 2012; Scheinberg 2015). In June 2016, we collected *A. valida* from Priest Landing by gathering *G. vermiculophylla* from the *Spartina*-mudflat ecotone and rinsing it in filtered seawater to dislodge associated epifaunal invertebrates. We then identified the dislodged amphipods to species under a dissecting scope. Both adult males and females (4.5–12 mm in length) were used for the experiment. We housed individual *A. valida* in plastic Reditainer® cups (~ 164 mL) that we filled with 150 mL of filtered seawater (~ 31 psu) and capped with plastic lids. We punctured the lids with ~ 1 mm holes to reduce evaporation while allowing for oxygen flow. Food was withheld from *A. valida* for 48 h prior to initiation of the experiment. Each amphipod was offered ~ 0.50 g wm of one of the three *G. vermiculophylla* treatment levels detailed below (n = 12). We spun the seaweed for 30 s prior to weighing. Autogenic controls were included in separate containers without an amphipod for each replicate. The experiment ran for seven days, and every other day we extracted 50 mL of water from each container, targeting amphipod waste that accumulated on the bottom, and replaced it with fresh, filtered seawater. Mortality of *A. valida* occurred in block 12 of the non-enriched and freshly collected treatment levels (n = 11, accordingly).

We used three treatment levels to determine the effect of nutrient content on amphipod feeding: nutrient-enriched, non-enriched, and freshly collected *G. vermiculophylla*. The freshly collected treatment level allowed us to assess whether growing the other treatment levels in laboratory conditions altered consumption by the grazers. *G. vermiculophylla* was grown in the laboratory prior to the feeding trial using the same method as described in the *Nutrient Enrichment Assay 'Fish Consumer'* section. The freshly collected treatment level consisted of *G. vermiculophylla* collected from the field at Priest Landing, rinsed, and defaunated on the same day that the experiment began.

Data Analysis For all assays, we calculated the consumption of seaweed biomass (g wm) and assessed data normality using the same methods as in the *Native vs. Non-Native Feeding Assays* experiments. For the epifaunal invertebrate consumer experiment, we tested for differences in consumed biomass (g wm) as a function of nutrient treatment level using a One-Way ANOVA (package 'stats'). For the fish consumer experiment, we tested for differences in consumed biomass (g wm) as a function of nutrient treatment level using paired *t*-tests (package 'stats') for both the no-choice and choice assays. The paired *t*-test was used for the no-choice assays because the same individual fish was used as a single replicate across both nutrient treatment levels.

Results

Native versus non-native feeding assays

Epifaunal Invertebrate Consumer At the end of the seven day choice and no-choice feeding assays, mud snail *I. obsleta* and mud crab *E. depressus* demonstrated differences in feeding preferences between the native *U. lactuca* and non-native *G. vermiculophylla.* In the no-choice feeding assays, *I. obsoleta* consumed significantly more, over 10 times more on average, *U. lactuca* than *G. vermiculophylla* (Wilcoxon rank sum test: W = 64.5, $p = 0.04$; Fig. 2a; see Appendix Table 1 for all mean ± SE consumed wet biomass values). However, for *E. depressus* higher variability in consumption of *U. lactuca* and *G. vermiculophylla* led to no statistical difference between treatment levels (Wilcoxon rank sum test: W = 42, $p = 0.60$; Fig. 2a). In the choice feeding assays, *I. obsoleta* consumed over 10 times more native *U. lactuca* biomass than non-native *G. vermiculophylla* biomass (Wilcoxon signed rank test: V = 42, $p = 0.02$; Fig. 2b). Similarly, *E. depressus* consumed significantly more *U. lactuca* biomass than *G. vermiculophylla*, consuming 3 times more of the native seaweed (Wilcoxon signed rank test: V = 55, $p < 0.01$; Fig. 2b).

Fish Consumer After 48 h, in the no-choice feeding assays, *L. rhomboides* ate 60% more on average of

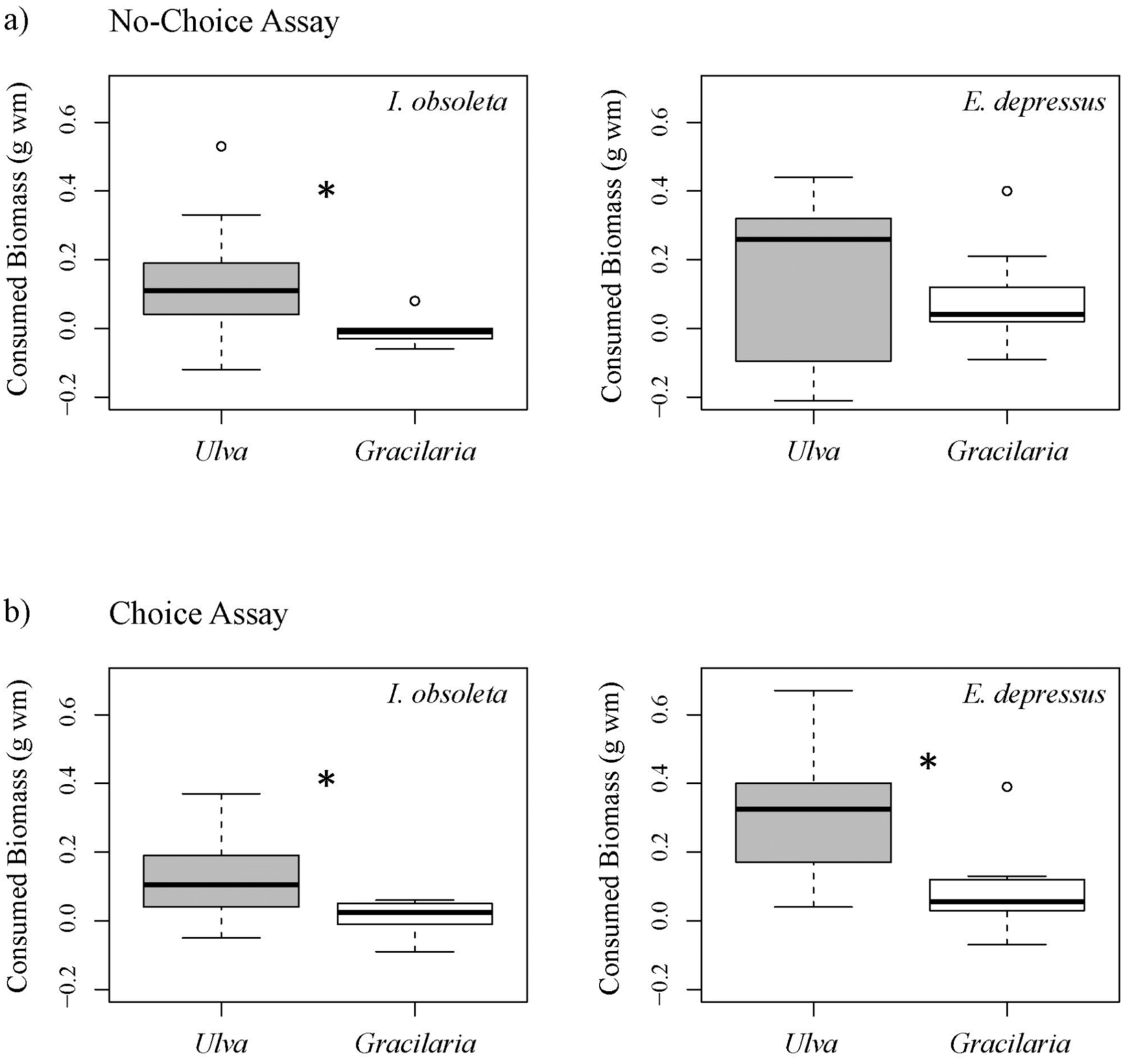

Fig. 2 Amount of biomass (g wm) of native (*Ulva lactuca*) and non-native (*Gracilaria vermiculophylla*) seaweed consumed by native *Ilyanassa obsoleta* and *Eurypanopeus depressus* in (a) no-choice (n = 10) and (b) choice (n = 10) feeding assays. In the no-choice feeding assays, the consumers were offered ~ 0.5 g of one seaweed species; in the choice feeding trials, invertebrate consumers were offered ~ 0.5 g of each seaweed species. Assays ran for seven days. Grey represents the *U. lactuca* treatment level, and white represents the *G. vermiculophylla* treatment level. The box and whisker plots represent the median (midline) and third and first quartiles (75th and 25th percentiles). The upper and lower dashed lines illustrate the maximum and minimum values up to 1.5 times the interquartile range; data points beyond that interval are represented as outliers (white dots). * indicates treatment levels that differed significantly

G. vermiculophylla than *U. lactuca*, though their consumption was not significantly different between the treatment levels due to large variance (Welch's *t*-test: $t_{4.18} = -1.01$, $p = 0.37$; Fig. 3a). In the choice feeding assays, *L. rhomboides* ate nearly 10 times more *G. vermiculophylla* than *U. lactuca,* showing a significant preference for the non-native seaweed (paired *t*-test: $t_7 = -4.51$, $p < 0.01$; Fig. 3b).

Nutrient enrichment assays

Fish Consumer In the no-choice feeding assays, *L. rhomboides* consumed similar amounts of *G. vermiculophylla* in the enriched (0.46 ± 0.12 g wm, mean ± SE) and non-enriched (0.39 ± 0.11 g wm) treatment levels over the 72 h assays (paired *t*-test: $t_9 = 0.48$, $p = 0.65$; Fig. 4a). However, in the choice feeding assay, *L. rhomboides* consumed twice as much of the enriched *G. vermiculophylla*, eating 0.31 g wm (±0.04) of the enriched seaweed versus 0.13 g wm (±0.04) of the non-enriched seaweed (paired *t*-test: $t_9 = 2.90$, $p = 0.02$; Fig. 4b).

Epifaunal Invertebrate Consumer At the end of the 7 day no-choice assay, *A. valida* consumed similar, minimal amounts of non-enriched *G. vermiculophylla* (0.03 ± 0.03 g wm, mean ± SE) as enriched (0.05 ± 0.03 g wm) or freshly collected (0.03 ± 0.02 g wm) *G. vermiculophylla*, with no significant difference among the treatment levels (One-Way ANOVA: $F_{2,31} = 0.32$, $p = 0.73$; Fig. 5). The lack of differences between the laboratory grown treatment level and the freshly collected treatment level, suggests that the laboratory conditions did not affect amphipod feeding.

Discussion

Understanding how an introduced primary producer is incorporated into a recipient food web is essential to predict its effects on ecosystem structure and function (e.g., Byers et al. 2010; Pintor and Byers 2015). In our system, both consumer identity and seaweed nutrient content determined the fate of non-native *G. vermiculophylla* within feeding assays. In the absence of a native seaweed (*U. lactuca*), mud crab *E. depressus* and pinfish *L. rhomboides* consumed *G. vermiculophylla*. However, the pinfish *L. rhomboides* consumed 7 times more *G. vermiculophylla*

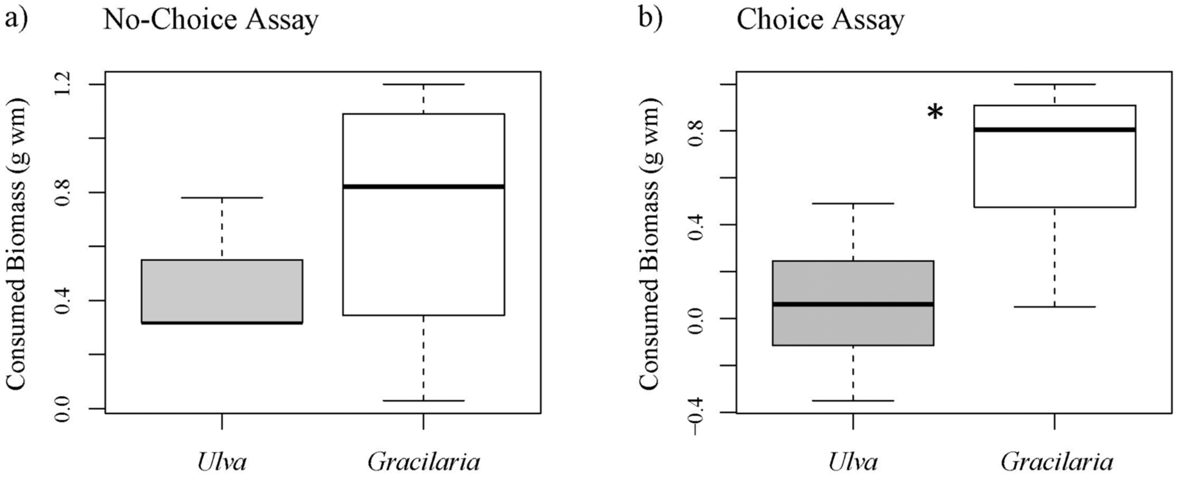

Fig. 3 Amount of biomass (g wm) of native (*Ulva lactuca*) and non-native (*Gracilaria vermiculophylla*) seaweed consumed by pinfish, *Lagodon rhomboides*, in the (a) no-choice (n = 4) and in the (b) choice (n = 8) feeding assays. In the no-choice feeding assays, the fish were offered ~ 1.0 g of one seaweed species; while in the choice feeding trials, fish were offered ~ 1.0 g of each species. Assays ran for 2 days. Grey represents the *U. lactuca* treatment level, and white represents the *G. vermiculophylla* treatment level. The box and whisker plots represent the median (midline) and third and first quartiles (75th and 25th percentiles). The upper and lower dashed lines illustrate the maximum and minimum values up to 1.5 times the interquartile range; data points beyond that interval are represented as outliers (white dots). * indicates treatment levels that differed significantly

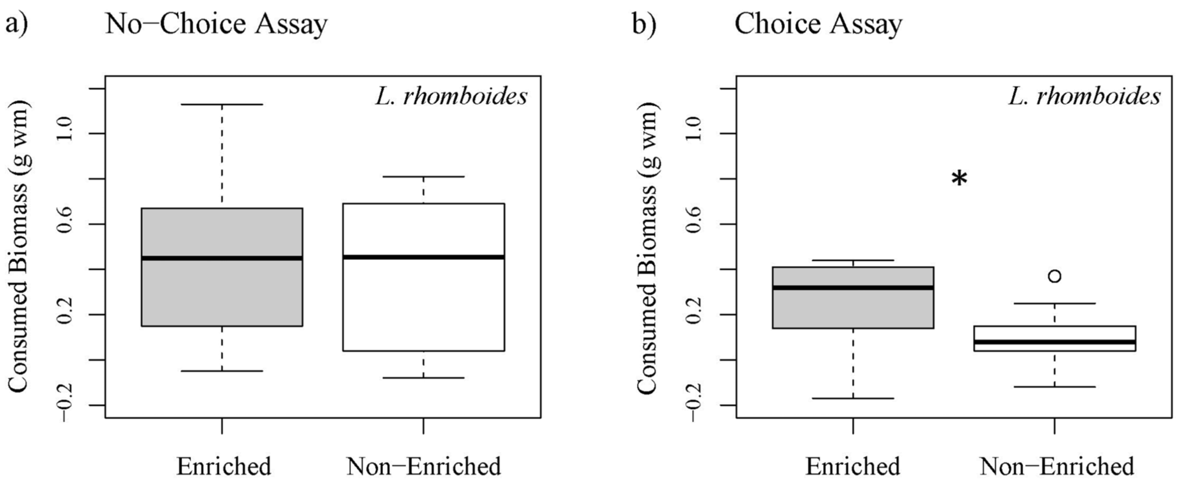

Fig. 4 Amount of *Gracilaria vermiculophylla* biomass (g wm) consumed by *Lagodon rhomboides* during (a) no-choice and (b) choice feeding assays. *G. vermiculophylla* treatment levels were nutrient-enriched (n = 10) and non-enriched (n = 10). In the no-choice feeding assays, the consumers were offered ~ 1.0 g of one enrichment treatment level; while in the choice feeding assay, fish were offered ~ 1.0 g of each enrichment treatment level. Assays ran for 3 days. Grey represents the nutrient-enriched treatment level, and white represents the non-enriched treatment level. The box and whisker plots represent the median (midline) and third and first quartiles (75th and 25th percentiles). The upper and lower dashed lines illustrate the maximum and minimum values up to 1.5 times the interquartile range; data points beyond that interval are represented as outliers (white dots). * indicates treatment levels that differed significantly

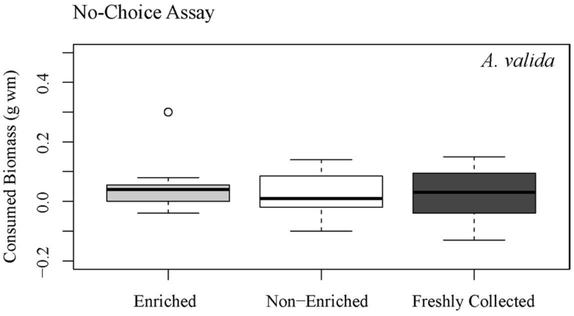

Fig. 5 Amount of *Gracilaria vermiculophylla* biomass consumed (g wm) by amphipods, *Ampithoe valida*, in the no-choice assay. *G. vermiculophylla* treatment levels were nutrient-enriched (n = 12), non-enriched (n = 11), and freshly collected (n = 11). Amphipods were offered ~ 0.5 g of *G. vermiculophylla*. Assays ran for 7 days. Data were analyzed using ANOVA. Light grey represents the nutrient-enriched treatment level, white represents the non-enriched treatment level, and dark grey represents the freshly collected treatment level. The box and whisker plots represent the median (midline) and third and first quartiles (75th and 25th percentiles). The upper and lower dashed lines illustrate the maximum and minimum values up to 1.5 times the interquartile range; data points beyond that interval are represented as outliers (white dots). * indicates treatment levels that differed significantly

than *E. depressus*, and within a shorter time frame. *L. rhomboides* was also the only consumer species to demonstrate a preference for the non-native seaweed over the native seaweed. The fish also preferred *G. vermiculophylla* when it was enriched. Thus, we provide insights about how *G. vermiculophylla* may be incorporated into the food webs of southeastern USA estuaries.

Seaweeds are important resources for generalist consumers in nearshore systems; however, non-native seaweeds can be less useful to native consumers given mismatched palatability. Although *G. vermiculophylla* provides an abundant resource, the common invertebrates, mud snail *I. obsoleta* and mud crab *E. depressus*, preferred native *U. lactuca* when given a choice. Within the same system, another common epifaunal invertebrate, the amphipod *Gammarus mucronatus*, similarly prefers to eat native *Spartina alterniflora* detritus over *G. vermiculophylla* (Wright et al. 2014). Our results also reflect studies from other regions of the *G. vermiculophylla* invasive range, in which native herbivores preferred native seaweeds over the introduced seaweed (Weinberger et al. 2008; Nejrup et al. 2012; Hu and Juan 2014) – a pattern attributed to high concentrations of wound-activated and inducible chemical defenses produced by the non-native populations of *G. vermiculophylla* (Nylund et al. 2011; Hamman et al. 2013; but see Bippus et al 2018). Though *U. lactuca* is chemically defended, the native seaweed produces secondary compounds that are qualitatively different from those of *G. vermiculophylla*. *U. lactuca* produces dimethylsulphoniopropionate (DMSP) (Stefels 2000; Van Alstyne and Puglisi 2007), while *G. vermiculophyllum* produces oxylipins (Nylund et al. 2011; Rempt et al. 2012). Given their sympatry with *U. lactuca*, the studied invertebrates may have evolved tolerances to *U. lactuca*'s chemical defense compounds, making the native seaweed a more palatable resource (Sotka and Hay 2002). In fact, DMSP and its biproducts can promote consumption by some native invertebrate consumers (Van Alstyne and Puglisi 2007). To understand the mechanisms behind the invertebrates' preferences for the native seaweed, feeding assays that isolate the chemical, nutritional, and physical differences between *U. lactuca* and *G. vermiculophylla* should be conducted.

In contrast to the invertebrates, pinfish *L. rhomboides* preferred to consume *G. vermiculophylla* over the native *U. lactuca*. Though this result has not previously been reported in our system, studies of other non-native seaweeds have found that they can be consumed by native grazers, occasionally at rates similar to consumption of native seaweeds (e.g., Rossi et al. 2009; Cacabelos et al. 2010; Bulleri and Malquori 2015). Not only did *L. rhomboides* prefer *G. vermiculophylla*, but the fish rapidly consumed on average nearly 10 times more of the non-native seaweed than the native seaweed in the choice assay. Previous research has documented rapid grazing of *Gracilaria* spp. by herbivorous fish in comparison to brown and green seaweeds (Ganesan et al. 2006). In our system, the rapid consumption of *G. vermiculophylla* by pinfish suggests that they are a plausible candidate for future experiments exploring top-down influences on the non-native seaweed.

In addition to differences between consumer species in their consumption of native *versus* non-native seaweeds, we observed differences in the role of nutrient content. In the no-choice trials, the amphipod *A. valida* and pinfish *L. rhomboides* consumed similar amounts of nutrient-enriched *versus* non-enriched *G. vermiculophylla*. However, *L. rhomboides* consumed significantly more enriched seaweed when presented with a choice between non-enriched and enriched *G. vermiculophylla*. One possible explanation of the difference between *A. valida* and *L. rhomboides* consumption of nutrient-enriched resources may lie in differences in nutritional requirements between the consumer species. Herbivores are generally nutrient limited, and thus the nutrient content of primary producers can dictate herbivore food selection (Mattson 1980; Hay 1991; Sterner and Hessen 1994; Elser et al. 2001; Fink and Von Elert 2006; Kraufvelin et al. 2006). However, organisms require different amounts of energy and nutrients based on their specific physiological constraints (Sterner and Elser 2002; Sterner and Hessen 1994). For example, herbivorous fishes must process large amounts of carbon to meet their nitrogen and phosphorus requirements (Hay 1991; Hood et al. 2005), suggesting that our additions of nitrogen and phosphorus may have improved the nutritional value for *L. rhomboides*. In fact, *L. rhomboides* have exhibited similar nutrient-driven consumption of seagrass *Halodule wrightii* (Heck et al. 2006), further illustrating the importance of high-nutrient food items in pinfish diets. Although the nutrients enhanced in our study appear to stimulate *L. rhomboides* feeding, enriched and unenriched *G. vermiculophylla* was consumed at statistically equivalent rates by *A. valida*. This may reflect the possibility that nutritional value of enriched and unenriched *G. vermiculophyll*a are of similar magnitude to *A. valida*. The congeneric *A. longimana* similarly does not select seaweed based on nutritional value because compensatory feeding behavior allows the amphipod to make up for lower nutritional values (Cruz-Rivera and Hay 2001).

A second explanation relates to the palatability of the seaweed. Nutrient availability can control the production of chemical defenses (Stefels 2000). For instance, DMSP content can be inversely related to nitrogen availability in the environment (Stefels 2000), while terpenoid metabolites can increase with nitrogen enrichment (Cronin and Hay 1996). If the concentrations of secondary compounds in *G. vermiculophylla* are linked to nutrient availability, the potential benefit of increased nutrient content for invertebrates may be outweighed by this chemical deterrence. Thus, our results suggest that the suite of herbivores present and the nutrient conditions within a recipient ecosystem may be important drivers in the incorporation of non-native seaweeds into recipient food webs. Further investigation is needed to clarify the ecological mechanisms (e.g., herbivore nutrient limitation and chemical defenses) behind the observed differences in consumption of nutrient-enriched *G. vermiculophylla* between consumer types.

Although the present study increases our knowledge of which species consume *G. vermiculophylla* in Georgia estuaries, we do not know the long-term effects of the seaweed's consumption on native grazer fitness. Consumption of non-native seaweeds has been linked to degraded metabolic and physiological conditions of both native invertebrate and fish grazers (e.g., Scheibling and Anthony 2001; Gollan and Wright 2006; Lyons and Scheibling 2007; Felline et al. 2012). For instance, the invasive seaweed *Caulerpa racemosa* causes reduced growth in sea urchins, *Paracentrotus lividus* (Tomas et al. 2011) and cellular and physiological alterations in white sea bream, *Diplodus sargus* (Felline et al. 2012), which may lead to reduced fitness and stocks over the long-term. Much like *L. rhomboides* in the present study, *D. sargus* and *P. lividus* prefer non-native *C. racemosa* to native seaweeds and other invasive seaweeds. For these native Mediterranean grazers, their preferences of the invasive seaweed suggest a mismatch between preference and fitness consequences that elucidates an ecological trap for the native grazers. This is a critical scenario to consider for *G. vermiculophylla* in southeastern estuaries. Therefore, we need research on the fitness consequences of *G. vermiculophylla* consumption on *L. rhomboides* to determine the overall positive or negative effect of the novel resource on consumer populations within this ecosystem.

Conclusion

Despite the potential of *G. vermiculophylla* to provide a novel, abundant primary resource within southeastern USA estuaries, we observed varied utilization of the non-native seaweed depending on consumer identity and seaweed nutrient content. Nonetheless, the mixed effects of *G. vermiculophylla* on grazer consumption highlights the need for more research on trophic interactions with non-native seaweeds globally. Furthermore, assessing the consumption of non-native seaweeds across an array of consumer species, macroalgal traits, and seasons will provide a more realistic illustration of seaweed-grazer interactions. Given that non-native seaweed species continue to be introduced across the world, more detailed analyses of their influence on trophic dynamics are necessary.

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Author Contributions LH, JB, and ES conceived and designed the studies. LH, KK, and TM ran the experiments and collected the data. LH analyzed the data. LH and JB wrote the manuscript. LH, JB, KK, TM, and ES reviewed and provided feedback on all drafts.

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Declarations

Conflict of Interests The authors have no relevant financial or non-financial interests to disclose.

Appendix

See Table 1

Table 1 Mean and standard error (±SE) of consumed seaweed biomass (g wet mass) for three native herbivores in the 'choice' and 'no-choice' *Native versus Non-native Feeding Assays*. Assays for *Ilyanassa obsoleta* and *Eurypanopeus depressus* ran for 7 days. Assays for *Lagodon rhomboides* ran for 2 days. Seaweed biomass consumption was calculated by subtracting the final seaweed biomass from the initial mass (g wm). A negative value indicates net seaweed growth. The invertebrate assays started with ~ 0.5 g wm per seaweed species; the fish assays started with ~ 1 g wm per species.

Feeding assay	Consumer species	Seaweed species	Consumed Seaweed Biomass (g wm)	
			Mean	±SE
Choice assay	*I. obsoleta*	*G. vermiculophylla*	0.01	0.02
		U. lactuca	0.13	0.04
	E. depressus	*G. vermiculophylla*	0.09	0.04
		U. lactuca	0.32	0.06
	L. rhomboides	*G. vermiculophylla*	0.68	0.11
		U. lactuca	0.07	0.1
No-choice assay	*I. obsoleta*	*G. vermiculophylla*	-0.01	0.01
		U. lactuca	0.14	0.07
	E. depressus	*G. vermiculophylla*	0.09	0.05
		U. lactuca	0.15	0.09
	L. rhomboides	*G. vermiculophylla*	0.72	0.26
		U. lactuca	0.44	0.12

References

Abreu MH, Pereira R, Yarish C, Buschmann AH, Sousa-Pinto I (2011a) IMTA with *Gracilaria vermiculophylla*: Productivity and nutrient removal performance of the seaweed in a land-based pilot scale system. Aquaculture 312(1–4):77–87

Abreu MH, Pereira R, Buschmann AH, Sousa-Pinto I, Yarish C (2011b) Nitrogen uptake responses of *Gracilaria vermiculophylla* (Ohmi) Papenfuss under combined and single addition of nitrate and ammonium. J Exp Mar Biol Ecol 407:190–199

Adams SM (1976) Feeding ecology of eelgrass fish communities. Trans Am Fish Soc 105:514–519

Bippus PM, Krueger-Hadfield SA, Sotka EE (2018) Palatability of an introduced seaweed does not differ between native and non-native populations. Mar Biol 165:39

Bishop MJ, Byers JE (2015) Predation risk predicts use of a novel habitat. Oikos 124:1225–1231

Britton-Simmons KH (2004) Direct and indirect effects of the introduced alga *Sargassum muticum* on benthic, subtidal communities of Washington state, USA. Mar Ecol Prog Ser 277:61–78

Bulleri F, Malquori F (2015) High tolerance to stimulated herbivory in the clonal seaweed *Caulerpa cylindracea*. Mar Environ Res 107:61–65

Byers JE, Gribben PE, Wright JT (2010) Variable direct and indirect effects of a habitat-modifying invasive species on mortality of native fauna. Ecology 91(6):1787–1798

Byers JE, Gribben PE, Yeager C, Sotka EE (2012) Impacts of an abundant introduced ecosystem engineer within mudflats of the southeastern US coast. Biol Invasions 14:2587–2600

Cacabelos E, Olabarria C, Incera M, Troncoso JS (2010) Do grazers prefer invasive seaweeds? J Exp Mar Biol Ecol 393:182–187

Callaway RM, Ridenour WM (2004) Novel weapons: Invasive success and the evolution of increased competitive ability. Front Ecol Environ 2(8):436–443

Cronin G, Hay ME (1996) Effects of light and nutrient availability on the growth, secondary chemistry, and resistance to herbivory of two brown seaweeds. Oikos 77:93–106

Cruz-Rivera E, Hay ME (2000) The effects of diet mixing on consumer fitness: macroalgae, epiphytes and animal matter as food for marine animals. Oecologia 123:252–261

Cruz-Rivera E, Hay ME (2001) Macroalgal traits and the feeding and fitness of an herbivorous amphipod: the roles of selectivity, mixing and compensation. Mar Ecol Prog Ser 218:249–266

Cummings DO, Williamson JE (2008) The role of herbivory and fouling on the invasive green alga *Caulerpa filiformis* in temperate Australian waters. Mar Freshw Res 59:279–290

Douglass JG, Duffy JE, Canuel EA (2011) Food web structure in a Chesapeake Bay eelgrass bed as determined through gut contents and ^{13}C and ^{15}N isotope analysis. Estuaries Coasts 34(4):701–711

Duarte C, Navarro JM, Acuña K, Gómez I (2010) Feeding preferences of the sandhopper *Orchestria tuberculate*: the importance of algal traits. Hydrobiologia 651:291–303

Duarte C, Acuña K, Navarro JM, Gómez I (2011) Intra-plant differences in seaweed nutritional quality and chemical defenses: Importance for the feeding behavior of the intertidal amphipod *Orchestroidea tuberculata*. J Sea Res 66:215–221

Elser JJ, Hayakawa K, Urabe J (2001) Nutrient limitation reduces food quality for zooplankton: *Daphnia* response to seston phosphorus enrichment. Ecology 82(3):898–903

Enge S, Sagerman J, Wikstrom SA, Pavia H (2017) A review of herbivore effects on seaweed invasions. Oceanogr Mar Biol Annu Rev 2017(55):421–440

Felline S, Caricato R, Cutignano A, Gorbi S, Lionetto MG, Mollo E, Regoli F, Terlizzi A (2012) Subtle effects of biological invasions: cellular and physiological responses of fish eating the exotic pest *Caulerpa racemosa*. PLoS ONE 7(6):e38763

Fink P, Von Elert E (2006) Physiological responses to stoichiometric constraints: nutrient limitation and compensatory feeding. Oikos 115:484–494

Freshwater DW, Montgomery F, Greene JK, Hamner RM, Williams M, Whitfield PE (2006) Distribution and identification of an invasive *Gracilaria* species that is hampering commercial fishing operations in southeastern North Carolina, USA. Biol Invasions 8:631–637

Ganesan M, Thiruppathi S, Sahu N, Rengarajan N, Veeragurunathan V, Jha B (2006) *In situ* observations on preferential grazing of seaweeds by some herbivores. Curr Sci 91(9):1256–1260

Giannotti AL, McGlathery KJ (2001) Consumption of *Ulva lactuca* (Chlorophyta) by the omnivorous mud snail *Ilyanassa obsoleta* (Say). J Phycol 37(2):209–215

Gollan JR, Wright JT (2006) Limited grazing pressure by native herbivores on the invasive seaweed *Caulerpa taxifolia* in a temperate Australian estuary. Mar Freshw Res 57(7):685–694

Gorman L, Kraemer GP, Yarish C, Min Boo S, Kim JK (2017) The effects of temperature on the growth rate and nitrogen content of invasive *Gracilaria vermiculophylla* and native *Gracilaria tikvahiae* from Long Island Sound, USA. Algae 32(1):57–66

Hammann M, Wang G, Rickert E, Boo SM, Weinberger F (2013) Invasion success of the seaweed *Gracilaria vermiculophylla* correlates with low palatability. Mar Ecol Prog Ser 486:93–103

Hammann M, Rempt M, Pohnert G, Wang G, Boo SM, Weinberger F (2016) Increased potential for wound activated production of Prostaglandin E_2 and related toxic compounds in non-native populations of *Gracilaria vermiculophylla*. Harmful Algae 51:81–88

Haram LE, Kinney KA, Sotka EE, Byers JE (2018) Mixed effects of an introduced ecosystem engineer on the foraging behavior and habitat selection of predators. Ecology 99:2751–2762

Haram LE, Sotka EE, Byers JE (2020) Effects of novel, non-native detritus on decomposition and invertebrate community assemblage. Mar Ecol Prog Ser 643:49–61

Hay ME (1991) Fish – seaweed interactions on coral reefs: effects of herbivorous fishes and adaptations of their prey. In: Sale PF (ed) The Ecology of Fishes on Coral Reefs. Academic Press. Elsevier. San Diego, California, USA, pp 96–119

Hay ME (1996) Marine chemical ecology: what's known and what's next? J Exp Mar Biol Ecol 200:103–134

Hay ME, Fenical W (1996) Chemical ecology and marine biodiversity: insights and products from the sea. Oceanography 9(1):10–20

Hay ME, Steinberg PD (1992) The chemical ecology of plant-herbivore interactions in marine versus terrestrial communities. In: Rosenthal GA, Berenbaum MR (eds) Herbivores: Their Interaction with Secondary Methabolites. Evolutionary and Ecological Processes. Academic Press. Elsevier. San Diego, California, USA, pp 371–413

Heck KL Jr, Valentine JF, Pennock JR, Chaplin G, Spitzer PM (2006) Effects of nutrient enrichment and grazing on shoalgrass *Halodule wrightii* and its epiphytes: results of a field experiment. Mar Ecol Prog Ser 326:145–156

Hood JM, Vanni MJ, Flecker AS (2005) Nutrient recycling by two phosphorus-rich grazing catfish: the potential for phosphorus-limitation of fish growth. Oecologia 146(2):247–257

Hu ZM, Juan LB (2014) Adaptation mechanisms and ecological consequences of seaweed invasions: a review case of agarophyte *Gracilaria vermiculophylla*. Biol Invasions 16(5):967–976

Jiménez RS, Hepburn CD, Hyndes GA, McLeod RJ, Taylor RB, Hurd CL (2015) Do native subtidal grazers eat the invasive kelp *Undaria pinnatifida*? Mar Biol. https://doi.org/10.1007/s00227-015-2757-y

Jormalainen V, Honkanen T (2008) Macroalgal chemical defenses and their roles in structuring temperate marine communities. In: in C.D. Amsler, (ed) Algal Chemical Ecology. Springer-Verlag, Berlin, Germany, pp 57–90

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17(4):164–170

Kollars NM, Byers JE, Sotka EE (2016) Invasive décor: an association between a native decorator worm and a non-native seaweed can be mutualistic. Mar Ecol Prog Ser 545:135–145

Kraufvelin P, Salovius S, Christie H, Moy FE, Karez R, Pedersen MF (2006) Eutrophication-induced changes in benthic algae affect the behavior and fitness of the marine amphipod *Gammarus locusta*. Aquat Bot 84:199–209

Lohrer AM, Whitlatch RB, Wada K, Fukui Y (2000) Home and away: comparisons of resource utilization by a marine species in native and invaded habitats. Biol Invasions 2:41–57

Lyons DA, Scheibling RA (2007) Differences in somatic and gonadic growth of sea urchins (*Stronglyocentrotus droebachiensis*) fed kelp and the invasive alga *Codium fragile* ssp. *tomentosoides* are related to energy acquisition. Mar Biol 152:285–295

MacDonald J (1982) Divergent life history patterns in the co-occurring intertidal crabs *Panopeus herbstii* and Eurypanopeus *depressus* (Crustacea: brachyura: xanthidae). Mar Ecol Prog Ser 8:173–180

Mann KH (1988) Production and use of detritus in various freshwater, estuarine and coastal marine ecosystems. Limnol Oceanogr 33(4):910–930

Mattson WJ Jr (1980) Herbivory in relation to plant nitrogen content. Annu Rev Ecol Syst 11:119–161

Monteiro CA, Aschwin HE, Santos ROP (2009) Macro- and mesoherbivores prefer native seaweeds over the invasive brown seaweed *Sargassum muticum*: a potential regulating role on invasions. Mar Biol 156:2505–2515

Nejrup LB, Pedersen MF, Vinzent J (2012) Grazer avoidance may explain the invasiveness of the red alga *Gracilaria* *vermiculophylla* in Scandinavian waters. Mar Biol 159:1703–1712

Nelson WG (1979) Experimental studies of selective predation on amphipods: consequences for amphipod distribution and abundance. J Exp Biol Ecol 38:225–245

Nicotri ME (1980) Factors involved in herbivore food preference. J Exp Mar Biol Ecol 42:13–26

Nylund GM, Weinberger F, Rempt M, Pohnert G (2011) Metabolic assessment of induced and activated chemical defence in the invasive red alga *Gracilaria vermiculophylla*. PLoS ONE 6(12):e29359

Ojeda FP, Munoz AA (1999) Feeding selectivity of the herbivorous fish *Scartichthys viridis*: effects on macroalgal community structure in a temperate rocky intertidal coastal zone. Mar Ecol Prog Ser 184:219–229

Pavia H, Toth GB (2008) Macroalgal models in testing and extending defense theories. Pages pp. In: Amsler CD (ed) Algal Chemical Ecology. Springer-Verlag, Berlin, Germany, pp 121–146

Pedersen MF, Johnsen KL (2017) Nutrient (N and P) dynamics of the invasive macroalgae *Gracilaria vermiculophylla*: nutrient uptake kinetics and nutrient release through decomposition. Mar Biol 164:172

Pedersen MF et al (2005) Biomass dynamics of exotic *Sargassum muticum* and native *Halidrys siliquosa* in Limfjorden, Denmark - Implications of species replacements on turnover rates. Aquat Bot 83:31–47

Pedersen MF et al (2016) Enemy release an unlikely explanation for the invasive potential of the brown alga *Sargassum muticum*: experimental results, literature review and meta-analysis. Mar Biol 163:1–14

Pelletreau KN, Targett NM (2008) New perspectives for addressing patterns of secondary metabolites in marine macroalgae. Pages pp. In: Amsler CD (ed) Algal Chemical Ecology. Springer-Verlag, Berlin, Germany, pp 121–146

Pintor LM, Byers JE (2015) Do native predators benefit from non-native prey? Ecol Lett 18:1174–1180

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation forStatistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rempt M, Weinberger F, Grosser K, Pohnert G (2012) Conserved and species-specific oxylipin pathways in the wound activated chemical defense of the noninvasive red alga *Gracilaria chilensis* and the invasive *Gracilaria vermiculophylla*. Beilstein J Org Chem 8:283–289

Reynolds LK, Carr LA, Boyer KE (2012) A non-native amphipod consumes eelgrass inflorescences in San Francisco Bay. Mar Ecol Prog Ser 451:107–118

Rodriguez LF (2006) Can invasive species facilitate native species? evidence of how, when, and why these impacts occur. Biol Invasions 8:927–939

Rossi F, Olabarria C, Incera M, Garrido J (2009) The trophic significance of the invasive seaweed *Sargassum muticum* in sandy beaches. J Sea Res 63:52–61

Scheibling RE, Anthony SX (2001) Feeding, growth and reproduction of sea urchins (*Strongylocentrotus droebachiensis*) on single and mixed diets of kelp (*Laminaria* spp.) and the invasive alga *Codium fragile* ssp. *tomentosoides*. Mar Biol 139:139–146

Scheinberg, L.A. 2015. Feeding behavior and population structure of *Ampithoe valida*: a bicoastal comparison. Masters Thesis. San Francisco State University. San Francisco, California, USA.

Sotka EE, Hay ME (2002) Geographic variation among herbivore populations in tolerance for a chemically rich seaweed. Ecology 83(10):2721–2735

Stefels J (2000) Physiological aspects of the production and conversion of marine algae and higher plants. J Sea Res 43:183–197

Sterner RW, Hessen DO (1994) Algal nutrient limitation and the nutrition of aquatic herbivores. Annu Rev Ecol Syst 25:1–29

Sterner RW, Elser JJ (2002) Ecological stoichiometry: the biology of elements from molecules to the biosphere. Princeton University Press, Princeton, New Jersey, USA

Stoner AW (1980) The feeding ecology of *Lagodon rhomboides* (Pisces: Sparidae): Variation and functional responses. US National Marine Fisheries Service Fishery Bulletin 78:337–352

Sumi CBT, Scheibling RE (2005) Role of grazing by sea urchins *Strongylocentrotus droebachiensis* in regulating the invasive alga *Codium fragile* ssp. *tomentosoides* in Nova Scotia. Mar Ecol Prog Ser 292:203–212

Teal J (1962) Energy flow in the salt marsh ecosystem of Georgia. Ecology 43(4):614–624

Thomsen MS, McGlathery KJ (2007) Stress tolerance of the invasive macroalgae *Codium fragile* and *Gracilaria vermiculophylla* in a soft-bottom turbid lagoon. Biol Invasions 9:499–513

Thomsen MS, Wernberg T, South PM, Schiel DR (2016) Non-native seaweeds drive changes in marine coastal communities around the world. In: Hu ZM, Fraser C (eds) Seaweed Phylogeography. Springer, Netherlands, pp 147–185

Tomas F, Cebrian E, Ballesteros E (2011) Differential herbivory of invasive algae by native fish in the Mediterranean Sea. Estuar Coast Shelf Sci 92:27–34

Van Alstyne KL, Puglisi MP (2007) DMSP in marine macroalgae and macroinvertebrates: distribution, function, and ecological impacts. Aquatic Science 69:394–402

Van Alstyne KL, Koellermeier L, Nelson TA (2007) Spatial variation in dimethylsulfonoipropionate (DMSP) production in *Ulva lactuca* (Chlorophyta) from Northeast Pacific. Mar Biol 150:1127–1135

Weinberger F, Buchholz B, Karez R, Wahl M (2008) The invasive red alga *Gracilaria vermiculophylla* in the Baltic Sea: adaptation to brackish water may compensate for light limitation. Aquat Biol 3:251–264

Winemiller KO, Akin S, Zeug SC (2007) Production sources and food web structure of a temperate tidal estuary: integration of dietary and stable isotope data. Mar Ecol Prog Ser 343:63–76

Wright JT, Byers JE, DeVore JL, Sotka EE (2014) Engineering or food? Mechanisms of facilitation by a habitat-forming invasive seaweed. Ecology 95(10):2699–2706