Early Strategies of Invasive Seaweeds:
The Recent Invasion of *Dasysiphonia* (formerly, “*Heterosiphonia*”) *japonica*
to the Western North Atlantic Ocean

By Christine Ramsay-Newton

B.S. in Biology, Providence College
M.S. in Biological Sciences, University of Rhode Island

A dissertation submitted to

The Faculty of
The College of Science of
Northeastern University
In partial fulfillment of the requirements
For the degree of Doctor of Philosophy

April 13, 2015

Dissertation directed by

(Anne) Randall Hughes
Assistant Professor
DEDICATION

To my family – Jason, Gabriella, Greyson, Grant and Gia – you have made this experience one fun and crazy, yet incredibly rewarding, adventure. Through all the ups and downs, I can always look to one of you for a smile or a laugh.

To my parents – Without your support and encouragement over the years, I never would have been able to accomplish all of this.
ACKNOWLEDGEMENTS

This dissertation would not have been possible without the guidance of my major professors, M.E.S. Bracken, A.R. Hughes and C.S. Thornber. In addition, the members of my committee, D. Cheney, D. Kimbro, and J. Grabowski provided valuable insights and fresh perspectives to this research.

I would like to thank the members of my lab for their assistance with this work, including former and current Bracken lab members, as well as the Hug-Bro lab members. I would also like to acknowledge my undergraduate field and laboratory assistants, past and present, both at Northeastern University and the University of Rhode Island. In particular, I am indebted to all of the diving buddies I have worked with to accomplish this subtidal research.

This research would not have been possible without the support of the following diving safety officers and their respective universities: S. Genovese, T. Lyman, and L. Magee (Northeastern University), A. Hanson (URI), and J. Godfrey (UConn). In addition, Northeastern University’s Marine Science Center and the University of Rhode Island’s Graduate School of Oceanography provided valuable outdoor space for running experiments.

I am particularly indebted to M. Guidone and N. Rohr, who have guided and supported my academic and professional life for the last eight years.

Funding for this research was provided by The Massachusetts Institute of Technology Sea Grant College Program, under National Oceanic and Atmospheric Administration Grant Number NA14OAR4170077, MIT SG Project Number 2014-
R/RCM-37, along with funding by National Science Foundation Award OCE-0963010 and Woods Hole Sea Grant (Subaward A100923).

Lastly, I would like to thank my friends and family, particularly my husband and parents, for supporting me throughout my entire graduate career. Without your assistance, this would have never been possible!
ABSTRACT OF DISSERTATION

Invasion biology has become a primary focus of research on global change due to the enormous ecological and economic impacts that these species can have on recipient communities. Ecologically, invasive species have been responsible for altering community structure, reducing native biodiversity, and disrupting ecosystem functioning. The economic impacts of invasive species can include altering fisheries and aquaculture, as well as decreases in recreation and tourism. However, as many invaders go unnoticed or unidentified, particularly in marine communities, much of the invasion biology research has been conducted on well-established invaders. Therefore, little is known about early invasion dynamics on invader characteristics and recipient communities.

The recent invasion of the red alga, Dasysiphonia (formerly, “Heterosiphonia”) japonica to the western North Atlantic Ocean provides us with a unique opportunity to study the early invasion dynamics of a marine macrophyte invader. Native to the Indo-Pacific region, Dasysiphonia was first reported as an invader in the eastern Atlantic Ocean in the 1980’s, before invading the western Atlantic Ocean in 2009 in Rhode Island (although molecular data suggest it was present as early as 2007 in Rhode Island waters). Based on temperature and salinity tolerances of the genetically identical European populations, Dasysiphonia has the potential to alter native biodiversity and ecosystem functioning in subtidal communities from Nova Scotia, Canada through Florida, USA.

We used this recent invasion to examine the early invasion dynamics of Dasysiphonia on recipient communities in the western Atlantic Ocean. Specifically, this research sought to: (1) report the currently invaded range of Dasysiphonia in the western Atlantic Ocean, (2) assess the impacts on native community structure and biodiversity
from *Dasysiphonia*, (3) investigate the abiotic and biotic factors contributing to invasion success of *Dasysiphonia*, and (4) determine the impacts from the invader on critical nearshore ecosystem processes.

We conducted subtidal community surveys at 19 sites in 2012 between Maine, USA and New York, USA to ascertain the current invaded range of *Dasysiphonia* in the western North Atlantic. *Dasysiphonia* was found at nearly all sites from Cape Elizabeth, Maine through Long Island Sound (New York). Abundances of *Dasysiphonia* averaged approximately 14% of the benthic community, however, we observed abundances of up to 80% were seen at multiple locations. In addition, we found community structure differed significantly between the northern and southern regions, which are separated by a well-known biogeographic barrier at Cape Cod, Massachusetts.

Important changes at the community and individual species level may occur immediately following an initial invasion as the invader is incorporated into the recipient community. We continued tracking abundances of *Dasysiphonia* and recipient community responses during the first four years of the invasion in the northern region, as well as explored the impacts this marine invader had on ecosystem functioning in the recipient community. At the community level, biodiversity of native macrophytes decreased to nearly half of pre-invasion levels and community composition shifted within only four years after the initial invasion of *Dasysiphonia*. Additionally, *Dasysiphonia* abundances decreased following the initial invasion. On an individual species level, we found evidence of plasticity in the invader with respect to nutrient uptake efficiency. Despite these changes in structure at both the community and individual species level, communities are able to successful respond to species invasion by altering the functional
mechanisms underlying the relationship between biodiversity and ecosystem functioning. Experiments during the initial invasion in 2011 showed non-invaded communities were more successful at nutrient uptake, however, as *Dasysiphonia* was incorporated into the community, changes at both the community and initial species level by 2013 allowed invaded communities to increase their overall nutrient uptake efficiencies and surpass those of non-invaded community assemblages.

The impacts and community responses to invasions are context dependent, as we were able to show for *Dasysiphonia*. During the first four years of invasion, abundances of *Dasysiphonia* were consistently higher (>200%) in the northern biogeographic providence (north of the biogeographical barrier, Cape Cod, MA), when compared to our surveys in the southern region, suggesting differences in biotic and abiotic conditions may have contributed to the success of *Dasysiphonia* within each region. Indeed, through controlled mesocosm experiments in each region, we found northern populations of *Dasysiphonia* grew 10 times faster than populations south of the biogeographical barrier. Preliminary evidence also suggested that consumption of *Dasysiphonia* by the native herbivore, *Lacuna vincta*, may be higher in the south, leading to the lower abundances of the invader we found in our subtidal surveys. This differential invasion strategy between biogeographic regions may have contributed to important community level responses as we found a strong negative correlation between *Dasysiphonia* abundance and native diversity in the northern biogeographic providence, however, through *in situ* manipulative experiments, we showed *Dasysiphonia* did not impact diversity in the southern region.
Our work highlights the importance of recognizing and identifying invasive species early in their invasion process, as important community and individual species level changes can occur within only 5 years following the initial invasion, including reductions in biodiversity and alterations of important ecosystem functions. However, the success and impacts of these invaders are context dependent and can vary with differences in biotic and abiotic conditions of the recipient community. Therefore the need to assess invader traits and community impacts across the entire invaded range is paramount, particularly if this range encompasses major differences in conditions, as in the invasion of *Dasysiphonia* to the western Atlantic Ocean.
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CHAPTER 1

INVASION OF THE RED SEAWEED *HETEROSIPHONIA JAPONICA* SPANS BIOGEOGRAPHIC PROVINCES IN THE WESTERN NORTH ATLANTIC OCEAN

Christine Newton*¹*, Matthew E.S. Bracken¹, Megan McConville², Katherine Rodrigue², Carol S. Thornber²

¹Northeastern University
Marine Science Center
430 Nahant Road
Nahant, MA 01908, USA

²Department of Biological Sciences
University of Rhode Island
120 Flagg Road
Kingston, RI 02881, USA

*Corresponding author: newton.c@husky.neu.edu

Manuscript published:
ABSTRACT:

The recent invasion of the red alga *Heterosiphonia japonica* in the western North Atlantic Ocean has provided a unique opportunity to study invasion dynamics across a biogeographical barrier. Native to the western North Pacific Ocean, initial collections in 2007 and 2009 restricted the western North Atlantic range of this invader to Rhode Island, USA. However, through subtidal community surveys, we document the presence of *Heterosiphonia* in coastal waters from Maine to New York, USA, a distance of more than 700 km. This geographical distribution spans a well-known biogeographical barrier at Cape Cod, Massachusetts. Despite significant differences in subtidal community structure north and south of Cape Cod, *Heterosiphonia* was found at all but two sites surveyed in both biogeographic provinces, suggesting that this invader is capable of rapid expansion over broad geographic ranges. Across all sites surveyed, *Heterosiphonia* comprised 14% of the subtidal benthic community. However, average abundances of nearly 80% were found at some locations. As a drifting macrophyte, *Heterosiphonia* was found as intertidal wrack in abundances of up to 65% of the biomass washed up along beaches surveyed. Our surveys suggest that the high abundance of *Heterosiphonia* has already led to marked changes in subtidal community structure; we found significantly lower species richness in recipient communities with higher *Heterosiphona* abundances. Based on temperature and salinity tolerances of the European populations, we believe *Heterosiphonia* has the potential to invade and alter subtidal communities from Florida to Newfoundlnd in the western North Atlantic.
KEYWORDS: *Heterosiphonia japonica*, biogeographical barrier, invasive species

INTRODUCTION:

Non-native species invasions have become a primary focus of research on global change in the past decade [1,2]. The importance of marine invasions is highlighted by the significant economic and ecological impacts often associated with these species following a successful invasion. While only a small fraction of all introduced species can successfully thrive in a new habitat, their impacts can be dramatic [3,4]. Economically, invasive marine species have been responsible for the collapse of fisheries and losses in aquaculture, tourism, and marine infrastructure [5]. Invaders may also have substantial ecological impacts by modifying the habitat in which they invade, displacing native species, and altering food webs and community structure [6]. Additionally, marine invasive species have been identified as a major threat to biodiversity [1,5,7].

The invasive red seaweed *Heterosiphonia japonica* Yendo (hereafter *Heterosiphonia*), recently discovered in the western North Atlantic Ocean, poses a threat to native biodiversity and ecosystem functioning. First reported in Rhode Island waters in 2007, this species is morphologically and genetically identical to invasive populations of *Heterosiphonia* in the eastern North Atlantic [8,9]. *Heterosiphonia* was first recorded in France in 1984 and has since become widespread along European coastlines [10]. While the exact vector of introduction to the western North Atlantic is unknown, this species was likely introduced from Europe via ballast water early in the new century [8].

In contrast to its European invaded range [10,11,12], *Heterosiphonia* is not particularly abundant in its native range in the western North Pacific Ocean, comprising less than 1% of the macroalgal biomass and only occurring sporadically throughout the year [13,14]. In both its
native and invaded ranges, *Heterosiphonia* occupies shallow, subtidal habitats and is present either on rocky substrata or epiphytic on other macroalgal species, although it has also been found in sandy and soft sediment habitats [11,13, C. Newton, pers. obs.].

Initial reports limited the western Atlantic distribution of this species to Rhode Island [8]. However, reports from the invasion of *Heterosiphonia* in Europe suggest that the species is capable of rapid dispersal associated with broad thermal and salinity tolerances and high fecundity due to vegetative propagation of fragmented pseudolaterals [15,16]. This has led to a wide geographic distribution in Europe, with reports of the invasive alga from Norway to Italy [10]. Based on thermal tolerances across its European range, *Heterosiphonia* has the potential to invade western Atlantic waters from Newfoundland through Florida [16].

Based on these predictions from the eastern Atlantic invasion of *Heterosiphonia*, we sought to: (1) ascertain the present invaded range and relative abundance of *Heterosiphonia* in western Atlantic coastal waters; (2) determine the biological attributes that are associated with recipient communities; (3) establish whether more diverse communities have higher resistance to *Heterosiphonia* invasion; and (4) assess the proportion of drift *Heterosiphonia* in wrack mats washed ashore. We addressed these goals by surveying shallow subtidal communities and adjacent beaches along the northwestern Atlantic shoreline from New York to Maine, USA.

**METHODS:**

We conducted subtidal community surveys at 19 sites between Cape Elizabeth, Maine (43°37’N, 70°12’W) and Waterford, Connecticut (41°17’N, 72°09’W), including Southold, New York (41°18’N, 71°55’W), during the summer of 2012 (Fig. 1). This geographic range covers over 700 km of coastline while spanning a well-known biogeographic barrier in the western
Atlantic Ocean; Cape Cod, Massachusetts, separates the Acadian biogeographic province from the more southerly Virginian province. These two provinces are characterized by marked differences in water temperature and community structure [17,18]. Cape Cod is a well-known southern limit for many cold water marine species, as the southward flowing Labrador Current brings down cooler waters, before swinging east along the arm of Cape Cod, and finally returning in a northeasterly direction. However, waters south of Cape Cod are more influenced by the warmer Gulf Stream, particularly during the summer months [17].

Surveys were conducted in both biogeographic provinces between 0 and 6.25 m depth using SCUBA, as *Heterosiphonia* is most commonly found within this depth range. Sites were chosen to include a variable range of exposure, from locations exposed to ocean swells to protected bays.

At each site, a 20m transect was haphazardly placed in the subtidal zone, at approximately the mid point of the species' typical depth range (mean depth = 2.0 ± 0.11 m). We placed a 0.0625 m$^2$ quadrat every 2 m along the transect. Within each quadrat, the percent cover of each macroalgal and sessile invertebrate species was recorded. When present, a subsample of *Heterosiphonia* individuals was collected from each site. Upon collection, specimens were returned to the laboratory, where field identifications were confirmed under a compound microscope (100X) using characteristics from Schneider [8]. All individuals collected were either vegetative or tetrasporic. No fertile gametophytes were found during our sampling. At an additional 12 sites within our subtidal survey range, we examined the intertidal and/or shallow subtidal zone for evidence of drifting *Heterosiphonia* individuals. At each of these sites, individuals were collected and identified under a field microscope (40X) or laboratory microscope (100X). Due to logistical constraints, we clustered all crustose coralline algal species
together, as *in situ* identifications to the species level proved impossible for this group. When possible, a subsample of *Heterosiphonia* individuals from most locations was pressed and deposited in the University of Rhode Island (KIRI) or Northeastern University (HNUB) herbarium collections.

We also conducted weekly surveys of intertidal wrack mats at five sites in the northern range of our surveys from 28 June 2012 through 02 August 2012 (Table 1). These sites were chosen to encompass a variety of exposures and local topographies. Surveys were conducted at low tide each week. Similar to our subtidal surveys, a 20m transect was laid parallel to the mean-low water line at each site and a 0.0625 m$^2$ quadrat was used to sample every 2 m along the transect. The contents of each quadrat were collected into individual bags and immediately returned to the laboratory where any *Heterosiphonia* present in the quadrat was sorted out. The wet weight of all *Heterosiphonia* and other remaining macrophytes present was recorded after being spun in a salad spinner 15X to remove excess moisture [6].

**Statistical Analyses:**

Multivariate data were analyzed using Primer v. 6.0 (Primer-E Ltd., Plymouth, UK) to compare differences in subtidal community structure. Bray-Curtis similarity matrices were constructed on square-root transformed percent-cover data. We then ran a PERMANOVA (Permutational Multivariate Analysis of Variance; ref. 19) to determine if community compositions differed north and south of Cape Cod, Massachusetts. Univariate data were analyzed using JMP v. 9.0 (SAS Institute, Inc., Cary, North Carolina, USA). Regression was used to determine the relationship between species richness and abundance of *Heterosiphonia*. We conducted analyses of variance (ANOVAs) to assess spatial and temporal differences for
intertidal drift surveys of *Heterosiphonia*. To assess temporal variability in our subtidal surveys we were only able to repeat subtidal surveys at four locations, two north (sites 14 & 15, Table 1) and two south (sites 21 & 22, Table 1). We were unable to satisfy the homogeneity of variances assumption for analyses of variances via transformation for these data [20]. Therefore, we used a generalized linear model (proc GENMOD in SAS v. 9.2, SAS Institute, Inc., Cary, North Carolina, USA) with a Poisson distribution and log link to assess temporal differences of *Heterosiphonia* abundance between early summer and late summer.

*Ethics Statement:*

No specific permits were required for the field surveys, as they were conducted from public access points or Northeastern University property (Marine Science Center, Nahant, Massachusetts, USA). The study did not involve any endangered or protected species or any protected locations.

**RESULTS:**

Subtidal community composition differed significantly between the Acadian province and the Virginian province (p < 0.001; Fig 2). Northern subtidal communities were primarily composed of *Chondrus crispus, Heterosiphonia japonica*, crustose coralline algal species, and *Corallina officinalis*, which collectively comprised over 60% of the sessile species cover (means of 20%, 17%, 12% and 11%, respectively). While *Chondrus* and *Heterosiphonia* remained the most abundant species in southern subtidal communities (13% and 7% of the cover, respectively), *Phyllophora pseudoceranoides* also made up a substantial portion of the subtidal community (9%). There was also a greater diversity in community structure at southern sites,
with 22 different species comprising 90% of the community. By contrast, only 13 species comprised 90% of the shallow subtidal community in the north (Fig. 2). Results were similar when *Heterosiphonia* was removed from the analysis (p < 0.001).

Despite these differences in community compositions, *Heterosiphonia* was present at all but two of the subtidal sites surveyed (it was absent at Nubble Light, York, Maine and Town Neck Beach, Sandwich, Massachusetts) in both the Acadian province and the Virginian province. Relative abundances of *Heterosiphonia* ranged from 0.0 to 100 percent coverage to the north of Cape Cod (mean = 17.34 ± 2.86 %), while relative abundances were slightly lower south of Cape Cod (0.0% to 52.63%, mean = 7.41 ± 1.19 %; one-way ANOVA, \( F_{1,183} = 11.35, p < 0.001 \)). The average abundance of *Heterosiphonia* was lower in subtidal communities where species richness was higher (\( R^2 = 0.30, p = 0.02; \) Fig. 3). During our surveys of intertidal wrack mats, *Heterosiphonia* comprised an average of 20% of biomass; however, abundances of up to 65% were seen on multiple occasions.

*Heterosiphonia* abundances also exhibited temporal and spatial variability, both subtidally and in intertidal wrack mats. Subtidal *Heterosiphonia* abundances were two orders of magnitude higher at sites surveyed during the early summer (May/June) than at the end of the summer (\( \chi^2 = 1676.52, p < 0.001; \) Table 2). While intertidal wrack mat surveys were not conducted during the month of May, the abundance of *Heterosiphonia* was 40% higher during June than any of the other months surveyed (\( F_{2,370} = 9.34, p <0.001; \) Table 2). As expected, we found differences among sites surveyed (\( F_{4,370} = 15.95, p <0.001 \)). There was also a significant site*week interaction for our intertidal drift surveys (p <0.001).

**DISCUSSION:**
While initial reports restricted the distribution of *Heterosiphonia* to Rhode Island [8,9], this invader now occurs across a much larger biogeographic range. From this study alone, we have determined *Heterosiphonia* has become established in subtidal communities along > 700 km of the western Atlantic coastline from Cape Elizabeth, Maine through Waterford, Connecticut. Furthermore, recent reports have documented the presence of *Heterosiphonia* in Atlantic Canada [9], and *Heterosiphonia* has been reported as far west as the mouth of the Connecticut River (J. Foertch, pers. comm.). This extensive range, with a continuous distribution spanning at least 700 km, became evident within only five years of the initial report of *Heterosiphonia* in Rhode Island in 2007 [9]. While we can not confirm how long *Heterosiphonia* may have been present (but unnoticed) in New England, if *Heterosiphonia* was indeed initially limited to sites in Rhode Island, as suggested by Schneider [8], then this incredibly rapid rate of expansion is comparable to the expansion throughout its invaded range along European coastlines; within 5 years of initial reports, the invader had spread > 830 km along the Norwegian coast [10,11]. Although the possibility of multiple introductions via shipping vectors throughout its western Atlantic range exists, it is also possible that *Heterosiphonia* successfully expanded its invaded range through rapid growth and nutrient uptake rates, high reproductive potential due to fragmentation, and release from natural herbivory (A. Drouin & N. Low, pers. comm.).

Based on the wide range of temperature and salinity tolerances of the European populations of *Heterosiphonia*, we believe this invader will continue to rapidly expand its geographic range along the western Atlantic coast, ultimately achieving a temperate to subtropical distribution and potentially invading locations from Florida to Newfoundland [16]. We are currently working to determine the lethal temperature and salinity ranges for the western
Atlantic Ocean populations of *Heterosiphonia*. However, these populations are an exact genetic match to European populations [8], for which the thermal and salinity tolerances are known (0°C to 30°C, 10 to >30 psu; ref. 16). Thus, whereas this invader’s eventual range will likely be impacted by changes in temperature and salinity associated with climate change, a more pressing current concern is the likelihood that it will continue to expand its range rapidly, both northward and southward, to fill its thermal niche (i.e., its temperature and salinity tolerances allow it to grow well beyond its current geographic range).

*Heterosiphonia* was able to invade subtidal communities both north and south of Cape Cod, Massachusetts, a well-known biogeographical barrier. Despite the historical differences in both abiotic conditions and biological community structure between the two biogeographic provinces [17,18], *Heterosiphonia* has become one of the most abundant macrophytes, on average, in these communities. However, the abundance of *Heterosiphonia* also appears to be spatially variable, with *Heterosiphonia* comprising up to 79% of total macrophyte cover at some locations, whereas in other communities where *Heterosiphonia* is present, it occupies < 1% of the shallow subtidal community (Table 1). These data may be the result of our survey design, which was intended to rapidly assess the invader’s geographic range by maximizing the number of sites visited over the course of four months. As a result, we were not able to visit all sites on a regular basis.

However, we were able to capture some of the temporal variability in *Heterosiphonia* abundances in subtidal communities. During this study, four sites (two north and two south of Cape Cod, Massachusetts) were surveyed both at the beginning of the summer (May/June) and at the end of the summer (August). *Heterosiphonia* abundances were two orders of magnitude higher during May/June than during the end of the summer (Table 2). However, populations of
*Heterosiphonia* appeared to be recovering following the end of this survey (September and October). Additionally, large populations of *Heterosiphonia* were present during the previous fall of 2011. Therefore, despite this decrease in abundance towards late summer, we postulate that *Heterosiphonia* populations may be experiencing a seasonal growth cycle, with extremely high abundances during the late spring (Table 2) and fall (late September – October). However, towards the middle of August, the abundance of *Heterosiphonia* was significantly reduced, even becoming undetectable in some locations where it was formerly abundant (Table 2). The seasonal pattern observed during 2012 is consistent with reproductive observations from European populations, where necrosis in cells of *Heterosiphonia* pseudolaterals was most prominently observed in late summer and fall [15], suggesting individuals were shedding small fragments. As fragmented pseudolaterals can function as vegetative propagules [15], the abscission of these structures during the late summer may lead to a secondary peak in the abundance of *Heterosiphonia* upon settlement and regrowth.

The temporal patterns observed in subtidal *Heterosiphonia* abundance paralleled patterns seen in intertidal wrack mats. Peak abundances of attached, subtidal *Heterosiphonia* were seen during May and began to decline in June (Table 2). In contrast, maximum intertidal wrack abundances did not begin to decline until July. This suggests that *Heterosiphonia* individuals became detached from the substratum during the late spring and early summer, existing primarily as drifting individuals. Indeed, many drifting specimens were observed during early summer months at various sites during our SCUBA surveys. The loss of these individuals from subtidal populations could further explain the decline in *Heterosiphonia* abundances seen during our surveys in late summer and provide further support for the likely importance of excised pseudolaterals as a means of reproduction for this invasive macrophyte, particularly in
contributing to a second peak in abundance during early fall. However, it is currently unknown whether *Heterosiphonia* populations will maintain their high abundances through winter conditions (e.g. lower temperature, higher storm frequency and intensity).

Our surveys suggest that *Heterosiphonia* may have already altered subtidal community structure in areas it has invaded, as we observed lower seaweed species richness in communities characterized by greater *Heterosiphonia* abundance. These patterns are consistent with local extinction of native macroalgae due to competition with *Heterosiphonia*. It is also possible that communities with greater native macrophyte diversity are more resistant to invasion by *Heterosiphonia* [21], and we are currently conducting experiments to evaluate these possibilities.

Very little is currently known about the impacts of invasive seaweed species; ecological impacts have only been studied for ~6% of the 277 known invasive seaweed species. Of these, only 6 studies have examined ecological impacts *in situ* [22,23]. Collectively, our observations highlight community characteristics and population fluctuations across the current known range of a newly-discovered invasive macrophyte. The invasion and expansion of *Heterosiphonia* across multiple biogeographic provinces in the western North Atlantic Ocean provides an opportunity to understand the spread, impacts, and mechanisms associated with a marine invasion, providing critical information for management and amelioration of the impacts of this species and other marine invaders.

**ACKNOWLEDGEMENTS:**

The authors would like to thank V. Perini, I. Rosenthal, and N. Low for their diving assistance and A. Saco for help with beach wrack surveys. We thank the diving safety officers and their respective universities for diving reciprocity: T. Lyman (Northeastern University), A.
Watson (University of Rhode Island), and J. Godfrey (University of Connecticut). This is contribution number 297 from the Marine Science Center of Northeastern University.

LITERATURE CITED:


Figure 1. Presence of *Heterosiphonia japonica* in the Western Atlantic Ocean. Numbers correspond to locations listed in Table 1 where *Heterosiphonia* was found in SCUBA, shallow subtidal, and intertidal surveys. Circles indicate locations of *in situ* SCUBA surveys, with filled circles corresponding to locations where *Heterosiphonia* was found and open circles indicating locations where *Heterosiphonia* was absent. Squares correspond to locations where *Heterosiphonina* was found drifting in the shallow subtidal or as intertidal wrack.
Figure 2. Relative abundances of sessile species (seaweeds and sessile invertebrates) in subtidal communities. North and south refer to the biogeographical barrier at Cape Cod, Massachusetts. Species listed comprised 80% of the overall community, and data are means ± 1 S.E.
Figure 3. Relationship between sessile species richness and *Heterosiphonia japonica* abundance. Data presented are per plot, across all sites (regression; $R^2 = 0.30$, $p = 0.02$).
<table>
<thead>
<tr>
<th>Location</th>
<th>Site Number</th>
<th>Latitude °N</th>
<th>Longitude °W</th>
<th>% cover of <em>Heterosiphonia</em> (mean ± S.E.)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Maine</strong></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Fort Williams State Park, Cape Elizabeth</td>
<td>1</td>
<td>43°37'31.15&quot;</td>
<td>70°12'46.73&quot;</td>
<td>0.28±0.28</td>
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<td>Two Lights State Park, Cape Elizabeth</td>
<td>2</td>
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<td>70°11'54.26&quot;</td>
<td>1.33±0.63</td>
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<tr>
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<td>70°13'04.99&quot;</td>
<td>5.39±1.91</td>
</tr>
<tr>
<td>Nubble Light, York</td>
<td>4</td>
<td>43°09'56.78&quot;</td>
<td>70°35'29.70&quot;</td>
<td>0</td>
</tr>
<tr>
<td><strong>New Hampshire</strong></td>
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<td></td>
<td></td>
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<tr>
<td>Rye Beach, Rye</td>
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<td>42°57'24.51&quot;</td>
<td>70°46'40.23&quot;</td>
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<td><strong>Massachusetts</strong></td>
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<tr>
<td>Magnolia Beach, Gloucester*</td>
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<tr>
<td>Singing Beach, Manchester*</td>
<td>9</td>
<td>42°34'06.37&quot;</td>
<td>70°45'39.85&quot;</td>
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<tr>
<td>Stinky Beach, Manchester*</td>
<td>10</td>
<td>42°33'54.11&quot;</td>
<td>70°47'11.18&quot;</td>
<td>P</td>
</tr>
<tr>
<td>West Beach, Beverly</td>
<td>11</td>
<td>42°33'41.56&quot;</td>
<td>70°48'15.80&quot;</td>
<td>36.74±14.28</td>
</tr>
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<td>Castle Rock, Marblehead</td>
<td>12</td>
<td>42°29'58.67&quot;</td>
<td>70°50'02.63&quot;</td>
<td>18.80±2.56</td>
</tr>
<tr>
<td>Kings Beach, Swampscott</td>
<td>13</td>
<td>42°27'58.22&quot;</td>
<td>70°55'15.64&quot;</td>
<td>P</td>
</tr>
<tr>
<td>Canoe Beach, Nahant</td>
<td>14</td>
<td>42°25'10.09&quot;</td>
<td>70°54'25.30&quot;</td>
<td>28.41±6.11</td>
</tr>
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<td>Pumphouse Beach, Nahant</td>
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<td>42°25'01.13&quot;</td>
<td>70°54'25.27&quot;</td>
<td>17.74±5.04</td>
</tr>
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<td>70°54'31.27&quot;</td>
<td>79.3±3.81</td>
</tr>
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<td>70°54'56.57&quot;</td>
<td>P</td>
</tr>
<tr>
<td>Bay Shore Drive, Plymouth</td>
<td>18</td>
<td>41°56'59.02&quot;</td>
<td>70°35'24.66&quot;</td>
<td>P</td>
</tr>
<tr>
<td>Town Neck Beach, Sandwich</td>
<td>19</td>
<td>41°46'22.19&quot;</td>
<td>70°29'30.42&quot;</td>
<td>0</td>
</tr>
<tr>
<td>South Beach, Edgartown</td>
<td>20</td>
<td>41°21'05.98&quot;</td>
<td>70°29'56.35&quot;</td>
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<tr>
<td><strong>Rhode Island</strong></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Kings Beach, Newport</td>
<td>21</td>
<td>41°27'15.65&quot;</td>
<td>71°20'35.70&quot;</td>
<td>2.34±1.11</td>
</tr>
<tr>
<td>Fort Adams, Newport</td>
<td>22</td>
<td>41°28'36.60&quot;</td>
<td>71°20'28.51&quot;</td>
<td>13.50±4.13</td>
</tr>
<tr>
<td>Fort Wetherill, Jamestown</td>
<td>23</td>
<td>41°28'45.77&quot;</td>
<td>71°21'40.69&quot;</td>
<td>18.64±10.83</td>
</tr>
<tr>
<td>State Pier #5, Narragansett</td>
<td>24</td>
<td>41°25'20.17&quot;</td>
<td>71°27'19.33&quot;</td>
<td>0.65±0.65</td>
</tr>
<tr>
<td>Camp Cronin State Park, Narragansett</td>
<td>25</td>
<td>41°21'42.70&quot;</td>
<td>71°29'18.99&quot;</td>
<td>P</td>
</tr>
<tr>
<td>Southern Light, Block Island</td>
<td>26</td>
<td>40°09'04.73&quot;</td>
<td>71°33'19.59&quot;</td>
<td>P</td>
</tr>
<tr>
<td>Quonochontaug Pond, Charlestown</td>
<td>27</td>
<td>41°20'25.32&quot;</td>
<td>71°43'12.04&quot;</td>
<td>P</td>
</tr>
<tr>
<td><strong>New York</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Latimer Reef, Southold</td>
<td>28</td>
<td>41°18'14.17&quot;</td>
<td>71°55'42.78&quot;</td>
<td>9.12±2.02</td>
</tr>
<tr>
<td><strong>Connecticut</strong></td>
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<td></td>
<td></td>
<td></td>
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<tr>
<td>Avery Point, Groton</td>
<td>29</td>
<td>41°18'54.15&quot;</td>
<td>72°03'49.89&quot;</td>
<td>0.36±0.36</td>
</tr>
<tr>
<td>Dock Road State Boat Ramp, Waterford</td>
<td>30</td>
<td>41°18'30.39&quot;</td>
<td>72°08'54.59&quot;</td>
<td>4.09±2.90</td>
</tr>
<tr>
<td>Two Tree Island, Waterford</td>
<td>31</td>
<td>41°17'38.50&quot;</td>
<td>72°09'07.98&quot;</td>
<td>23.10±4.88</td>
</tr>
</tbody>
</table>
Notes: Site numbers correspond to labels in Figure 1. $P$ indicates locations where *Heterosiphonia* was observed drifting in the shallow subtidal but quantitative surveys were not conducted, and * indicates locations of weekly intertidal surveys.
Table 2. Seasonality of *Heterosiphonia japonica* abundances.

<table>
<thead>
<tr>
<th></th>
<th>Subtidal (Percent Cover)</th>
<th>Intertidal Wrack (g/m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>North</td>
<td>South</td>
</tr>
<tr>
<td>Early</td>
<td>43.80±7.38</td>
<td>7.65±2.35</td>
</tr>
<tr>
<td>Mid</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Late</td>
<td>0.24±0.15</td>
<td>0.09±0.07</td>
</tr>
</tbody>
</table>

*Notes:* Within subtidal communities, *Heterosiphonia* abundance was at least two orders of magnitude higher in early summer (May/June) than during late summer (August; $\chi^2 = 1676.52$, p < 0.001). At least twice as much *Heterosiphonia* biomass was found in intertidal wrack mats during June than in other months ($F_{6,45} = 12.66$, p <0.001).
CHAPTER 2

COMMUNITY RESPONSES, ECOSYSTEM FUNCTIONING AND INVADER PLASTICITY

FOLLOWING THE RECENT INVASION OF DASYSIPHONIA ("HETEROSIPHONIA")

JAPONICA TO THE WESTERN NORTH ATLANTIC OCEAN

Christine Ramsay-Newton¹*, Annick Drouin²³, A. Randall Hughes¹, Matthew E.S. Bracken⁴

¹Marine Science Center, Northeastern University, Nahant, MA 01908,
² Institut Maurice Lamontagne, Fisheries and Océans Canada, Québec, Canada G5H 3Z4,
³ Institut des sciences de la mer, Université du Québec à Rimouski, Québec, Canada, G5L 3A1,
⁴ Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697-2525

*Author for correspondence: newton.c@husky.neu.edu,
Phone: +1(781) 581-7370
Fax: +1(781) 581-6076

Manuscript in preparation for publication in Biological Invasions
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 that may take place at the species level immediately following an invasion. This study examined the recent invasion of the red alga, Dasysiphonia (formerly, Heterosiphonia) japonica to the western North Atlantic Ocean. Within four years of the initial invasion, community composition had changed and biodiversity had decreased to nearly half of pre-invasion levels. In addition, the relative proportion of Dasysiphonia decreased over our four-year study from its initial invasion levels. On an individual species level, we found evidence of plasticity in the invader with respect to nutrient uptake following the initial invasion. Using realistic changes in community structure, we also showed that invaded communities can respond successfully to species invasions by altering the functional mechanisms underlying relationships between biodiversity and ecosystem processes. In particular, we evaluated the relationship between biodiversity and nutrient uptake in invaded and uninvaded assemblages. During the initial invasion in 2011, uninvaded communities performed better with respect to nutrient uptake, however, as the invasion progressed, by 2013, the performance of the uninvaded communities dropped, while those invaded communities increased their overall nutrient uptake efficiency. All of these changes, at the species, community and ecosystem levels, occurred within only five years of the initial invasion, highlighting the importance of identifying species invasions early and monitoring their effects through time.

KEY WORDS: Invasive species, biodiversity, ecosystem functioning, phenotypic plasticity, nutrient uptake, Dasysiphonia japonica
INTRODUCTION:

Invasive species, particularly in marine systems, have been identified as a major threat to the community structure and the biodiversity of recipient communities (Parker et al. 1999, Stachowicz et al. 2002, Jones and Thornber 2010). Non-native marine species are often able to tolerate a wide range of abiotic conditions and are often competitively superior to native species in areas such as growth, defense, nutrient uptake and palatability (Theoharides and Dukes 2007, Hayes and Barry 2008). Without some level of biological 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 impact food webs, as well as alter community and ecosystem processes (Parker et al. 1999, Grosholz 2002, Williams and Smith 2007, Thomsen et al. 2009, Ehrenfeld 2010).

As major contributors to the global biodiversity crisis, invasive species have great potential to impact the diversity of systems (Molnar et al. 2008), and as such, may subsequently impact ecosystem functioning (Bracken and Williams 2013). As ecosystem processes depend on the functional properties of species, changes in the diversity and composition of these species, whether due to non-native species or other impacts, have the potential to alter the functional properties of each ecosystem as well (Bracken et al. 2008, Naeem et al. 2012, Bracken and Williams 2013). However, as Sousa et al. (2011) reported, only 4% of all studies published in Biological Invasions from 1999 to 2009 reported invasive species impacts on ecosystem functioning.

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 the impacts on both of these processes. Native to the Indo-Pacific region, *Dasysiphonia* was first reported in Rhode Island waters in 2009 (Schneider 2010), although molecular data suggest this invader was present in the area as early as 2007 (Savoie and Saunders 2013). Since then, *Dasysiphonia* has spread over 700km 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 (COI-5P mitochondrial barcode; Schneider 2010). Based on the distribution and temperature tolerances of genetically identical 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 changes in diversity are already occurring in invaded communities along the western North Atlantic from the invasion of *Dasysiphonia* (Newton et al. 2013, Low et al. 2014), although the generality of these results needs to be examined further.

As primary producers, invasive marine seaweeds can have substantial impacts on recipient communities (Schaffelke and Hewitt 2007, Williams and Smith 2007). Through increased competition with native macrophytes, invasive seaweeds have the potential to alter the abundance and diversity of recipient communities. These changes, along with potential structural changes in habitat from the invader, can lead to changes in the associated fauna, as well as changes in ecosystem functioning of the recipient community (Schaffelke and Hewitt 2007,
Thomsen et al. 2009). Ecological impacts have only been studied in situ for ~6% of the 277 known invasive seaweed species, and in all cases, only the effects after a long term history in their invaded habitat are 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 empirical evidence is known about invasion-mediated changes that may occur early in the invasion process and the long-term responses of communities and ecosystems to invasions (Strayer 2012).

Using the recent invasion of Dasysiphonia to the western North Atlantic ocean, this research aims (1) to determine the early effects of the invasive seaweed Dasysiphonia on biodiversity and community composition in the recently invaded western North Atlantic ocean, (2) to quantify the direct and indirect effects of Dasysiphonia on community and ecosystem processes (nitrate use efficiency) in recipient communities, as nitrate is a critical limiting nutrient in nearshore environments in the western North Atlantic (Perini and Bracken 2014), and (3) to assess any changes that may occur in invader traits following the initial invasion. These objectives were addressed in a four-year study using a combination of in situ community surveys and laboratory uptake experiments that incorporated realistic changes in community structure.

METHODS:

Dasysiphonia was first reported at our study site in Nahant, Massachusetts in 2010 (Canoe Beach; 42°25’12.6”N, 70°54’21.3”W; Low et al. 2014). Canoe Beach is a semi-protected rocky site, with 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 and diving program at the Marine Science Center,
we have a reliable yearly record of the macrofaunal 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 to this region, as our study sites are located directly adjacent to Northeastern University’s Marine Science Center. Further evidence of this early capture of the invasion is suggested by the fact at the beginning of our study, *Dasysiphonia* was not present at some of our study sites (see “*In situ* surveys”). However, by the following year, *Dasysiphonia* was found at all of our study sites, and by 2012, it 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 2011-2014 in Nahant, Massachusetts. *Dasysiphonia* was first reported at some sites in this area in 2010 (Low et al. 2014), however, it had not fully colonized the area until 2012 (Ramsay-Newton, *pers. obs.*). Therefore, in 2011, surveys were conducted in a site that had been invaded by *Dasysiphonia*, (Canoe Beach East) as well as a nearby site that had not yet been invaded (Canoe Beach West). 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 (Ramsay-Newton, *pers. obs.*). 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 site surveys.

Quantitative SCUBA surveys were conducted during summer peak growth season of *Dasysiphonia* between 1.6m and 5.1m depth (below mean lower-low water) using randomly placed 0.0625m$^2$ quadrats (n = 7-21/year). Seaweed community composition was assessed either
by destructively sampling the entire quadrat to obtain the dry weights of each species in the lab or by measuring the percent coverage of each species in situ. 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 is altered in response to invasion mediated changes in the community, we conducted nutrient uptake experiments to measure nitrate use efficiency. 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 2011 survey data from Nahant, Massachusetts, we created realistic seaweed community assemblages that represented the relative abundances of seaweed species from both our invaded (Canoe Beach East) and non-invaded (Canoe Beach West) sites (Table 1; Appendix 1). A third treatment, identical invaded assemblages but with Dasysiphonia removed, was used to assess whether potential impacts were due to changes in the community or changes in 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., 2014). 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).

For each trial, seaweeds were collected no more than 18 hours in advance, spun to remove excess water and weighed to obtain a total of 6 g of seaweed per chamber. A single assemblage or monoculture was placed in each chamber and allowed to acclimate for 10 minutes before seawater was spiked with a NaNO₃ stock solution to the appropriate concentration (2, 15, 30, or 50 µmol L⁻¹). Water samples were collected every 15 minutes over the 2-hour 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, Colorado, 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 depletion of nitrate 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⁻¹h⁻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:

\[ V = \frac{V_{max} X S}{K_s + S}, \]  
(Eq. 1)

where \( V \) (µmol g⁻¹h⁻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 linear models to fit the data:
\[ V = m \times S + b, \quad \text{(Eq. 2)} \]

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 (\( \alpha \)) for each assemblage, which represents the slope of the relationship at low nitrate concentrations. For assemblages in which a Michaelis-Menten model was used,

\[ \alpha = \frac{V_{\text{max}}}{K_s}, \quad \text{(Eq. 3)} \]

whereas in assemblages where a linear fit model was appropriate,

\[ \alpha = m. \quad \text{(Eq. 4)} \]

To examine whether the performance of a community is impacted by the presence or absence of *Dasysiphonia* in the community and the mechanisms underlying any relationships between community composition and ecosystem function, we calculated two metrics for the effects of species assemblage on uptake: \( D_{\text{mean}} \) and \( D_{\text{max}} \). These metrics are used to examine the complementarily or resource partitioning that exists in a community with respect to biodiversity and nitrate uptake as different species in the community use non-overlapping resources (Bracken and Williams 2013). Specifically, these metrics are used to indicate whether the performance (e.g. nutrient uptake) of a diverse assemblage is predicted by the mean (\( D_{\text{mean}} \)) of each
component species or the best performing component species ($D_{max}$). $D_{mean}$ is an indicator of non-transgressive overyielding:

$$D_{mean} = (P - M_{mean})/M_{mean},$$  \hspace{1cm} (Eq. 5)

where $P$ was 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 analysis:**

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 and years using a two-way analysis of variance (ANOVA) on log-transformed data with fixed factors. Tukey post-hoc tests were run on 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, North Carolina, 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; PRIMER v. 6.0; Primer-E Ltd., Plymouth, UK). Nutrient uptake data were analyzed using one-sample t tests with a null hypothesis of $\alpha$ (or $D_{\text{mean}}$ or $D_{\text{max}}$) = 0.

RESULTS:

In situ surveys:

Over the course of the study (2011-2014), we found the macroalgal community in Nahant, Massachusetts changed both in terms of biodiversity and community composition (Table 1). In 2011, species richness was nearly 2 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 re-sampling of our previously uninvaded site showed similar, but lower levels of biodiversity than both our sites in 2011 ($F_{1,36} = 5.71$, $p = 0.023$; Figure 1). In addition, we found 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 non-invaded site was significantly different, prior to the invasion in 2011 and following the invasion in 2014 (Global $R = 0.97$, $p = 0.01$; Figure 2). The relative proportion of 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 ($F_{3,56} = 6.36$, $p < 0.001$; Figure 3). Although this proportion fluctuated across years, it should be noted that all years tended to decrease in the relative abundance of Dasysiphonia from its initial invasion in 2011.

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 $\alpha = 0.26$; Figure 4; Low et al., 2014). However, in 2012 and 2013, uptake efficiencies of *Dasysiphonia* decreased and were comparable to the average of all other species.

We examined the impacts of *Dasysiphonia* on nutrient uptake in a community context, specifically by comparing whether each realistic multi-species assemblage of seaweeds performed better than the average performance of the component species ($D_{\text{mean}}$), or the best performing component species in the assemblage ($D_{\text{max}}$). In the multi-species assemblages created to represent our sites that had not been invaded by *Dasysiphonia*, we found assemblages performed better than the average of the component species in 2011 ($D_{\text{mean}} > 0$; Figure 5a). However, by 2013, the average uptake efficiency of non-invaded assemblages had declined to a level predicted from the performance of each component species ($D_{\text{mean}} \sim 0$; Figure 5a). A slight downward trend in the uptake efficiency of these assemblages was also observed with respect to $D_{\text{max}}$ (Figure 5b).

In contrast to our non-invaded assemblages, the assemblages that had been created to represent our *Dasysiphonia* invaded site showed evidence of increasing efficiency of nitrate uptake from 2011 to 2013 using both of our efficiency metrics ($D_{\text{mean}}$ and $D_{\text{max}} > 0$; Figure 5a & 5b). This increase only occurred in the assemblages that included *Dasysiphonia*: when we ran the uptake trials using invaded assemblages without *Dasysiphonia*, no such patterns were seen in either $D_{\text{mean}}$ or $D_{\text{max}}$ (“Invaded [Dasysiphonia removed]”; Figure 5a & 5b).

**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 about changes in invader performance during the first years of its invasion. By comparing nearby communities that had and had not yet been invaded, we were able to show lower species richness immediately following the initial invasion of Dasysiphonia in 2011, before diversity declined to nearly half of its initial diversity, four years later in 2014. Along with this reduction in biodiversity, the composition of the recipient community was changed following the invasion of Dasysiphonia. We have shown that with these realistic structural changes, communities are able to respond successfully to species invasions by altering the functional mechanisms (e.g. complementarity, or resource partitioning) behind ecosystem processes, specifically nutrient uptake. Complementarity exists when different species utilize non-overlapping recourses, such as nitrate, across a resource gradient to increase 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 increased 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 as Dasysiphonia was incorporated into the community. By 2013, the performance of the invaded community assemblages far surpassed not only the expected average performance of the community ($D_{\text{mean}}$), but also the uptake efficiency of the best performing component species ($D_{\text{max}}$).

Evidence for functional changes to Dasysiphonia’s invasion at the community level is seen when we remove Dasysiphonia from the invaded community assemblages. At the initial invasion in 2011, invaded communities performed equally well whether or not Dasysiphonia was
part of the system, suggesting this invader did not play a substantial role with respect to native species. However, by 2013, when *Dasysiphonia* was removed from invaded assemblages, the overall performance of the community dropped substantially (Figures 5a & 5b, “Invaded” & “Invaded [*Dasysiphonia* removed]”).

Not only did changes take place at the community level, but we also saw evidence of changes in the invader itself in the form of phenotypic plasticity with respect to nutrient uptake. During the initial invasion in 2011, nitrate uptake rates of *Dasysiphonia* were nearly an order of magnitude higher than any native species. 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. 2014). However, as the invasion progressed and the community structure changed, the uptake efficiency of *Dasysiphonia* was reduced 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 (Ramsay-Newton, *unpub data*). This phenotypic plasticity 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 (Newton et al. 2013), trait plasticity may be necessary to reduce intraspecific competition as the invader is incorporated into 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).

By incorporating realism and increased time scales into our research which captured the initial invasion, we were able to link invasion-mediated changes in community structure with
changes in ecosystem function, while also demonstrating plasticity of the invader. Our research has shown a drastic shift in responses at both the community and ecosystem level in response to a recent algal invader. Initially, Dasysiphonia was a better competitor for resources than native species, and thus the overall production of the community suffered. However, within five years of the initial invasion, Dasysiphonia had reduced its uptake efficiency as an individual species, and thus the overall production 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 plasticity. 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 incorporating realism into invasion research, not only through using realistic changes in community structure, but also through capturing the full range of responses by the invader as well as the recipient community. As the global biodiversity crisis is largely driven by anthropogenic causes, species losses are not likely to be random, therefore, incorporating realistic changes in diversity into invasion research is necessary to adequately assess impacts on both community and ecosystem level processes.

ACKNOWLEDGEMENTS:

We would like to thank N. Low, V. Perini, I. Rosenfield, and V. Selesnick for diving and laboratory assistance. K. Benes provided additional laboratory assistance. We would also like to acknowledge Northeastern University’s Marine Science Center Diving Program and the following Diving Safety Officers: L. Bentley-Magee, S. Genovese and T. Lyman. This publication is partially the result of research sponsored by The Massachusetts Institute of Technology Sea Grant College Program, under National Oceanic and Atmospheric
Administration Grant Number NA14OAR4170077, MIT SG Project Number 2014-R/RCM-37, along with funding by National Science Foundation Award OCE-0963010 and Woods Hole SeaGrant (Subaward A100923) to M.E.S.B and C.S.T. This is contribution number XXX from the Marine Science Center of Northeastern University.

LITERATURE CITED:


Bracken MES, Jones E, Williams SL (2011) Herbivores, tidal elevation, and species richness simultaneously mediate nitrate uptake by seaweed assemblages Ecology 92:1083-1093


Cardinale BJ et al. (2012) Biodiversity loss and its impact on humanity Nature 486

Davidson AM, Jennions M, Nicotra AB (2011) Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis Ecology Letters 14:419-431


Hooper DU et al. (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change Nature 486:105-109

Jones E, Thornber CS (2010) Effects of habitat-modifying invasive macroalgae on epiphytic algal communities Marine Ecology Progress Series 400:87-100


Low NHN, Drouin A, Marks CJ, Bracken MES (2014) Invader traits and community context contribute to the recent invasion success of the macroalga Heterosiphonia japonica on New England rocky reefs Biological Invasions doi:10.1007/s10530-014-0724-z


Newton C, Bracken MES, McConville M, Rodrigue K, Thornber CS (2013) Invasion of the red seaweed Heterosiphonia japonica spans biogeographic provinces in the Western North Atlantic Ocean PLOS ONE 8:e62261

Parker IM et al. (1999) Impact: toward a framework for understanding the ecological effects of invaders Biological Invasions 1:3-19


Power LD, Cardinale BJ (2009) Species richness enhances both algal biomass and rates of oxygen production in aquatic microcosms Oikos 118:1703-1711


Savoie AM, Saunders GW (2013) First record of the invasive red alga Heterosiphonia japonica (Ceramiales, Rhodophyta) in Canada BioInvasion Records 2:27-32


Simberloff D, Gibbons L (2004) Now you see them, now you don't! - population crashes of established introduced species Biological Invasions 6:161-172


Figure 1. Community biodiversity at non-invaded and invaded sites in the four years following the initial invasion of Dasysiphonia japonica. Letters indicate differences in species richness based on a two-way ANOVA with Invasion Status and Year as factors. Sample size is indicated in parentheses.
**Figure 2.** MSDS plot of community structure showing significant changes in the composition of the subtidal benthic community following the invasion of *Dasysiphonia japonica*. 
Figure 3. The relative proportion of *Dasysiphonia japonica* in the subtidal benthic community in the four 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.
Figure 4. Nitrate uptake efficiency (µmol/g/h) of individual component species in monoculture across three years (2011-2013).
Figure 5. Community performance (nutrient uptake efficiency) in the three 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 ($D_{\text{mean}}$) of each component species (a) or the best performing ($D_{\text{max}}$) component species (b). Performances greater than zero indicate increased resource partitioning, or complementarity, thereby increasing the overall uptake efficiency of the community.
<table>
<thead>
<tr>
<th>Species</th>
<th>2011</th>
<th>2012</th>
<th>2013</th>
<th>2014</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Non-invaded</td>
<td>Invaded</td>
<td>Invaded</td>
<td>(Previously)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Non-invaded</td>
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<td><em>Ahnfeltia plicata</em></td>
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<td>3.00±1.18</td>
<td>0.18±0.18</td>
<td>1.10±1.10</td>
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<td><em>Bonnemaisonia hamifera</em></td>
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<td>0.07±0.04</td>
<td>4.07±2.05</td>
<td>1.25±1.25</td>
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<td>Botryloides diegensis</td>
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<td>1.17±0.55</td>
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<td>Bugula spp.</td>
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</tr>
<tr>
<td><em>Ceramium deslongchampii</em></td>
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<td><em>Chondrus crispus</em></td>
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<td>12.26±3.09</td>
<td>37.24±5.98</td>
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<td>0.56±0.56</td>
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<td>Codium fragile</td>
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</tr>
<tr>
<td>*Corallina officinalis</td>
<td>21.40±5.09</td>
<td>3.09±1.40</td>
<td>9.94±2.96</td>
<td>16.17±6.25</td>
</tr>
<tr>
<td>Crustose spp.</td>
<td>20.98±4.41</td>
<td>24.42±3.88</td>
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<td></td>
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<tr>
<td>Cystoclonium purpuratum</td>
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<td></td>
<td>0.57±0.45</td>
<td>18.47±5.91</td>
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<tr>
<td><em>Dasysiphonia japonica</em></td>
<td>2.10±0.80</td>
<td>49.45±5.33</td>
<td>14.90±4.45</td>
<td>21.15±5.05</td>
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<tr>
<td><em>Desmarestia spp.</em></td>
<td>1.80±0.85</td>
<td>1.65±1.01</td>
<td>2.50±1.82</td>
<td>8.83±5.04</td>
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<td>Euthora cristata</td>
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<td></td>
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<td>Erythrotrichia carnea</td>
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<td>Hildenbrandia rubra</td>
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<td></td>
<td>0.08±0.08</td>
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<td>Hypnea musciformis</td>
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<td></td>
<td>1.91±1.48</td>
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<td>Lithothamnion glaciale</td>
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<td>0.47±0.34</td>
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<td>Palmaria palmata</td>
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<td><em>Phycodrys rubens</em></td>
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<td>0.21±0.16</td>
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<td>Polysiphonia denudata</td>
<td>0.31±0.28</td>
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<tr>
<td><em>Polysiphonia fucoides</em></td>
<td>18.80±5.26</td>
<td>0.25±0.16</td>
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<td>3.48±3.48</td>
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<td>Polysiphonia haveyi</td>
<td>0.01±0.01</td>
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</tr>
<tr>
<td>Polysiphonia nigra</td>
<td>0.05±0.03</td>
<td>0.01±0.01</td>
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<tr>
<td><em>Polysiphonia stricta</em></td>
<td>0.58±0.43</td>
<td>2.26±1.65</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 1 Community composition of our non-invaded and invaded sites from 2011-2014. 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 percent cover +/- standard error. * indicates those species which were used during our nutrient uptake experiments (see Appendix 1 for experimental assemblages).

<table>
<thead>
<tr>
<th>Species</th>
<th>2011</th>
<th>2012</th>
<th>2013</th>
<th>2014</th>
<th>2015</th>
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<td>Rhodomela confervoides</td>
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<td>Ulva spp.</td>
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<td>0.15±0.12</td>
<td>0.05±0.05</td>
<td>1.18±0.54</td>
<td>1.46±0.91</td>
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</table>
APPENDICES:

APPENDIX 1 Composition of experimental assemblages used for nutrient uptake trials. Realistic assemblages are based on 2011 in situ community surveys from invaded and non-invaded sites. Species data are reported in grams (wet weight).

<table>
<thead>
<tr>
<th>Species Richness</th>
<th>Anfeltia plicata</th>
<th>Bonemaisonia hamifera</th>
<th>Ceramium spp.</th>
<th>Chondrus crispus</th>
<th>Corallina officinalis</th>
<th>Dasypodium rubens</th>
<th>Desmarestia aculeata</th>
<th>Phycodrys rubens</th>
<th>Polysiphonia fucoides</th>
<th>Polysiphonia strica</th>
<th>Polysiphonia stricta</th>
<th>Polysiphonia striata</th>
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<td>Invaded-1</td>
<td>5</td>
<td>0.5</td>
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<td>0</td>
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<td>0.1</td>
<td>5.2</td>
<td>0.1</td>
<td>0</td>
<td>0</td>
<td>0</td>
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<tr>
<td>Invaded-2</td>
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<td>0</td>
<td>0</td>
<td>1.5</td>
<td>0</td>
<td>4.0</td>
<td>0.5</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
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<tr>
<td>Invaded-3</td>
<td>4</td>
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<td>Invaded-4</td>
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<td>0</td>
<td>0</td>
<td>1.5</td>
<td>0</td>
<td>4.5</td>
<td>0</td>
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<td>0</td>
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<td>1.1</td>
<td>0</td>
<td>4.4</td>
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<td>0.1</td>
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<td>Invaded-9</td>
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<td>2.7</td>
<td>0.2</td>
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<td>Invaded-17</td>
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<td>0</td>
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CHAPTER 3

CONTEXT DEPENDENCY OF EARLY INVASION STRATEGIES: INVASION OF THE
RED ALGA, *DASYSIPHONIA* (“*HETEROSIPHONIA*”) *JAPONICA* TO THE WESTERN
NORTH ATLANTIC OCEAN ACROSS TWO BIOGEOGRAPHIC REGIONS

Christine Ramsay-Newton\(^1\)*, Matthew E.S. Bracken\(^2\), A. Randall Hughes\(^1\), Carol S. Thornber\(^3\)

\(^1\)Marine Science Center, Northeastern University, Nahant, MA 01908
\(^2\)University of California-Irvine, Irvine, CA 92697
\(^3\)University of Rhode Island, Kingston, RI 02881

*Author for correspondence: newton.c@husky.neu.edu,
Telephone: +1(781) 581-7370

Manuscript in preparation for publication in *Global Change Biology*
ABSTRACT:

Species invasions have become a primary focus of global change research. Yet little is known about the ecological processes early in the invasion, at both the individual and community level. We tracked abundances of a recent red algal invader, Dasysiphonia (formerly, “Heterosiphonia”) japonica in two biogeographic regions in the western North Atlantic Ocean. Higher abundances of the invasive alga (> 200% higher) were consistently found north of Cape Cod, Massachusetts, suggesting that differences in biotic and/or abiotic factors between the two regions may contribute to the success of this invader. Dasysiphonia grew 10 times faster in the northern region than south of Cape Cod, Massachusetts, a well-known biogeographical barrier. Consumption of Dasysiphonia by the native herbivore tended to be lower in the north, which may also contribute to the observed higher abundances. Temperature varied predictably across regions, with higher temperatures in the south. Previous experiments have demonstrated higher Dasysiphonia growth rates at higher temperatures, suggesting that regional temperature differences are not driving the patterns observed here. The different responses and roles of Dasysiphonia north and south of Cape Cod may result in important community level differences, as biodiversity declined in the northern region following the invasion of Dasysiphonia, whereas diversity was not impacted by the invader south of the biogeographical barrier.

KEY WORDS: Dasysiphonia japonica; herbivory; invasive species; biogeographical barrier; Cape Cod, Massachusetts; biodiversity; early invasion; growth rate

INTRODUCTION:
Species invasions have been increasing in frequency and intensity worldwide (Ruiz et al. 2000, McGeoch et al. 2010). Invasive species have dramatic, and often detrimental, effects on the communities in which they invade, such as declines in native biodiversity and disruptions to the ecosystem functioning of the recipient community (Molnar et al. 2008, Newton et al. 2013). These impacts have been documented in a wide variety of systems and taxonomic groups (Pyšek and Richardson 2010, Vila et al. 2011). As such, the desire to predict invasion success has become paramount in invasion biology research. Generally, the balance between species interactions and environmental conditions controls the success of an invader (Facon et al. 2006). Yet the impacts of individual species invaders vary greatly and individual recipient community conditions differ as well (Thomsen et al. 2011). This has led to great debate among researchers over the best ways to predict invasive success, suggesting there is no universal metric to measure impact or success of invaders (Vila et al. 2011, Pyšek et al. 2012).

Since the classic work of Elton (1958), researchers have explored why a particular invasive species is successful, with the goal of predicting the risk associated with future introductions. A number of traits have been identified as determining the invasiveness of a species across a wide range of taxonomic groups. Physiological tolerances, life history characteristics and biotic interactions have been shown to be traits most likely to predict the success of an invader (Miller and Ruiz 2009, Van Kleunen et al. 2010). For example, within invasive marine seaweeds, morphological traits such as filamentous construction is beneficial to invaders in areas with high disturbance potential, yet a corticated or leathery morphology is more likely to be successful in habitats with low disturbance (Williams and Smith 2007). Yet these characteristics vary with each particular invader, and some traits (i.e. palatability, nutrient uptake) may vary even within individual populations of an invader.
Therefore, due to the species specific nature of these traits, the relative importance of each of these traits as to predicting invasive success is poorly understood (Thomsen et al. 2011, Andreakis and Schaffelke 2012).

While determining invader traits is important, the characteristics of a community also play a role in whether a species will successfully invade a community (Olyarnik et al. 2008). Communities with higher native biodiversity have been shown to resist invasions better than those communities with lower native diversity (Thomsen et al. 2009, Altieri et al. 2010, Kimbro et al. 2013). This is likely due to the stronger species interactions, including the greater utilization of limiting resources by the native members of the community, such as space or nutrient availability (Stachowicz et al. 1999). Although higher diversity may reduce invader success, once an invader has become established in a region, it poses a critical threat to native biodiversity (Bax et al. 2003, Molnar et al. 2008, Butchart et al. 2010). However, much of the experimental literature surrounding biodiversity impacts has evaluated the effects of random diversity changes (Cardinale et al. 2006, Worm et al. 2006). We just beginning to explore of how realistic (often anthropogenic driven) changes in diversity are affecting communities interactions (Selmants et al. 2012, Bracken and Williams 2013). Therefore, the need to incorporate realistic communities, based on actual survey data, into our experimental designs is paramount.

The recent invasion of the subtidal red alga, *Dasysiphonia* (formerly, “*Heterosiphonia*”) *japonica* (hereafter, *Dasysiphonia*) to the western North Atlantic Ocean poses a critical threat to the biodiversity and functioning of marine ecosystems. *Dasysiphonia* was first reported in Rhode Island in 2009 (Schneider 2010), although molecular data suggests it was present in Rhode Island by 2007 (Savoie and Saunders 2013). Since this initial invasion, *Dasysiphonia* has colonized a continuous distribution north through Cape Elizabeth, Maine and south through
Long Island Sound in New York (Newton et al. 2013). Based on the temperature and salinity tolerances of the invasive European population of Dasysiphonia (which are a genetic match to western Atlantic populations [COI-5P mitochondrial barcode]), Dasysiphonia has the potential to invade subtidal communities from Florida to Newfoundland (Bjaerke and Rueness 2004, Newton et al. 2013). Indeed, a secondary population of Dasysiphonia was reported from Nova Scotia, Canada in 2012 (Savoie and Saunders 2013).

The current invaded range of Dasysiphonia crosses a well-known biogeographical barrier at Cape Cod, Massachusetts (Allee 1923, Vermeij 1978). Biogeographical barriers create distinct transitions of abiotic and biotic conditions that often prevent floral and faunal mixing, leading to distinct communities in each region. In marine systems, these barriers are often land structures, such as islands or peninsulas. In the western Atlantic Ocean, the Cape Cod barrier separates the northerly Gulf of Maine/Bay of Fundy ecoregion (Acadian Maritime province) from the southerly Virginian ecoregion (Virginian Maritime province; Spalding et al. 2007). Each of these regions is characterized by distinct abiotic and biotic conditions (Bertness et al. 1999). For example, the northerly Gulf of Maine/Bay of Fundy region is heavily influenced by colder water flowing south along the Labrador Current, while the warmer water of the Gulf Stream dominates the southerly Virginian region. This has led to distinct biological communities within each biogeographic region, including differences in the abundance of the invasive Dasysiphonia (Newton et al. 2013). During subtidal communities surveys, Dasysiphonia was found to be 220 times more abundant on average at sites in the northern region during the initial five years of the invasion (2011-2014; Figure 1). The relationship between biodiversity and Dasysiphonia abundance also differed between the two regions. In the northern region, increased Dasysiphonia abundance was negatively correlated with native biodiversity in recipient communities ($R^2 =$
0.79, p = 0.001; Figure 2; Newton et al. 2013), yet no relationship between biodiversity and Dasysiphonia abundance was found in the southern biogeographic region ($R^2 = 0.00, p = 0.87$; Figure 2; Newton et al. 2013).

These observations of consistently higher abundances of Dasysiphonia in the northern biogeographic region and differences in native biodiversity led us to examine how the invasion strategy of and community responses to Dasysiphonia differed across biogeographical regions. As the invasion of Dasysiphonia is ecologically recent, it provides a unique opportunity to study early invasion dynamics, including invasion success and community responses. In addition, this study seeks to explore the individual traits and community characteristics that make Dasysiphonia a successful invader by taking advantage of the invasive range of the invader across two biogeographic regions. Specifically, we sought to (1) understand the biotic and abiotic factors that lead to the successful invasion of Dasysiphonia in different biographical regions, and (2) determine the impacts on biodiversity and structure of recipient communities in both regions.

**METHODS:**

*Biotic and abiotic experiments:*

To assess biotic factors, specifically growth and herbivory, we conducted simultaneous mesocosm experiments in both biogeographic regions: northern experiments were conducted at Northeastern University’s Marine Science Center (Nahant, MA; 42.25N, 70.54W) and southern experiments were conducted at the University of Rhode Island’s Narragansett Bay Campus (Narragansett, RI; 41.25N, 71.25W). Each of these locations provided large outdoor seawater tables, supplied with filtered ambient temperature seawater, allowing us to maintain natural
differences in abiotic conditions between the two regions. Mesocosms for our growth assays were constructed of clear 1 L plastic containers with four large mesh-covered holes around the circumference of the container to maintain adequate seawater flow. For the herbivory assays, we used a 0.5 L plastic container and added a mesh barrier within to create an herbivore chamber and a non-herbivore chamber in each mesocosm. To assess how community context, or the presence of other native macrophytes, may affect growth or herbivory in a realistic context, we used two treatments for both assays – a monoculture of Dasysiphonia, and a polyculture with Dasysiphonia and the three most abundant species common to both regions (Newton et al. 2013).

Growth assays were conducted monthly during the summer of 2014 (May – September), at each of our facilities north and south of Cape Cod, MA. Macroalgae (Chondrus crispus, Dasysiphonia japonica, Corallina officinalis, and Polysiphonia fucoides; Newton et al. 2013) were collected using SCUBA from sites nearby each of the experimental facilities, allowing us to maintain any natural variation between the two regions. Once the macroalgae had been collected, it was sorted, spin-dried to a constant wet weight and introduced into the mesocosms such that the total wet weight of macroalgae in each mesocosm was 6.0 g. Following the 3-day growth period, the individuals were spin-dried and re-weighed. The biomass specific growth rates of Dasysiphonia in monoculture and in polyculture were assessed with a two-way fixed-factor ANOVA (Region X Treatment) to determine whether region or the presence of other species affected the growth rates of Dasysiphonia. Data from each month were combined into one overall growth metric, as our focus is on regional differences and we found no significant interactions involving time. We were often unable to find C. officinalis at our southern sites, so we excluded it from our analyses in the south. We ran additional northern polyculture trials
without *C. officinalis* and found that its presence or absence did not affect growth rates of other species in the polyculture (*F*<sub>1,15</sub> = 0.98, *p* = 0.33, C. Ramsay-Newton, *unpublished data*).

Feeding assays were conducted in both biogeographic regions during July 2014 to determine whether the native herbivore, *Lacuna vincta* showed a preference in consumption of *Dasysiphonia* over the three most common native species to both biogeographic regions. Thus, treatments for our feeding assays were identical to the growth assays (*Dasysiphonia* monoculture and one polyculture containing an equivalent amount of each species). The herbivores were collected from the same sites as the algae in both regions and were starved for a minimum of 24 hours prior to the initiation of the experiment. We maintained a total of 6.0 g (wet mass) of algae for each mesocosm, however, to account for our divided feeding chambers, we placed a total of 3.0 g of macroalgae on each side of the mesh barrier. *L. vincta* were introduced into one chamber of each mesocosm and maintained at a density of 3–4 grazers per a gram of algal wet mass (C. Ramsay-Newton, *unpublished data*). After three days, we carefully separated the algae and the herbivores and determined the final wet mass of each algal species.

To calculate the amount of algae consumed by the herbivores, we subtracted the biomass specific autogenic growth (no herbivore chamber; growth only) from the biomass specific change in wet mass of the herbivory chamber (growth and herbivory) for each species in each mesocosm. To test for preference in consumption of *Dasysiphonia*, we compared the expected consumption of *Dasysiphonia* in the absence of native species (monoculture treatment) with the actual consumption of *Dasysiphonia* in the presence of native species (polyculture treatment). These data were analyzed with a two-way fixed factor ANOVA (Region X Treatment).

Abiotic conditions north and south of the biogeographical barrier were taken from buoys near our experimental sites (North, NERACOOS Gulf of Maine A – Massachusetts Bay [42.52N,
70.56W]; South, NERRS NAXR1_WQ [41.57N, 71.32W]). The average daily temperature and salinity was downloaded for each year (2012-2014) through the Northeast Regional Association of Coastal and Ocean Observing Systems, a division of the Integrated Ocean Observing System (www.neracoos.org). Regional differences in temperature and salinity during the peak growth season of *Dasysiphonia* (May-October) were then analyzed using a two-way fixed factor Analysis of Variance (ANOVA, Region X Year; JMP v. 11.0, SAS Institute, Inc. Cary, North Carolina, USA). While the actual temperatures and salinities within our experimental mesocosm sites differed slightly from these buoy temperatures, this bias was present within both geographic regions.

*Biodiversity experiment:*

We conducted an *in situ* removal experiment at three sites north and three sites south of the biogeographic barrier (Cape Cod, MA) identified from previous surveys (Newton et al. 2013). During the summer of 2012, we established 45 0.0625 m² plots within the subtidal *Dasysiphonia* zone (1-6 m below MLLW; C. Ramsay-Newton, personal observation) using marine epoxy and cable ties. Plots were randomly assigned such that one-third were experimental plots with *Dasysiphonia* removed, one-third were non-removal (control) plots, and one-third served as procedural controls to account for the disturbance of algal removal. These plots were initially surveyed to ensure no *a priori* differences among treatments with respect to species diversity (North: $F_{2,177} = 0.27, p = 0.77$; South: $F_{2,128} = 0.73, p = 0.54$). The plots were visited every 2-4 weeks during peak growth periods (May – October) during our two-year experiment, concluding in October 2013.

During each visit, the percent cover of all sessile species was recorded for each plot. Experimental plots were then maintained by carefully removing *Dasysiphonia* regrowth by hand.
to ensure limited disturbance to the surrounding benthic community. The mean amount of *Dasysiphonia* removed was determined and an equivalent amount of biomass was removed from the procedural control plots. Species in these procedural control plots were removed in proportion to their abundance.

During the course of our two-year experiment, the northern region experienced a number of large storms, which resulted in substantial habitat disturbances at each of our northern sites (C. Ramsay-Newton, *personal observation*). Consequentially, we lost or were unable to survey approximately 80% of our established plots, despite our best attempts at monthly plot maintenance and repair. However, our southern sites remained relatively undisturbed. Therefore, we only have reliable data from the southern biogeographic region.

Univariate data were analyzed using a repeated measures ANOVA to assess the impacts of treatment and duration (time) on species richness in the southern plots with JMP v. 11.0. We also conducted a one-way ANOVA on the final sampling date to assess if there were any final treatment effects on species richness in the south. Differences in community composition among the three treatments at the conclusion of the experiment were assessed by calculating a Bray-Curtis similarity matrix on square root transformed data, constructing an nMDS (non-metric Multidimensional Scaling) plot and calculating an Analysis of Similarity (ANOSIM). Multivariate data was analyzed using PRIMER v. 6.0 (Primer-E Ltd., Plymouth, UK).

**RESULTS:**

*Biotic and abiotic differences:*

*Dasysiphonia* grew an order of magnitude larger in the north (0.030±0.009 g/d/d) than in the southern region (0.003±0.004 g/d/d; $F_{1,118} = 7.69$, $p = 0.006$; Figure 4). Consistently higher
growth was seen in the north whether *Dasysiphonia* was grown alone in monoculture, or in realistic polycultures with the three most abundant species common to both regions ($F_{1,118} = 0.11$, $p = 0.74$). Although not statistically significant, the growth of *Dasysiphonia* in polyculture was higher in the northern region than in the south.

When given a choice of food source, preferential consumption of *Dasysiphonia* by the native herbivore, *L. vincta*, was generally higher in the south, however, this was not statistically significant ($F_{1,32} = 0.21$, $p = 0.64$; Figure 5). Across both regions, consumption tended to be higher when *Dasysiphonia* was offered to herbivores with other native species in polyculture than when it the only food choice offered to herbivores, although this was not statistically significant ($F_{1,32} = 2.20$, $p = 0.15$).

Temperature was higher in the south during the peak growth season for each year (2012-2014; Figure 3), and on average was 11%, or approximately two degrees C, higher overall (North mean: $15.99\pm0.33^\circ$C, South mean: $17.81\pm0.35^\circ$C). Overall yearly temperatures (Figure 3) reached a maximum of $22.9^\circ$C in the north (2012) and $24.5^\circ$C in the south (2013). Differences in salinity between the two regions were also observed, but the direction and magnitude varied across all three years. Further, the maximum range of the salinities between the two regions was less than 5.0 psu (minimum: 27.4 psu [2013 North]; maximum: 32.1 psu [2012 South]).

*Biodiversity Experiment:*

Following our two-year species removal experiment, species diversity did not differ across any of our removal treatments in the southern region (repeated measures MANOVA: $F_{2,76} = 0.07$, $p = 0.93$; ANOVA[Final plot differences]: $F_{2,116} = 1.99$, $p = 0.76$; Figure 6). Community composition at the conclusion of our species removals also did not differ across treatments (ANOSIM, Global $R = -0.001$, $p = 0.76$; Figure 7).
DISCUSSION:

The higher abundances of *Dasysiphonia* found in the north are consistent with biotic differences between the two regional populations. *Dasysiphonia* grew ten times faster in the northern region than in the south. Higher growth was observed whether *Dasysiphonia* was grown alone, or in realistic polycultures with other native species (Figure 4). It is unlikely these growth differences were due to the abiotic conditions we tested (temperature or salinity). While we observed higher growth in populations of *Dasysiphonia* acclimated to colder temperatures, controlled laboratory experiments from genetically identical European populations of *Dasysiphonia* have shown higher growth associated with warmer temperatures (Bjaerke and Rueness 2004). However, the summer maximum temperatures observed in both western Atlantic biogeographic regions fall well within the optimal growth range for European populations of *Dasysiphonia* (19-24°C; Bjaerke and Rueness 2004). Interestingly, during the summer in which these monthly growth assays were conducted (May 2014-August 2014), the temperature in the northern region, where the higher growth of *Dasysiphonia* was observed, only reached the optimal growth range on ten days. In contrast, the southern region, which experienced lower growth rates of *Dasysiphonia*, reached the optimal growth range on 64 days during the summer of 2014. This observation may suggest temperature adaptation or plasticity of the invader since its initial invasion from Europe in 2007. It is possible the two populations may be genetically evolving independently from one another, as the genetic identity of our northern specimens has not been confirmed. However, a secondary population of *Dasysiphonia* from Nova Scotia, Canada, also located in the same northern biogeographic region, has been confirmed to be
genetically identical to southern populations of *Dasysiphonia* in Rhode Island (COI-5P mitochondrial barcode; Savoie and Saunders 2013).

With respect to salinity, reduced *Dasysiphonia* growth has been observed in the European populations at salinities less than 15psu (Bjaerke and Rueness 2004). As the range of salinities observed between our biogeographic regions was well above 15psu and differed, on average, by less that 5 psu, it is unlikely salinity differences contributed to the differences in *Dasysiphonia* abundances between the two regions in the Western Atlantic. Therefore, while temperature may have been a contributing factor, it is likely there are additional differences between the two biogeographic regions that also contributed to the higher abundances of *Dasysiphonia* found north of Cape Cod, MA.

Statistical analyses did not confirm differences in consumption of *Dasysiphonia* by native herbivores between the two regions, potentially due to the high variability of consumption rates within treatments. However, *L. vincta* tended to consume more *Dasysiphonia* in the southern region, particularly when given a choice among *Dasysiphonia* and three native species. If indeed there is preferential herbivory of the invasive macroalga when in polyculture with native species, this preference would run counter to the enemy release hypothesis (Colautti et al. 2004), which suggests invaders are successful due to release from herbivory in their invaded range (Elton 1958). However, further evidence is necessary to support this hypothesis with respect to *Dasysiphonia*. In addition, consumption of macroalgae can be affected by a number of different factors, including chemical defenses, temperature, availability of other food items, or differences within the herbivores themselves (Morelissen and Harley 2007, Lyons et al. 2010). While *Dasysiphonia* contains only trace amounts of dimethylsulfide, a common herbivore deterrent in marine macroalgae, other sulfur compounds may be present in larger amounts (K. van Alstyne,
personal communication). In addition, differences in average temperatures between the two regions may have also affected herbivory rates of *L. vincta*. Therefore, it is difficult to determine which other factors, or combination of factors, may contribute to any differences that may be observed in feeding rates between the two biogeographic regions.

Growth rates of the invasive macroalgae were an order of magnitude slower in the south, where reduced abundances of the invasive macroalgae are observed (Newton et al. 2013). While abundances of *Dasysiphonia* are lower in the southern region than the northern region, the invader is still the third most abundant macrophyte from the 2012 survey of southern sites, representing an average of 7.41±1.19% of the subtidal community in these areas (Newton et al. 2013). However, our manipulative experiment confirmed that *Dasysiphonia* is not impacting biodiversity or community composition in this region. The lack of an experimental effect is consistent with survey results demonstrating no relationship between *Dasysiphonia* abundance and native algal species diversity (Figure 2). In contrast, there is a negative relationship between *Dasysiphonia* abundance and species richness in the north (Figure 2; Newton et al. 2013).

Our results highlight the context-dependency of invasions, both in terms of invader traits and community responses. Invader traits, such as growth rates and palatability may differ between recipient communities, as we have shown with *Dasysiphonia*, which may suggest differential invasion strategies by the same species in different recipient regions. Indeed, the context-dependency of invader traits has been shown with other macrophyte species, and has important implications for biological controls across different recipient regions (Shea et al. 2005). Furthermore, the responses of the recipient community are also context dependent, as some regions may have little to no long-term impacts on biodiversity or community structure from invasive species, as invaders successfully assimilates themselves into the recipient
community, as we observed in our southern biogeographic region. However, in a different, yet nearby, region, the same invader may have larger long-term impacts on biodiversity, as we observed from community surveys in the north. These differences in invader traits, community responses and abiotic conditions within invaded ranges can lead to variable impacts of invaders, reported for Dasysiphonia (present study), as well as other marine invaders (Thomsen et al. 2011). With increasing invasion frequencies world-wide, the need to investigate the context dependency of impacts across the entire invaded range is paramount for assessment and control of non-native species, as invasion strategies and community responses can be species- and region-specific, particularly if this invaded range encompasses major abiotic and biotic differences, as in the Western Atlantic invasion of Dasysiphonia.

ACKNOWLEDGEMENTS:

We would like to thank K. Benes, A. Claros, A. Drouin, N. Low, C. Marks, M. McConville, J.B. Ramsay, M. Roberts, K. Rodrigue, I. Rosenthal, V. Selsnick, S. Smith, and V. Perini for their diving and laboratory assistance. This work was funded by the National Science Foundation (OCE-0963010 to G. Trussell et al. as part of the Academic Research Infrastructure Recovery and Reinvestment Program), Woods Hole Sea Grant (Subaward A100923 to MESB and CST) and MIT Sea Grant (Project Number 2014-R/RCM-37 to ARH). This material is based upon work supported in part by the National Science Foundation EPSCoR Cooperative Agreement #EPS-1004057. This is publication number XXX from the Marine Science Center of Northeastern University.

LITERATURE CITED:


Elton, C. 1958. The ecology of invasions by animals and plants, Methuen, London.


Figure 1. Relative proportion of *Dasysiphonia japonica* at sites north and south of the biogeographical barrier at Cape Cod, Massachusetts. *Dasysiphonia* was >200% more abundant in northern regions during the first 5 years of invasion.
Figure 2. Native biodiversity of recipient communities declines with increasing Dasysiphonia japonica abundance at sites north of Cape Cod, Massachusetts (top), while no correlation between biodiversity and invader abundance is seen in observational surveys at sites south of the major biogeographical barrier (bottom). (Data adapted from Newton et al. 2013).
Figure 3. Temperature variation between the two biogeographic regions north and south of Cape Cod, Massachusetts during the initial invasion. Daily water temperatures reached the optimal growth range of *Dasysiphonia japonica* (top panel, grey box) during each year in each region. Each year, temperatures reached the optimal growth range of *Dasysiphonia* as determined by Bjaerke and Rueness (2004). On average, temperatures were 11% higher in the southern region during the peak growth season of *Dasysiphonia* (May-October; bottom panel).
Figure 4. Mean daily biomass specific growth +/- 1 standard error of *Dasysiphonia japonica* was 10 times faster in the region north of Cape Cod, Massachusetts than in the south ($F_{1,118} = 7.69$, $p = 0.006$). Growth of *Dasysiphonia* was higher in the north regardless of whether *Dasysiphonia* was grown in monoculture and in polyculture with three most abundant algal species common to both regions ($F_{1,118} = 0.11$, $p = 0.74$).
Figure 5. Consumption of *Dasysiphonia japonica* by the native herbivore, *Lacuna vincta* tended to be higher in the south than in the region north of Cape Cod, Massachusetts, although this was not statistically significant ($F_{1,32} = 0.21, p = 0.64$). *Lacuna* tended to consume more *Dasysiphonia* in polycultures with 3 additional native species common to both regions, than in no-choice monocultures ($F_{1,32} = 2.20, p = 0.15$).
Figure 6. Dasysiphonia japonica had no impact on final native biodiversity following a two year in situ removal experiment ($F_{2,16} = 1.99$, $p = 0.76$).
Figure 7. Community composition was not impacted by *Dasysiphonia japonica* following a two-year *in situ* removal experiment (ANOSIM, Global $R = -0.001$, $p = 0.76$).