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Species, community, and ecosystem-level responses following the invasion of the red alga *Dasysiphonia japonica* to the western North Atlantic Ocean

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Abstract Species invasions have been increasing in frequency worldwide, yet critical gaps remain in our understanding of how invaders affect community structure and ecosystem functioning, particularly during the initial stages of invasion. Even less is known about changes in the invader that may take place immediately following an invasion. This study examined the recent invasion of the red macroalga *Dasysiphonia* (formerly, *Heterosiphonia*) *japonica* to the western North Atlantic Ocean with the aim of filling in gaps in our understanding of the impacts that invasive seaweeds have at the species, community and ecosystem levels immediately following their establishment. Within 5 years of invasion, community composition had changed and biodiversity had decreased to nearly half of pre-invasion levels. In addition, the relative proportion of *Dasysiphonia* decreased by 35% over our four-year study from initially high levels shortly after establishment. We found evidence that functional traits of this initially aggressive invader changed over time, as it ultimately became a less aggressive, co-inhabiting member of the local algal community, particularly with respect to nutrient uptake and relative abundances, although native diversity remained low relative to pre-invasion levels. Using these realistic changes in community structure, including decreases in biodiversity, we also showed that nutrient uptake of algal assemblages changed over time, suggesting changes in the functional characteristics of invaded communities, with implications for ecosystem-level processes such as nutrient fluxes. This study provides rare empirical evidence about the successional stages occurring at the individual, community, and ecosystem levels during the first 5 years of an invasion.

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Introduction

Invasive species have been identified as a major threat to the community structure and biodiversity of

recipient communities (Parker et al. 1999; Stachowicz et al. 2002; Molnar et al. 2008; Butchart et al. 2010; Jones and Thornber 2010; Ojaveer et al. 2014). For example, in marine ecosystems, non-native species are often able to tolerate a wide range of abiotic conditions and are often competitively superior to native species with respect to growth, defense, and nutrient uptake, and they are often less palatable than native species (Theoharides and Dukes 2007; Hayes and Barry 2008; Low et al. 2015). Without some level of biological or environmental control, invaders have the potential to dominate the recipient community, in terms of abundance and processes (Vila et al. 2011; Newton et al. 2013). In addition, invaders can have indirect effects on species at different trophic levels, and these effects can impact food webs and alter community and ecosystem processes (Parker et al. 1999; Grosholz 2002; Williams and Smith 2007; Thomsen et al. 2009; Ehrenfeld 2010; Katsanevakis et al. 2014).

Because ecosystem-level processes depend on the functional properties of component species, changes in the diversity and composition of communities, whether due to non-native species or other impacts, have the potential to alter the functional properties of ecosystems (Bracken et al. 2008; Naeem et al. 2012; Bracken and Williams 2013). However, Sousa et al. (2011) noted that only 4% of all studies published in *Biological Invasions* from 1999 to 2009 reported the impacts of invasive species on ecosystem functioning. Additionally, in a recent European review of marine invasions, Katsanevakis et al. (2014) noted that only 13% of reported impacts on ecosystem services from invasive marine species were from manipulative and/or mensurative (e.g. "Pre- vs. Post-Invasion"), citing expert judgment and/or "dubious correlations" as the remaining lines of evidence.

As with other invasive marine species, invasive marine seaweeds have been shown to have substantial impacts on recipient communities (Schaffelke and Hewitt 2007; Williams and Smith 2007; Thomsen et al. 2012). For example, invasive seaweeds have the potential to alter the abundance and diversity of recipient communities through increased competition with native macrophytes (Davidson et al. 2015) and cause potential structural changes in habitat which can lead to changes in the associated fauna, as well as subsequent changes in ecosystem functioning of the recipient community (Schaffelke and Hewitt 2007; Thomsen et al. 2009, 2012). However, as with other

marine invaders, ecological impacts have only been studied in situ for ~6% of the 277 known invasive seaweed species, and in all cases, only effects after the invader had been present in their invaded habitat for many years have been documented (Williams and Smith 2007; Thomsen et al. 2009). Capturing any potential changes that may have occurred immediately following the invasion is difficult. Therefore, little is known about invasion-mediated changes that may occur early in the invasion process and changes in invader roles and impacts over time (Strayer 2012).

The recent invasion of the red alga *Dasysiphonia* (formerly, *Heterosiphonia*) *japonica* (hereafter, *Dasysiphonia*) to the western North Atlantic Ocean threatens both community structure and ecosystem functioning and therefore provides a unique opportunity to understand and quantify invasion impacts on both of these processes immediately following the invasion. Native to the Indo-Pacific region, *Dasysiphonia* was first reported in Rhode Island waters in 2009 (Schneider 2010), although molecular data suggest that this invader was present in the area as early as 2007 (Savoie and Saunders 2013). Since then, *Dasysiphonia* has spread over 700 km in coastal waters and now occupies an invaded range from Maine through New York, with an additional population reported in 2012 in Nova Scotia, Canada (Newton et al. 2013; Savoie and Saunders 2013). Initial samples collected from Rhode Island are a genetic match to samples from invaded populations in Europe (Schneider 2010). Based on the distribution and temperature tolerances of European populations (Bjaerke and Rueness 2004), *Dasysiphonia* has the potential to invade coastal habitats in the western North Atlantic from Florida to Newfoundland (Newton et al. 2013). In addition, in a qualitative assessment of impacts from marine invasive species, Molnar et al. (2008) characterized *Dasysiphonia* as an invader with severe ecological impacts that threatens to disrupt entire ecosystem processes. Indeed, early reports suggest that changes in diversity are already occurring in invaded communities along the western North Atlantic coast following the invasion of *Dasysiphonia* (Newton et al. 2013; Low et al. 2015). While tracking the initial invasion in 2012, negative correlations were found between *Dasysiphonia* abundance and native macrophyte diversity along the western North Atlantic coast (Newton et al. 2013; Low et al. 2015). However, it is unclear whether these negative relationships

remain consistent over time. In addition, the impacts associated with these changes on recipient community structure and functioning have not been identified for this recent algal invader.

Here, we addressed these knowledge gaps by (1) assessing the early changes in biodiversity and community composition in the recipient community following the establishment of *Dasysiphonia*, (2) quantifying the direct and indirect effects of *Dasysiphonia* on community and ecosystem processes (nitrate use efficiency) in recipient communities, and (3) determining any changes in invader traits (e.g., nitrate uptake efficiency) following the initial invasion. These objectives were addressed in a four-year study using a combination of in situ community surveys and laboratory nitrate uptake experiments that incorporated realistic changes in community structure.

Methods

Dasysiphonia was first reported at our study sites in Nahant, Massachusetts, USA in 2010 (Canoe Beach East and Canoe Beach West; 42°25′12.6″N, 70°54′21.3″W; Low et al. 2015). Both Canoe Beach East and Canoe Beach West are semi-protected rocky sites characterized by a combination of subtidal cobble and large boulder fields. Nutrient availability fluctuates seasonally, with significantly lower nitrate availability during summer months (Perini and Bracken 2014). Due to the active research diving program at Northeastern University's Marine Science Center, we have a reliable yearly record of the macroalgal community from faculty, graduate student and undergraduate certified scientific divers, many of who have been trained in marine botany. We are thus relatively confident that we identified *Dasysiphonia* at an unusually early stage in its invasion in this region, as our study sites are located directly adjacent to the Marine Science Center. Further evidence of our early observation and study of the invasion is suggested by the fact at the beginning of our study, *Dasysiphonia* was not present at one of our study sites (see "In situ surveys"). However, by the following year, 2012, *Dasysiphonia* was found at all of our study sites, and was present in a nearly continuous distribution from Maine through New York (Newton et al. 2013), with an additional population reported in Nova Scotia, Canada in 2012 (Savoie and Saunders 2013).

In situ surveys

We conducted in situ seaweed community composition surveys from 2011 to 2014 in Nahant, MA. *Dasysiphonia* was first reported at some sites in this area in 2010 (Low et al. 2015), however, it had not fully colonized the area until 2012 (C. Ramsay-Newton, *personal observation*). Therefore, in 2011, surveys were conducted at two sites, Canoe Beach East (hereafter, "invaded"), where *Dasysiphonia* comprised 49.4% of total macroalgal biomass during our initial surveys in 2011 and at nearby Canoe Beach West (hereafter "uninvaded" or "previously uninvaded" site), where *Dasysiphonia* comprised <2% of the total macroalgal biomass in 2011. In 2012 and 2013, surveys were conducted at Canoe Beach East (invaded site) only, as the entire region had been impacted by *Dasysiphonia*, including our previously non-invaded site (C. Ramsay-Newton, *personal observation*). In 2014, we re-surveyed Canoe Beach West (our previously non-invaded site that was now invaded), as well as continued our Canoe Beach East (invaded) site surveys.

Quantitative SCUBA surveys were conducted during *Dasysiphonia*'s summer peak growth period at depths between 1.6 and 5.1 m below mean lower-low water using randomly placed 25 cm × 25 cm quadrats (n = 5–21 per year). Seaweed community composition was assessed either by destructively sampling the entire quadrat to obtain the dry weights of each species in the lab (2011 data) or by measuring the percent coverage of each species in situ (2012–2014 data). Visual estimates of seaweed cover and dry biomass measurements from plot clearings were highly correlated ($R^2 = 0.83, p < 0.001$). To compare data across years using these different sampling techniques, we report the relative percentages (of either dry mass or percent cover) of each species in this study.

Nutrient uptake experiments

To assess how the critical ecosystem function of nutrient cycling was altered in response to invasion mediated changes in the community through time, we conducted nutrient uptake experiments to measure nitrate use efficiency in 2011, 2012, and 2013. Nitrate is an important growth-limiting nutrient for seaweeds in near-shore subtidal communities, including our

study site of Nahant, Massachusetts (Perini and Bracken 2014). Using our data from collections of biomass during the surveys conducted in 2011, we created realistic seaweed community polyculture assemblages that replicated the relative abundances of seaweed species from both our invaded (Canoe Beach East) and non-invaded (Canoe Beach West) sites (Table 1; Online Resource 1). These realistic seaweed community assemblages were created by collecting all upright seaweeds in $n = 10$ quadrats (25 cm × 25 cm) in each location, sorting them in the lab to species, and determining the relative abundance (wet weight) of each species in each plot. Each polyculure assemblage was standardized to total weight of 6 g. A third treatment, identical to the invaded assemblages but with *Dasysiphonia* removed, was used to assess whether potential impacts were due to changes in the community or to the presence of the invader itself. We also included monoculture assemblages of each component species to assess nitrate uptake on an individual species level.

Nitrate uptake rates were measured for each realistic polyculture assemblage, and for all individual component species at four different nitrate concentrations (2, 15, 30, and 50 µmol L^{-1}) using clear acrylic 1-L plastic containers filled with re-circulating artificial seawater (35 ppt). Each chamber was placed in a chilled water bath, such that water temperatures and light levels in each chamber were kept within the ranges of local in situ conditions (13–15 °C and 350.5 ± 25 µmol photons m^{-2} s^{-1}, respectively; Low et al. 2015). Each chamber was also outfitted with a pump to maintain high turbulence, as nutrient uptake and photosynthetic rates of seaweeds are hindered at low velocities (Barr et al. 2008).

Seaweed was collected from our invaded site (Canoe Beach East) via SCUBA no more than 18 h prior to each trial to capture any trait changes in the invader and community response through time. Seaweeds were spun to remove excess water and weighed to create each realistic assemblage or monoculture. A single assemblage or monoculture was placed in each chamber and allowed to acclimate for 10 min before seawater was spiked with a NaNO$_3$ stock solution to the appropriate concentration (2, 15, 30, or 50 µmol L^{-1}). Water samples were collected every 15 min over the 2-h trial to assess nitrate depletion in the water column. The nitrate concentration in each water sample was determined using a

QuickChem 8500 Series FIA + analyzer (Lachat Instruments, Loveland, CO, USA). At the conclusion of each trial, seaweeds were removed from the chambers and oven-dried at 60 °C to obtain a dry weight for each component species in the assemblage.

The rate of nitrate depletion in the water column of each chamber was divided by the dry weight of seaweed in the chamber to obtain a biomass specific nitrate uptake rate (µmol g^{-1} h^1). The rate was then plotted as a function of initial nitrate concentration and fitted to Michaelis–Menten models using nonlinear curve-fitting techniques to determine the parameters for each assemblage:

$$V = (V_{max} \times S) / (K_s + S), \tag{1}$$

where V (µmol g^{-1} h^1) was the uptake rate, V_{max} was the maximum uptake rate of a species or assemblage, S (µmol/L) was the initial nitrate concentration and K_s was defined as the initial concentration at $V_{max}/2$. We also used liner models to fit the data:

$$V = m \times S + b, \tag{2}$$

where m was the slope of the liner relationship and b was the intercept. Michaelis–Menten models and linear models were verified using the corrected Akaike Information Criterion (AIC), to determine the most appropriate model for each assemblage. The preferred model was the one with the minimum AIC value. We calculated the nitrate uptake coefficient (α) for each assemblage, which represents the slope of the relationship at low nitrate concentrations. For assemblages in which a Michaelis–Menten model was used,

$$\alpha = V_{max}/K_s, \tag{3}$$

whereas in assemblages where a linear fit model was appropriate,

$$\alpha = m. \tag{4}$$

To examine whether the performance of a community was impacted by the presence or absence of *Dasysiphonia* in the community and the mechanisms underlying any relationships between community composition and nitrate uptake, we calculated two metrics for the effects of species assemblage on uptake: D_{mean} and D_{max}. These metrics are used to evaluate whether assemblages exhibit overyielding, consistent with complementarity or facilitation, as different species in the community use non-

Table 1 Community composition of our non-invaded and invaded sites from 2011 to 2014

Species	2011		2012	2013	2014	
	Non-invaded	Invaded	Invaded	Invaded	Previously non-invaded	Invaded
Ahnfeltia plicata	1.39 ± 0.87	3.00 ± 1.18	0.18 ± 0.18			1.10 ± 1.10
Bonnemaisonia hamifera	3.75 ± 2.28	0.07 ± 0.04	4.07 ± 2.05		1.25 ± 1.25	
Botryoloides diegensis			1.17 ± 0.55	3.29 ± 1.41	0.63 ± 0.63	
Bugula spp.				0.82 ± 0.49		
Ceramium deslongchampii	0.20 ± 0.11	0.16 ± 0.08	0.56 ± 0.39	0.38 ± 0.38		0.30 ± 0.30
Chaetomorpha spp.	0.15 ± 0.11	0.01 ± 0.01	0.15 ± 0.15	0.38 ± 0.28	0.87 ± 0.87	0.37 ± 0.37
Chaetomorpha melagonium	0.02 ± 0.01	0.01 ± 0.00				
Chondrus crispus	44.15 ± 4.87	34.33 ± 4.81	12.26 ± 3.09	13.24 ± 3.03	37.24 ± 5.98	44.37 ± 2.88
Cladophora spp.	0.23 ± 0.11		0.21 ± 0.21	0.56 ± 0.56		
Codium fragile	0.01 ± 0.01					
Corallina officinalis	21.40 ± 5.09	3.09 ± 1.40	9.94 ± 2.96	12.29 ± 2.60	16.17 ± 6.25	
Crustose spp.			20.98 ± 4.41	24.42 ± 3.88		
Cystoclonium purpuratum				0.57 ± 0.45	3.48 ± 3.48	18.47 ± 5.91
Dasysiphonia japonica	2.10 ± 0.80	49.45 ± 5.33	14.90 ± 4.45	40.26 ± 4.74	16.97 ± 4.26	21.15 ± 5.05
Desmarestia spp.	1.80 ± 0.85	1.65 ± 1.01			2.50 ± 1.82	8.83 ± 5.04
Euthora cristata	0.06 ± 0.03					
Erythrotrichia carnea		0.15 ± 0.15				
Hildenbrandia rubra			0.08 ± 0.08			
Hypnea musciformis			1.91 ± 1.48			
Lithothamnion glaciale			0.47 ± 0.34			
Palmaria palmata						
Phycodrys rubens	0.07 ± 0.05	0.21 ± 0.16	0.75 ± 0.53			3.66 ± 2.90
Phyllophora pseudoceranoides	0.01 ± 0.01	0.03 ± 0.03				
Polyides rotundus		0.99 ± 0.99	0.75 ± 0.56			
Polysiphonia spp.			21.21 ± 5.46	0.26 ± 0.26		
Polysiphonia denudata	0.31 ± 0.28					
Polysiphonia fucoides	18.80 ± 5.26	0.25 ± 0.16			3.48 ± 3.48	
Polysiphonia haveyi	0.01 ± 0.01					
Polysiphonia nigra	0.05 ± 0.03	0.01 ± 0.01				
Polysiphonia stricta	0.58 ± 0.43	2.26 ± 1.65				
Porphyra spp.	0.01 ± 0.00	0.01 ± 0.01				
Saccharina spp.	0.02 ± 0.02	4.19 ± 3.77			13.53 ± 4.08	
Spermothamnion repens			9.50 ± 3.54		2.43 ± 1.49	0.73 ± 0.73
Rhodomela confervoides	1.97 ± 0.99					
Ulva spp.	0.16 ± 0.12	0.15 ± 0.12	0.05 ± 0.05	1.18 ± 0.54	1.46 ± 0.91	0.30 ± 0.30

Invaded sites were surveyed each year, while our non-invaded site was surveyed prior to *Dasysiphonia japonica* invasion and re-surveyed in 2014 after *Dasysiphonia* had invaded. Results are reported in relative percentages ± standard error

* Indicates those species which were used during our nutrient uptake experiments (see Online Resource 1 for experimental assemblages)

overlapping resources (Bracken and Williams 2013). Specifically, we compared the performance (i.e., nutrient uptake) of a diverse assemblage to the mean performance of the component species (D_{mean}) or to the best performing component species (D_{max}). D_{mean} is an indicator of non-transgressive overyielding:

$$D_{mean} = (P-M_{mean})/M_{mean}, \qquad (5)$$

where P was the uptake coefficient of a given assemblage and M_{mean} was the predicted uptake coefficient based on a weighted average of the component species' uptake coefficients when measured in monoculture (Power and Cardinale 2009; Bracken et al. 2011). We also calculated D_{max} as an indicator of transgressive overyielding:

$$D_{max} = (P-M_{max})/M_{max},$$

where M_{max} was the uptake coefficient of the best-performing component species when measured in monoculture (Loreau 1998; Bracken et al. 2011).

Statistical analyses

We calculated species richness at both Canoe Beach West (previously uninvaded) and Canoe Beach East (invaded) at the beginning and conclusion of this study (2011 and 2014, respectively) and analyzed differences in sites (Invaded and non-invaded/previously un-invaded) and years (2011 and 2014) using a two-way analysis of variance (ANOVA) on log-transformed data with fixed factors. Tukey post hoc tests were run on statistically significant effects. We also used a one-way analysis of variance to calculate differences in species richness and the relative proportion of *Dasysiphonia* across all four sampling years at our continuously sampled Canoe Beach East (invaded) site. Univariate data were analyzed using JMP v. 11.0 (SAS Institute, Inc., Cary, NC, USA). Differences in macroalgal community composition across sites between 2011 and 2014 were assessed by calculating a Bray–Curtis similarity matrix on square root transformed data, followed by an analysis of similarity (ANOSIM) and the construction of an nMDS (non-metric Multidimensional Scaling) plot (PRIMER v. 6.0; Primer-E Ltd., Plymouth, UK). Nutrient uptake data were analyzed using a generalized linear model (proc GENMOD in SAS v. 9.4, SAS Institute, Inc. Cary, NC, USA) with a gamma

distribution and log link to assess differences in D_{mean} or D_{max} for community assemblages with and without *Dasysiphonia*. Our model included year (2011, 2012, and 2013), treatment (invaded, non-invaded, and invaded [*Dasysiphonia removed*]), and a "Year × Treatment" interaction.

Results

In situ surveys

Following the invasion of *Dasysiphonia* in Nahant, MA in 2011, the macroalgal community changed both in terms of biodiversity and community composition (Figs. 1, 2; Table 1). In 2011, species richness was nearly two times greater at our site that had not yet been invaded by *Dasysiphonia* when compared to our invaded site. By 2014, both our invaded site and our previously uninvaded site—which had been subsequently invaded by *Dasysiphonia*—were characterized by similar levels of biodiversity which were lower than both sites in 2011 ($F_{1,36} = 43.38$, $p = 0.002$; Fig. 1; Table 2). In addition, we found that the composition of the macroalgal community at our invaded site remained fairly consistent from 2011 to 2014; however, the composition of the macroalgal community at our initially non-invaded site changed significantly, shifting to a community composition similar to our invaded site in 2014 (Global R = 0.97, $p = 0.01$; Fig. 2; Table 1). The relative proportion of
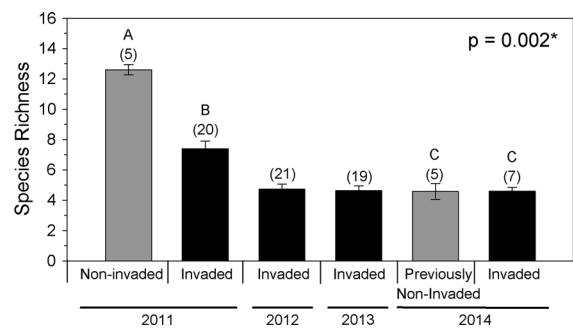
Fig. 1 Community biodiversity at non-invaded and invaded sites in the 4 years following the initial invasion of *Dasysiphonia japonica. Letters* indicate differences in species richness based on a two-way ANOVA with Invasion Status (invaded and non-invaded/previously non-invaded) and year (2011 and 2014) as factors. Sample size is indicated in *parentheses*
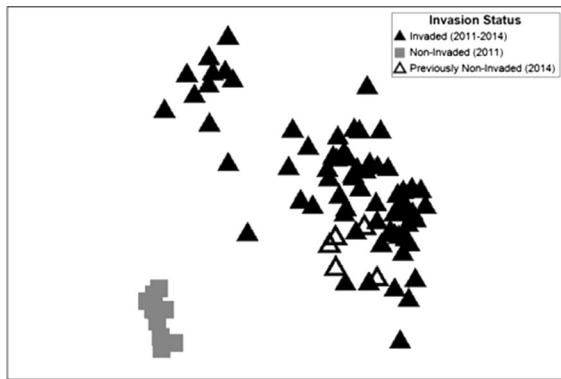
Fig. 2 MDS plot of community structure showing the community composition of the subtidal benthic community prior to the invasion of *Dasysiphonia japonica* significant changes in the composition of the subtidal benthic community before and after the invasion of *Dasysiphonia japonica* across all 4 years (2011–2014)

Fig. 3 The relative proportion of *Dasysiphonia japonica* in the subtidal benthic community in the 4 years following the initial invasion of *Dasysiphonia*. *Letters* indicate significant differences between years based on a one-way ANOVA. Sample size is indicated within *parentheses*

Dasysiphonia at the invaded site also decreased significantly from 56% of the macroalgal community in 2011 to only 21% of the macroalgal community in 2014 ($F_{3\ 56} = 6.36$, $p < 0.001$; Fig. 3). Although this proportion fluctuated across years, it should be noted that the relative abundance of *Dasysiphonia* was lower in subsequent years relative to abundances measured in 2011, immediately following its initial invasion (although this was not statistically significant in 2013).
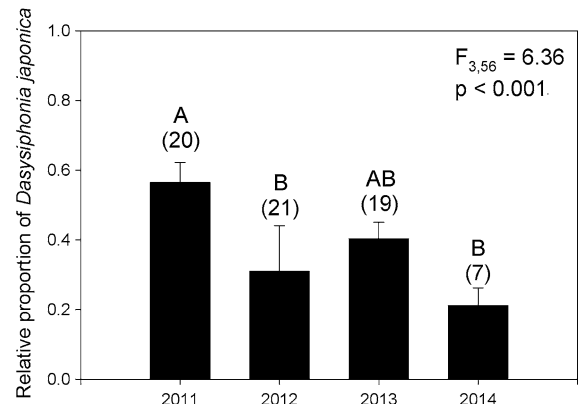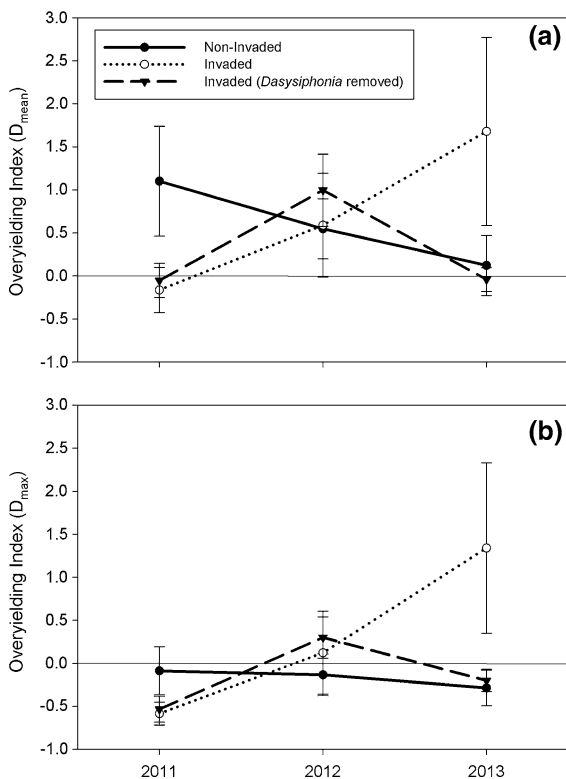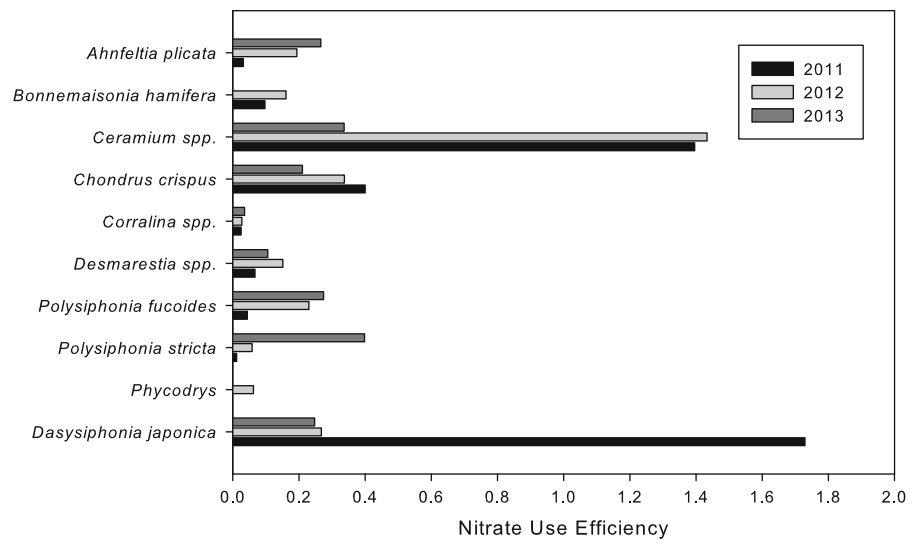
Nutrient uptake

On an individual species level, in 2011, *Dasysiphonia* had an uptake efficiency nearly an order of magnitude higher than the average of all other component species (*Dasysiphonia* $\alpha = 1.73$, all other component species mean $\alpha = 0.26$; Fig. 4; Low et al. 2015). However, in 2012 and 2013, uptake efficiencies of *Dasysiphonia*

decreased and were comparable to the average of all other species.

When the impacts of *Dasysiphonia* on nutrient uptake were assessed in a community context, we found that non-transgressive overyielding in nutrient uptake (D_{mean} values) of "invaded" community assemblages tended to increase as the invasion progressed between 2011 and 2013 (GENMOD: $D_{mean} > 0$; $z = -2.29$, $p = 0.022$, "Invaded" in 2011 vs. 2013; Fig. 5a). Initially, assemblages containing *Dasysiphonia* performed as predicted by the component species ($z = -0.71$, $p = 0.477$), but by 2013, assemblages containing *Dasysiphonia* were characterized by higher nitrate uptake efficiency than predicted by the component species ($z = 2.62$, $p = 0.009$). In contrast, overyielding in our "non-invaded" assemblages, which were characterized by relatively high D_{mean} values in 2011 ($z = 1.76$, $p = 0.079$), declined through 2012 and 2013, so that performance of the community assemblage was predicted by the average performance of each component species by 2013 ($D_{mean} \sim 0$; Fig. 5a; $z = 0.09$, $p = 0.925$). With respect to transgressive overyielding (D_{max}), we found that assemblages were actually underyielding relative to the best-performing component species (*Dasysiphonia*) in 2011 ($D_{max} < 0$; $z = 2.81$, $p = 0.058$). However, in 2012 and 2013, assemblages were performing as well as their best-performing component species ($D_{max} \sim 0$; $p > 0.80$; Fig. 5b). A "Year × Treatment" interaction (GENMOD: $X^2 = 9.15$, $df = 4$, $p = 0.058$) was present in the "Invaded" treatment (2011 < 0: $z = -2.41$,

Table 2 Results of the two-way ANOVA with Year (2011 and 2014) and Invasion Status

Effect	df	F	p value
Year	1	54.89	<0.001
Invasion Status	1	12.09	0.001
Year × Invasion Status	1	11.82	0.002
Error	33		

(Non-invaded/previously non-invaded and Invaded) as fixed factors to assess differences in species richness

Fig. 4 Nitrate uptake efficiency (μmol/g/h) of individual component species in monoculture across 3 years (2011–2013)

Fig. 5 Community performance (nutrient uptake efficiency) in the 3 years following the initial invasion of *Dasysiphonia japonica* across three groups of realistic community assemblages. The performance of a diverse, realistic assemblage is predicted by the mean (D_{mean}) of each component species **a** or the best performing (D_{max}) component species **b**. Performances greater than zero indicate increased resource partitioning, or complementarity, thereby increasing the overall uptake efficiency of the community

$p = 0.016$; $2012 = 0$: $z = 0.21$, $p = 0.834$; $2013 > 0$: $z = 2.12$, $p = 0.034$), yet was not present in the "Non-invaded" assemblages ($p > 0.30$ for all years). When we ran the uptake trials using invaded assemblages without *Dasysiphonia*, no such patterns were seen in either D_{mean} or D_{max}, indicating no overall change in overyielding between 2011 and 2013 ("Invaded [*Dasysiphonia* removed]"; Fig. 5a, b).

Discussion

Our research shows significant changes in macroalgal biodiversity and an ecosystem function (nitrate uptake) immediately following the invasion of *Dasysiphonia* and provides empirical evidence documenting changes in invader performance during the first years following its establishment. By comparing adjacent invaded and uninvaded communities, we were able to characterize both the initial decline in species richness immediately following the initial invasion of *Dasysiphonia* in 2011 and the subsequent invasion and reduction in biodiversity in a previously uninvaded community. Although we focus only on a single uninvaded and single invaded site, these reductions in biodiversity align well with results found at multiple sites throughout the invaded region of *Dasysiphonia* in the western North Atlantic (Newton et al. 2013; Low et al. 2015).

Along with this reduction in biodiversity, the composition of the recipient community changed

following the invasion of *Dasysiphonia*. The composition of the site that was initially uninvaded in 2011 became similar to the invaded site by 2014 when *Daysiphonia* had fully colonized the area. The changes in species abundance and community composition resulting from the invasion of *Dasysiphonia* affected nutrient uptake, highlighting impacts of the invader on an important ecosystem process; moreover, the functional mechanisms (e.g., complementarity) influencing ecosystem processes changed within the first 4 years of the initial invasion. Complementarity occurs when different species utilize non-overlapping resources, such as nitrate, across a resource gradient, increasing the overall performance of the community. While experiments during the initial stages of the invasion of *Dasysiphonia* in 2011 suggested that non-invaded communities were more successful at nutrient uptake and thus exhibited higher complementarity, as the invasion progressed, changes at both the community and individual species level allowed invaded communities to shift their resource partitioning and thus increase the overall efficiency of the community. By 2013, the performance of the invaded community assemblages surpassed not only the expected average performance of the community (D_{mean}), but also the uptake efficiency of the best performing component species (D_{max}).

Evidence for functional responses to *Dasysiphonia*'s invasion at the community level was highlighted by our removal of *Dasysiphonia* from invaded community assemblages. During the initial invasion in 2011, invaded communities performed equally well regardless of whether *Dasysiphonia* was included, suggesting that this invader did not interact substantially with the species that remained in invaded assemblages. However, by 2013, when *Dasysisphonia* was removed from invaded assemblages, the overall performance of the community dropped substantially (Fig. 5a, b, "Invaded" & "Invaded [*Dasysiphonia* removed]"), demonstrating that *Dasysiponia* was interacting with and complementing native species with respect to nutrient uptake.

Not only did changes take place at the community level, but we also saw evidence of changes in the traits of the invader itself with respect to nutrient uptake. During the initial invasion in 2011, the nitrate uptake efficiency of *Dasysiphonia* was nearly an order of magnitude higher than the average uptake of native species (1.73 vs. 0.26, respectively). This increased

efficiency is likely one of several traits that contributed to the initial invasive success of *Dasysiphonia*, along with higher growth rates and decreased herbivory when compared to native species (Low et al. 2015; C. Ramsay-Newton, *unpublished data*). However, as the invasion progressed and the community structure changed, the uptake efficiency of *Dasysiphonia* declined to levels comparable to those of native species. In addition, by 2014, *Dasysiphonia* was no longer competitively superior to native species in terms of growth rate or decreased herbivory (C. Ramsay-Newton, *unpublished data*). This shift in traits may be beneficial to invasive species when initially competing for resources during the initial invasion. However, as the invader reduces interspecific competition, by increasing its abundance during the course of the initial invasion and reducing native biodiversity (Newton et al. 2013; present study), changes in functional traits may be necessary to reduce intraspecific competition as the invader becomes the dominant member of the recipient community. Indeed, phenotypic plasticity has been shown to be greater in non-native species, particularly in response to greater resource availability (Simberloff and Gibbons 2004; Strayer et al. 2006; Davidson et al. 2011; Strayer 2012).

Immediately following its invasion, *Dasysiphonia* was an aggressive invader and competitor with native species, as evidenced by the initially high relative abundances and nutrient uptake rates of *Dasysiphonia*, as well as the decreases in community diversity associated with invasion. Yet, within only 5 years of its initial report, *Dasysiphonia* had been functionally incorporated into the local macroalgal community, as reflected in lower uptake rates and an increase in metrics that indicate complementarity or niche partitioning. However, this incorporation of the invader was accompanied by serious impacts to the native community with respect to native species abundance and diversity. By incorporating these realistic community changes along with increased time scales into our research, we were able to link invasion-mediated changes in community structure with changes in ecosystem functioning, while also documenting functional changes in the invader itself. Our research highlights dramatic and rapid shifts in responses at individual, community, and ecosystem levels associated with a recent macroalgal invader. Initially, *Dasysiphonia* was a better competitor for resources

than native species, and thus the overall efficiency of the community suffered. However, within 5 years of the initial invasion, *Dasysiphonia* had reduced its nutrient uptake efficiency, and the nitrate uptake efficiency of the community stabilized. We were able to capture not only the initial invasion of *Dasysiphonia*, but also the rapid response of the community and invader in terms of community structure, ecosystem functioning and invader traits at these sites in the western North Atlantic. This is not often the case, as lag times between initial introductions, range expansions and ecosystem impacts can last from decades to centuries (Simberloff 2011). Our work also further highlights the importance of capturing the full range of responses by the invader as well as the recipient community, including during the initial invasion, to adequately assess the mechanisms behind these impacts on the individual, community, and ecosystem level responses.

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