

Invasive seaweeds transform habitat structure and increase biodiversity of associated species

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Summary

1. The visual landscape of marine and terrestrial systems is changing as a result of anthropogenic factors. Often these shifts involve introduced species that are morphologically dissimilar to native species, creating a unique biogenic structure and habitat for associated species within the landscape. While community-level changes as a result of introduced species have been documented in both terrestrial and marine systems, it is still unclear how long-term shifts in species composition will affect habitat complexity or its potential to influence the biodiversity of species that occur at the base of the food web.

2. We analysed quadrat photos collected at several subtidal sites in the Gulf of Maine over a 30+ year period, and collected individual seaweed species to determine their complexity and the biodiversity of meso-invertebrates associated with each species.

3. By coupling the relationship of 30+ years of shifts in seaweed assemblages, morphological structure of the seaweed assemblage, and their meso-invertebrates, we determined introduced seaweeds have increased by up to 90%, corresponding to a rise in two-dimensional (2D) structure, and a decline in canopy height of subtidal rocky habitats. The highly complex two-dimensional habitat provided by introduced filamentous red seaweeds supports two to three times more meso-invertebrate individuals and species that form the base of the food web than simpler forms of morphological habitat.

4. Synthesis. The present study demonstrates a long-term shift in foundation species towards a dominance of invasive seaweeds that directly reduce canopy height and increase the 2D biogenic structure of the habitat. These introduced seaweeds harbour greater biodiversity of species found at the base of the food web than seaweeds with simpler forms such as the native kelp species. Such shifts in habitat structure will propagate to food webs by influencing the structure of lower trophic-level meso-invertebrates and indirectly upper trophic-level species that feed on these invertebrates and use the seaweed structure as refuge.

Key-words: ecosystem change, food webs, habitat complexity, invasive species, kelp loss, temperate reef habitats

Introduction

Foundation species facilitate biodiversity through the creation of local conditions that modify and stabilize a habitat (Dayton 1972). They can co-occur in assemblages of multiple foundation species (Gribben *et al.* 2009), or they can form one-way,

nested facilitation cascades (Bruno & Bertness 2001; Bruno, Stachowicz & Bertness 2003; Altieri *et al.* 2010; Angelini & Silliman 2014). The relative contribution of foundation species to ecosystem function may stem from their morphological structure which has been measured using a composite of species-specific trait-based metrics such as size, number of branches or size of air bladders (Bishop *et al.* 2009; Bishop, Fraser & Gribben 2013; Wright *et al.* 2014) and mathematical

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relationships of species complexity (e.g. Gunnarsson 1992; McAbendroth *et al.* 2005). Their structure can be of primary importance for facilitating species coexistence by allowing smaller organisms to find refuge from competitors or predators (Dayton 1972; Jones, Lawton & Shachak 1994; Warfe & Barmuta 2004; Bertness *et al.* 2006; Crain & Bertness 2006; Angelini *et al.* 2011; Bishop, Fraser & Gribben 2013). It can also determine the outcome of predator–prey interactions (Warfe & Barmuta 2004), identity of associated species (Carr 1989; Lazzari & Stone 2006) and size of associated individuals (Hacker & Steneck 1990; McAbendroth *et al.* 2005). As such, the morphological structure of foundation species provides a vital link to organisms throughout the food web, beginning with smaller invertebrates (e.g. mussels, snails, insects; Altieri, Silliman & Bertness 2007; Dijkstra, Boudreau & Dionne 2012; Adkins & Rieske 2013; Angelini & Silliman 2014), which are important prey species for higher trophic-level organisms.

Species introductions and environmental forcing have contributed to dramatic shifts in species composition in marine and terrestrial ecosystems (Vitousek *et al.* 1987; Meiners 2007; Byers 2009; Dijkstra, Westerman & Harris 2011; McIntyre *et al.* 2015; Verges *et al.* 2016). These shifts can result in a change in the morphological structure of the landscape, which can in turn lead to dissimilar patterns of abundance and richness of species in the associated community. In a desolate landscape, introduced species add biogenic structure to increase biodiversity and food web structure (Crooks 2002; Burlakova, Karatayev & Karatayev 2012; Byers *et al.* 2012). Introduced species often establish in areas that already have existing biogenic structure (Meiners, Pickett & Cadenasso 2002; Meiners, Cadenasso & Pickett 2004; Gribben *et al.* 2009). In such cases, these species represent additions that may or may not add greater structure to a landscape or alter the function of an ecosystem (Ellison *et al.* 2005; Crain, Albertson & Bertness 2008). While community-level changes as a result of introduced species have been documented in both terrestrial and marine systems (e.g. Able & Hagan 2000; Silliman & Bertness 2004; Schmidt & Scheibling 2006; Drouin, McKindsey & Johnson 2012; Rodwald 2013; Maggi *et al.* 2015), studies examining long-term shifts in species assemblages and relating these shifts to habitat structure and biodiversity of lower trophic-level species are rare.

There have been few prior studies of changes in habitat structure resulting from long-term shifts in foundation species, particularly in marine environments. A previous study in a terrestrial system found a shift from a native to an introduced dominant species increased the canopy height of terrestrial forests in Hawaii with unknown consequences for species that use this ecosystem (Asner *et al.* 2008). Changes in species composition observed in many temperate reef ecosystems are more rapid than that of terrestrial landscapes or the rocky reef systems in the US Pacific Northwest (Harris & Tyrrell 2001; Connell *et al.* 2008; Elahi *et al.* 2013; McIntyre *et al.* 2015). Given that the structure of a community and the facilitation of associated organisms can be heavily influenced by the

unique morphology of a particular species, it is important to have a mechanistic understanding of how long-term shifts in species composition will affect habitat structure and diversity species.

Temperate seaweed assemblages promote biodiversity and stability through their added physical structure (e.g. Graham 2004). Kelp forests are among the most productive systems in the ocean (Mann 1973; Hoegh-Guldberg & Bruno 2010). They occur along the majority of temperate ecosystem coastlines, and their physical structure provides habitat for a wide variety of organisms including commercially important species such as fish, crabs and lobsters (Bologna & Steneck 1993; Carr 1994; Paddock & Estes 2000). Previous studies report that on many coasts that experience high levels of human activity, kelp forests have been replaced by mats of introduced seaweeds (Boudouresque & Verlaque 2002; Airoldi & Beck 2007; Connell *et al.* 2008; Wernberg *et al.* 2016). The morphological structure of these introduced seaweeds is varied and may be quite different from those of the resident species.

In the Gulf of Maine, rocky subtidal communities are changing at unprecedented rates (Harris & Tyrrell 2001; Steneck & Carlton 2001; Harris & Jones 2005; Mathieson *et al.* 2008a,b; Steneck *et al.* 2013). These communities were transformed from a historical kelp bed community to one dominated by sea urchin barrens in the early 1980s (Steneck *et al.* 2013). Overfishing of sea urchins, beginning in 1987, led to a reversion to seaweed-dominated communities, but the new communities included a series of introduced seaweed species (e.g. Harris & Tyrrell 2001; Harris & Jones 2005; Mathieson *et al.* 2008b), many of which are turf-forming (<10 cm tall, densely packed fronds, lax branches and filamentous, see Connell, Foster & Airoldi 2014). We used field surveys to examine long-term (+30 years) changes in seaweed assemblages. We coupled these data with measurements of seaweed complexity (morphology) to investigate the effects of introduced species on habitat complexity. We also removed, identified and counted meso-invertebrates associated with individual seaweed species and then used these values to examine the relationship between introduced seaweeds and meso-invertebrate biodiversity. As introduced seaweeds are habitat-forming species that often represent a unique growth form in the invaded ecosystem and associated species use this form as substrata or refuge from competitors or predators, we expect the introduced seaweeds in the Gulf of Maine to have an impact on the complexity of the biogenic habitat and its inhabitants.

Materials and methods

LONG-TERM SHIFTS IN SPECIES COMPOSITION

Long-term shifts in seaweed composition were examined using slides and digital photographs (10–20 photos/site/time period) of 0.25-m² quadrats, collected at a depth of c. 8 m at four sites at the Isles of Shoals (Appendix S1, Supporting Information). The photos were analysed using CPCe v4.1 (Coral Point Count with Excel extensions).

A new code was written to accommodate the seaweed species in the Gulf of Maine. Percent cover was determined through point count analysis in which 200 points were randomly placed on the image and the species under each point was identified. For years in which we did not have photographs, we used values of mean and standard deviations obtained from the literature (Appendix S2) and observations of dominance.

INDIVIDUAL STRUCTURAL COMPLEXITY AND BIODIVERSITY

To investigate the effects of introduced seaweeds on habitat structure, we collected individuals (15 per species) of native (i.e. *Saccharina latissima*, *Ulva* spp., *Chondrus crispus*, *Desmarestia aculeata* and *Cystoclonium purpureum*) and introduced species (i.e. *Codium fragile* subsp. *fragile*, *Bonnemaisonia hamifera* and *Dasysiphonia japonica*). To prevent meso-invertebrates from swimming away or dropping off the seaweed during collection, individual seaweeds were covered with a bag and subsequently picked from the holdfast off of the substrate. The bag was immediately tied shut. Five replicates of each species were removed from three of four sites (Appledore Island, Lunging Island and White Island). Once collected, individual thalli were pressed and dried, and each individual was photographed, and a measure of 2D complexity (fractal dimension) was calculated. We used a measure of fractal dimension, as it uses the perimeter of the structural profile of individual seaweed species and thus morphological comparisons can be made across species (Tokeshi & Arakaki 2012). To calculate fractal dimension, images were imported into the image analysis program ImageJ (Rasband 1997–2016; Abramoff, Magalhaes & Ram 2004). Images were converted to binary images and outlined for fractal analysis. Fractal analysis in ImageJ is calculated using the box count method. The box count is an iterative process in which boxes, from large to small, are placed along the perimeter of the seaweed. ImageJ then plots the log of the number of boxes against the log of the box size. This gives a straight line with a negative slope (m), and fractal dimension (D) can be calculated as $D = 1 - m$. These samples were collected from the New Hampshire coast, pressed and then dried. To accompany this 2D measure of structural complexity, we measured heights of collected seaweeds and complemented these values with published values to be certain we captured the range of heights of the different seaweed species (Appendix S3).

Complexity values of *S. latissima* were calculated from pressed samples without holdfasts. To be sure these values did not vary from those with intact holdfasts, we compared complexity values of *S. latissima* with and without holdfasts using digitized samples collected from various locations in the Gulf of Maine (Cashes Ledge, Isles of Shoals, Cape Neddick, Maine and Rye, New Hampshire). Digitized images were downloaded from the University of New Hampshire's Herbarium portal and complexity (fractal dimension) was analysed for individual *S. latissima* ($n = 8$) with and without the holdfast. A t -test was used to test for mean differences in complexity between holdfast bearing *S. latissima* (1.084 ± 0.011) and the same individual alga without its holdfast (1.07 ± 0.017). Results show no significance difference in complexity of *S. latissima* with or without its holdfast ($t = 2.49$, $P = 0.11$). Complexity of *Neosiphonia* spp., a prevalent genus in the Gulf of Maine was analysed using samples archived at the University of New Hampshire's Hodgeson Herbarium. *Neosiphonia* spp. is divided into two morphologically indistinct species (*Neosiphonia harveyi* and *Neosiphonia japonica*) whose invasion status is still under debate (Savoie & Saunders 2015). Here, we list *Neosiphonia* spp. as introduced as it

first appeared at the Isles of Shoals in 1990 (Mathieson *et al.* 2008c).

To examine relationships between introduced seaweed species, abundance and richness of meso-invertebrates, we removed associated meso-invertebrates by placing each alga in a freshwater bath for c. 2 min as per Holmlund, Peterson & Hay (1990). This method euthanizes meso-invertebrates so they drop off the seaweed and all remaining individuals were picked off using tweezers under a dissecting scope. Meso-invertebrates from each thallus were placed in a labelled vile with ethanol for future analysis. All individuals were then counted and identified. We aggregated individual amphipods, caprellids and isopods into their respective groups as prior research has shown that this level of taxonomic resolution shows similar results to those conducted at finer scale resolutions (Sommerfeld & Clark 1995; Chapman 1998).

HABITAT STRUCTURAL COMPLEXITY AND BIODIVERSITY

To investigate the effect of long-term shifts in seaweed assemblages on habitat complexity, we used individual mean and standard deviations of dominant (i.e. those that comprised at least 5–10% of species composition at any one point in time, Fig. 1) seaweed species collected from subtidal sites at the Isles of Shoals (Appendix S1). We then used seaweed percent cover, measured from 0.25-m² quadrats, to weight the long-term values of habitat complexity. If values of percent cover were taken from the literature, we used the mean and standard deviation of individual (or group) seaweed percent cover to calculate habitat complexity. Using weighted percent cover allowed us to account for the densities and not just the presence or absence of seaweed species at any given time. We then modelled long-term shifts in meso-invertebrates associated with each habitat type by combining a weighted percent cover of seaweeds with the number of meso-invertebrate individuals and species associated with each seaweed species. *Neosiphonia* spp. was a common member of the seaweed assemblage throughout the study period. However, we did not find it during our recent sampling surveys at our study sites. To account for the meso-invertebrate abundance and richness associated with *Neosiphonia* spp., we used averaged meso-invertebrate numbers and species associated with *C. purpureum* and *D. japonica*. We did this as the complexity of *Neosiphonia* spp., calculated from herbarium pressed samples, was intermediate between the two species and we found a strong correlation between complexity and meso-invertebrate abundance and richness.

STATISTICAL ANALYSIS

Statistical analyses were generated using JMP software (JMP12, SAS Institute, Cary, NC, USA) and the PRIMERv6 with PERMANOVA extension package. We used two-way permutation multivariate analysis (PERMANOVA) with site and decade as the interaction terms to test differences in species composition among decades on untransformed data. Least squares regression of mean meso-invertebrate numbers and species richness collected from individual seaweed species was used to relate variation in meso-invertebrate abundance, and richness with seaweed complexity. Mann–Whitney U tests with seaweeds grouped as native and introduced was used to determine differences in seaweed complexity, meso-invertebrate abundance and species richness. The relationship between time and habitat complexity, meso-invertebrate abundance and richness was determined using least squares regression.

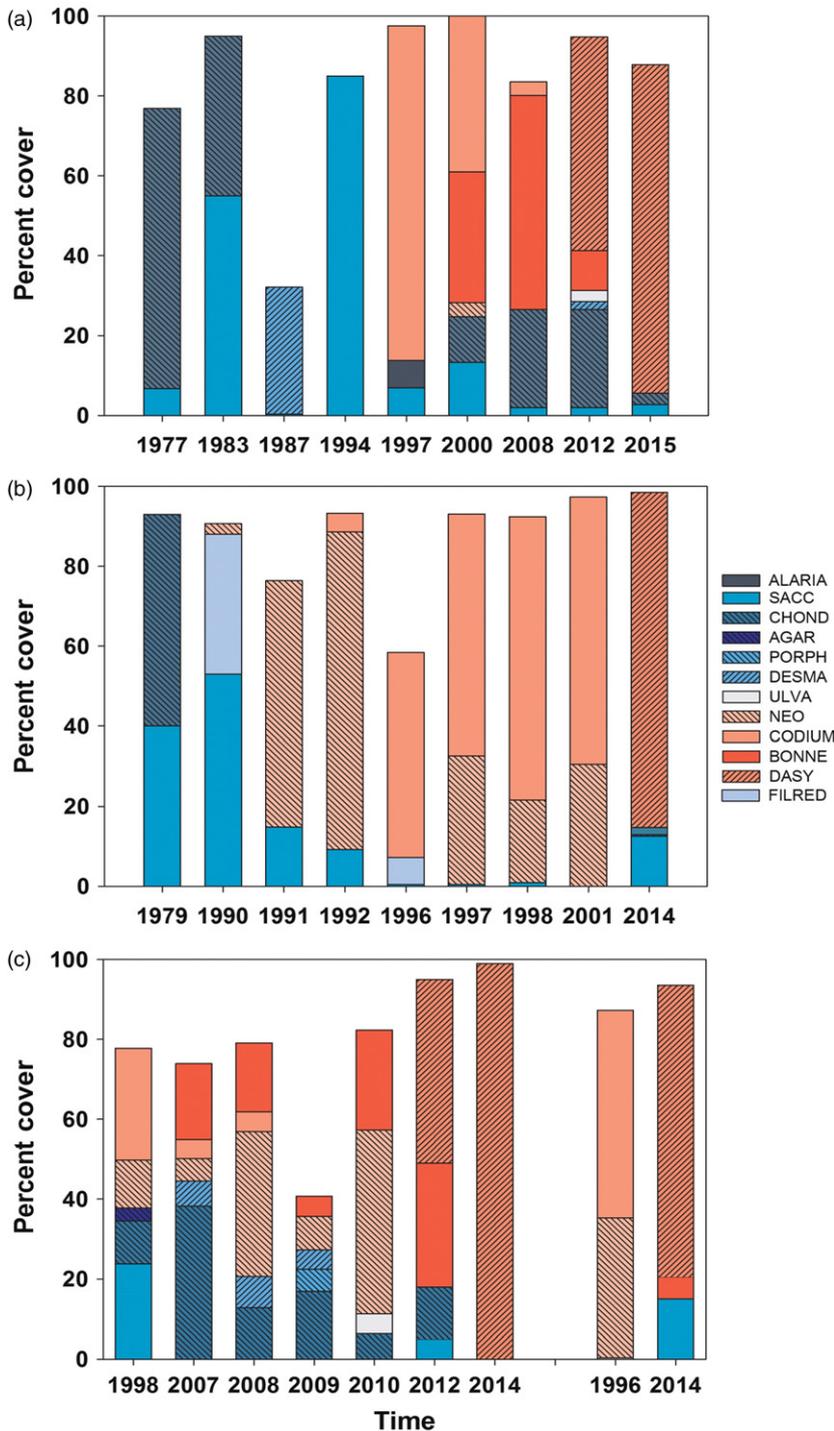


Fig. 1. Long-term trends in the dominance of seaweed assemblages at four sites at the Isles of Shoals. Blue colours represent native species while pink colours represent introduced or cryptogenic species. The assemblages at all four sites have undergone dramatic shifts in seaweed assemblages beginning with a system dominated by *Saccharina latissima* and *Chondrus crispus* in the 1970s and 1980s. In the 1990s, they transitioned to introduced assemblages dominated by the green fleece alga (*Codium fragile* subsp. *fragile*) and to a lesser extent *Neosiphonia* spp. By early 2000s, the assemblages were dominated by red filamentous introduced alga (*Neosiphonia* spp., *Bonnemaisonia hamifera*, *Dasyisiphonia japonica*). *Alaria* (*Alaria esculenta*), *Sacc* (*Saccharina latissima*), *Chond* (*Chondrus crispus*), *Agar* (*Agarum clathratum*), *Porph* (*Porphyr* spp.), *Desma* (*Desmarestia aculeata*), *Ulva* (*Ulva* spp.), *Neo* (*Neosiphonia* spp.), *Codium* (*Codium fragile* sp. *fragile*), *Bonne* (*Bonnemaisonia hamifera*), *Dasy* (*Dasyisiphonia japonica*), *Filred* (Filamentous red seaweed) (a) Star Island, (b) Appledore Island, (c) White Island (left side, 1998 to 2014) and Lunging Island (right side, 1996 and 2014 only).

Results

TEMPORAL SHIFTS IN SPECIES COMPOSITION

Multivariate analyses confirmed that species composition has changed since the 1970s. The analysis of untransformed data revealed a strong effect of decade on species composition (pseudo- $F_{4,26} = 2.26$, $P < 0.002$), with no effect of site (pseudo- $F_{3,26} = 0.46$, $P < 0.98$), or interaction between site and decade (pseudo- $F_{5,26} = 0.69$, $P < 0.88$). Overall, the seaweed assemblage has shifted from an historical community

dominated by kelp beds in the 1970s and early 1980s to one that is now primarily composed of introduced seaweed species (Fig. 1, Appendix S6). Although the green siphonaceous alga *C. f. subsp. fragile* was introduced to the Isles of Shoals in 1983, it did not become a dominant member of the community until the 1990s. *C. f. subsp. fragile* and to a lesser extent the red filamentous species, *Neosiphonia* spp. were dominant at this time (Carlton & Scanlon 1985). *Neosiphonia* spp. and *B. hamifera* replaced *C. f. subsp. fragile* as the dominant species in the late 2000s. Since 2012, the red filamentous alga *D. japonica* is the dominant seaweed at the Isles of Shoals.

INDIVIDUAL STRUCTURAL COMPLEXITY AND MESO-INVERTEBRATE BIODIVERSITY

Seaweed species collected from different sites were combined for all statistical analyses as there were no significant differences in complexity among species collected from different sites (Appendix S4). The primary structural differences are illustrated in Fig. 2; kelps such as *S. latissima* consist of flattened elongate blades on cylindrical stipes, while *C. f.* subsp. *fragile* forms elongate cylindrical branches. *Ulva* spp. forms flat blades and *C. crispus* forms upright branching bushes with narrow blades. The four remaining red species and *D. aculeata* form bushy arborescent thalli with thin and complex branching. There were differences in complexity among

individual seaweed species (Fig. 3, $P < 0.05$). As many of the introduced seaweeds are either branched or filamentous, they had the greatest complexity values as compared to native seaweed species whose morphology spans from blades to filamentous forms (Fig. 4).

Heights of seaweed species varied with the greatest heights found in most native species (e.g. *S. latissima*, *D. aculeata* and *C. purpureum*; Fig. 2). Introduced species were short with height values ranging from 0.2 to 1.0 m (*C. f.* subsp. *fragile* can reach 1.0 m in protected sites).

Ninety-three per cent of the variance in meso-invertebrate abundance and 71% of the variance in species richness was explained by complexity ($P < 0.001$, $R^2 = 0.93$, $P = 0.005$, $R^2 = 0.71$ respectively; Fig. 3). Numbers of meso-

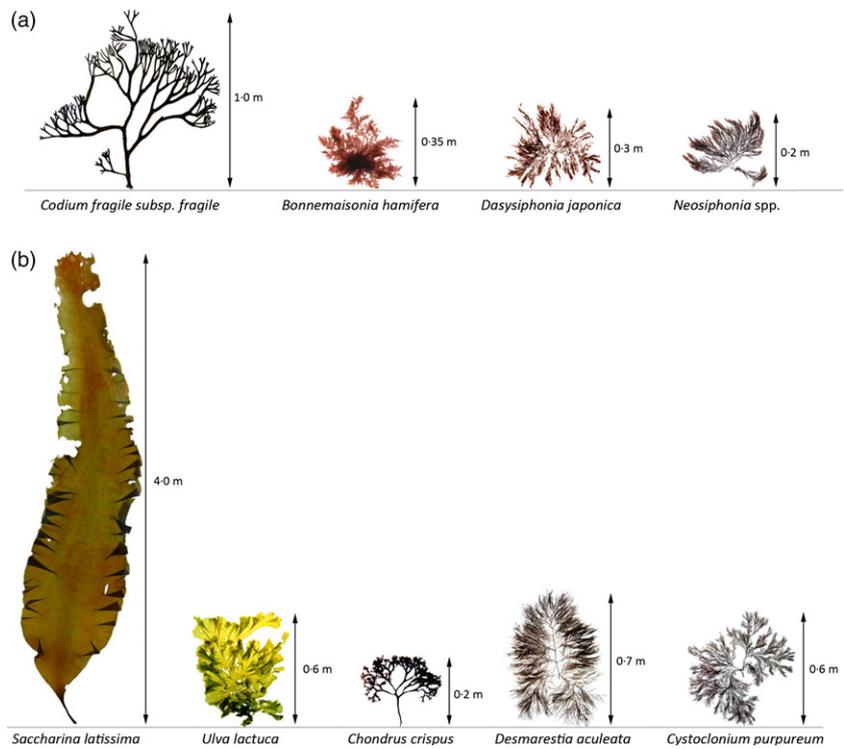


Fig. 2. Heights of introduced (a) and native (b) seaweed species that were commonly found between the late 1970s and 2015. To capture the full range of algal heights, values were taken from *in situ* sampling and a variety of sources (see Appendix S3).

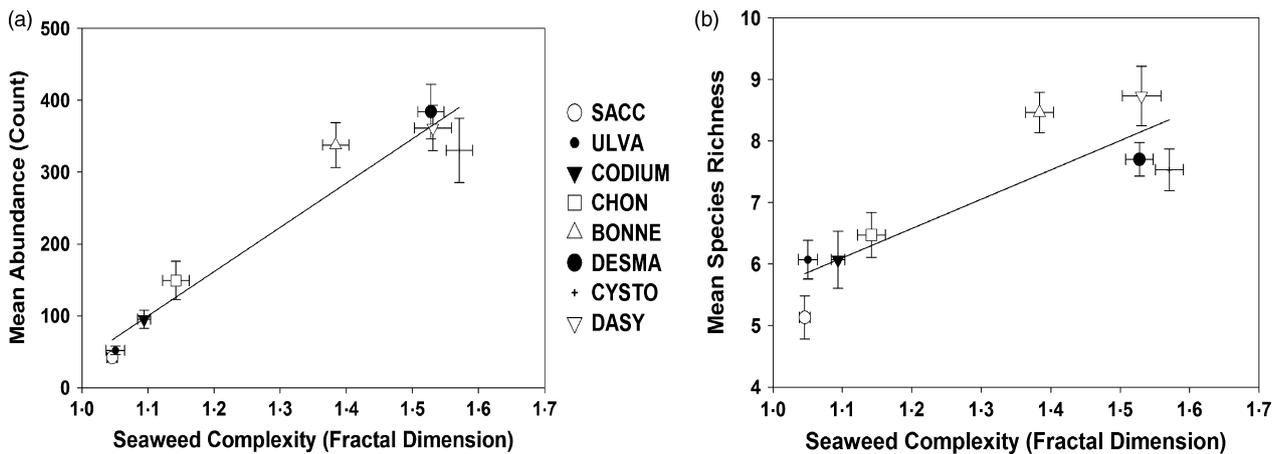


Fig. 3. Mean meso-invertebrate abundance and richness (a and b respectively) plotted against individual seaweed complexity. Middle symbols are representative of those in both figures. Meso-invertebrate abundance and richness showed a significant positive regression with individual seaweed complexity ($R^2 = 0.93$, $P < 0.01$, $R^2 = 0.71$, $P < 0.01$ respectively). Error bars are two SEs.

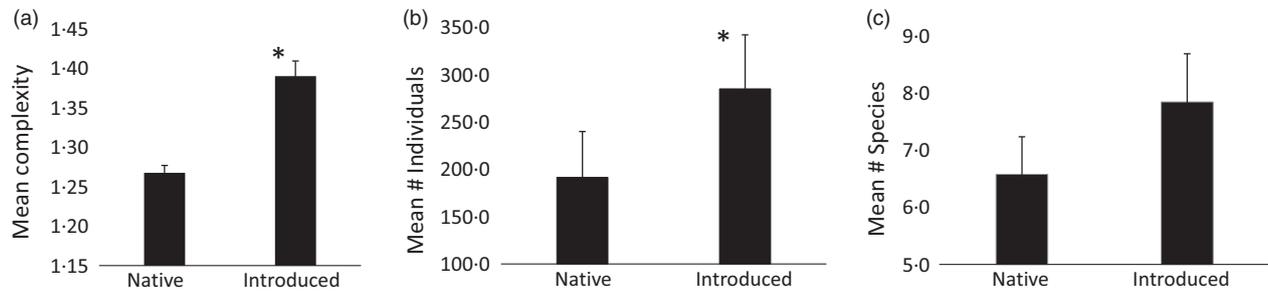


Fig. 4. Seaweed complexity (a), associated meso-invertebrate abundance (b) and species richness (c) of native and introduced species. Complexity of seaweeds and abundance of meso-invertebrates is greater on introduced than native seaweeds. No significant difference in meso-invertebrate species richness was found between native and introduced seaweeds.

Table 1. Mean densities (\pm SE) of dominant meso-invertebrate associated with each seaweed species. Amphipods and the subgroup, Caprellids, were the most abundant group of species

Species	Amphipods	Caprellids	Isopods	<i>L. vincta</i>	<i>M. helacinus</i>	<i>M. lunata</i>	<i>M. edulis</i>
<i>Dasyisiphonia japonica</i>	263.53 (\pm 15.96)	23.07 (\pm 0.83)	0.31 (\pm 0.00)	0.036 (\pm 0.00)	0.44 (\pm 0.00)	12.47 (\pm 1.20)	16.73 (\pm 1.78)
<i>Bonnemaisonia hamifera</i>	232.5 (\pm 22.51)	71.86 (\pm 3.36)	2.81 (\pm 0.21)	0.20 (\pm 0.00)	1.16 (\pm 0.02)	15.48 (\pm 2.29)	18.90 (\pm 5.71)
<i>Codium fragile</i> subsp. <i>fragile</i>	31.68 (\pm 1.73)	24.41 (\pm 2.33)	0.94 (\pm 0.00)	0.29 (\pm 0.00)	1.87 (\pm 0.01)	0.29 (\pm 0.00)	40.53 (\pm 5.07)
<i>Saccharina latissima</i>	35.51 (\pm 3.60)	8.42 (\pm 0.13)	0.14 (\pm 0.00)	33.98 (\pm 3.25)	3.17 (\pm 0.00)	6.70 (\pm 0.01)	12.08 (\pm 0.32)
<i>Ulva lactuca</i>	29.86 (\pm 1.41)	11.25 (\pm 0.25)	0.20 (\pm 0.00)	12.37 (\pm 0.15)	12.89 (\pm 0.36)	13.70 (\pm 0.36)	18.92 (\pm 0.77)
<i>Desmarestia aculeata</i>	115.73 (\pm 17.85)	152.73 (\pm 2.31)	6.19 (\pm 0.48)	0.87 (\pm 0.01)	5.75 (\pm 0.34)	9.61 (\pm 0.91)	31.98 (\pm 7.26)
<i>Cystoclonium purpureum</i>	174.47 (\pm 22.84)	26.54 (\pm 7.33)	3.44 (\pm 0.17)	1.12 (\pm 0.02)	1.32 (\pm 0.05)	1.70 (\pm 0.04)	13.62 (\pm 1.06)
<i>Dumontia contorta</i>	16.81 (\pm 0.32)	88.6 (\pm 5.27)	0.33 (\pm 0.00)	0.50 (\pm 0.00)	4.16 (\pm 0.30)	0 (\pm 0.00)	19.80 (\pm 0.34)
<i>Chondrus crispus</i>	109.93 (\pm 15.78)	3.85 (\pm 0.11)	0.46 (\pm 0.00)	5.72 (\pm 1.40)	2.40 (\pm 0.02)	13.63 (\pm 0.97)	5.60 (\pm 0.16)

invertebrates associated with individual seaweed species were similar among specific morphological groups of seaweeds (Appendix S5). Greater numbers of meso-invertebrates were found on branched or filamentous forms of seaweed ($\chi^2 = 6.55$, $P = 0.01$; Fig. 3). A variety of meso-invertebrates were found on native and invasive seaweeds with amphipods as the dominant group in highly complex seaweeds and in *C. crispus* (Table 1). Amphipods, caprellids, and mussels were the dominant meso-invertebrates found on *C. f.* subsp. *fragile* while *Lacuna vincta*, *Mytilus edulis* and amphipods were abundant on *Ulva* spp. A number of meso-invertebrates were equally numerous on *S. latissima*, including amphipods, mussels and several gastropod species (*L. vincta*, *Margarite helacinus*, and *Mitrella lunata*). No difference in meso-invertebrate species richness was observed between introduced and native seaweeds ($P = 0.23$, $\chi^2 = 2.46$; Fig. 4c).

LONG-TERM SHIFTS IN HABITAT COMPLEXITY AND BIODIVERSITY

Complexity increased as a function of time at all sites at the Isles of Shoals (Star, $R^2 = 0.58$, $P = 0.01$; Appledore $R^2 = 0.40$, $P = 0.05$; White, $R^2 = 0.59$, $P = 0.05$; Fig. 5). In the late 1970s, complexity of seaweed assemblages was 0.87 (± 0.03) and 1.02 (± 0.03) at Star and Appledore islands

respectively (Fig. 5a and b). In the mid-1990s, complexity was 0.92 (± 0.05) at White Island (Fig. 5c) and 1.11 (± 0.06) at Lunging Island (Appendix S6). By the mid 2010s, complexity had risen to 1.37 (± 0.05), 1.46 (± 0.06), 1.51 (± 0.001), and 1.35 (± 0.04) at Star, Appledore, White and Lunging Islands.

Concurrent with increasing complexity was a rise in modelled meso-invertebrate abundance (Star, $R^2 = 0.63$, $P = 0.01$; Appledore, $R^2 = 0.44$, $P = 0.4$; White, $R^2 = 0.85$, $P = 0.005$). At Star and Appledore Islands abundance had risen from 108.0 (± 5.9) to 289.6 (± 9.9) and 96.2 (± 2.3) to 315.6 (± 13.2) respectively. In the mid-1990s, associated modelled meso-invertebrate abundance was 89.7 (± 4.2) at White and 170.0 (± 8.9) at Lunging Islands and increased to 356.5 (± 1.8) and 288.6 (± 8.3) respectively (Fig. 5, Appendix S6). Modelled meso-invertebrate species richness followed the same trend, increasing with time (Star, $R^2 = 0.48$, $P = 0.2$; Appledore, $R^2 = 0.47$, $P < 0.04$; White, $R^2 = 0.70$, $P = 0.02$). Species richness rose from 4.9 (± 0.2) to 6.65 (± 0.2) at Star, 5.5 (± 0.1) to 8.2 (± 0.4) at Appledore, 4.64 (± 0.2) to 8.6 (± 0.1) at White and 5.8 (± 0.3) to 7.6 (± 0.2) at Lunging Islands.

Discussion

This study demonstrates that the composition of foundation temperate reef assemblages in the Gulf of Maine has

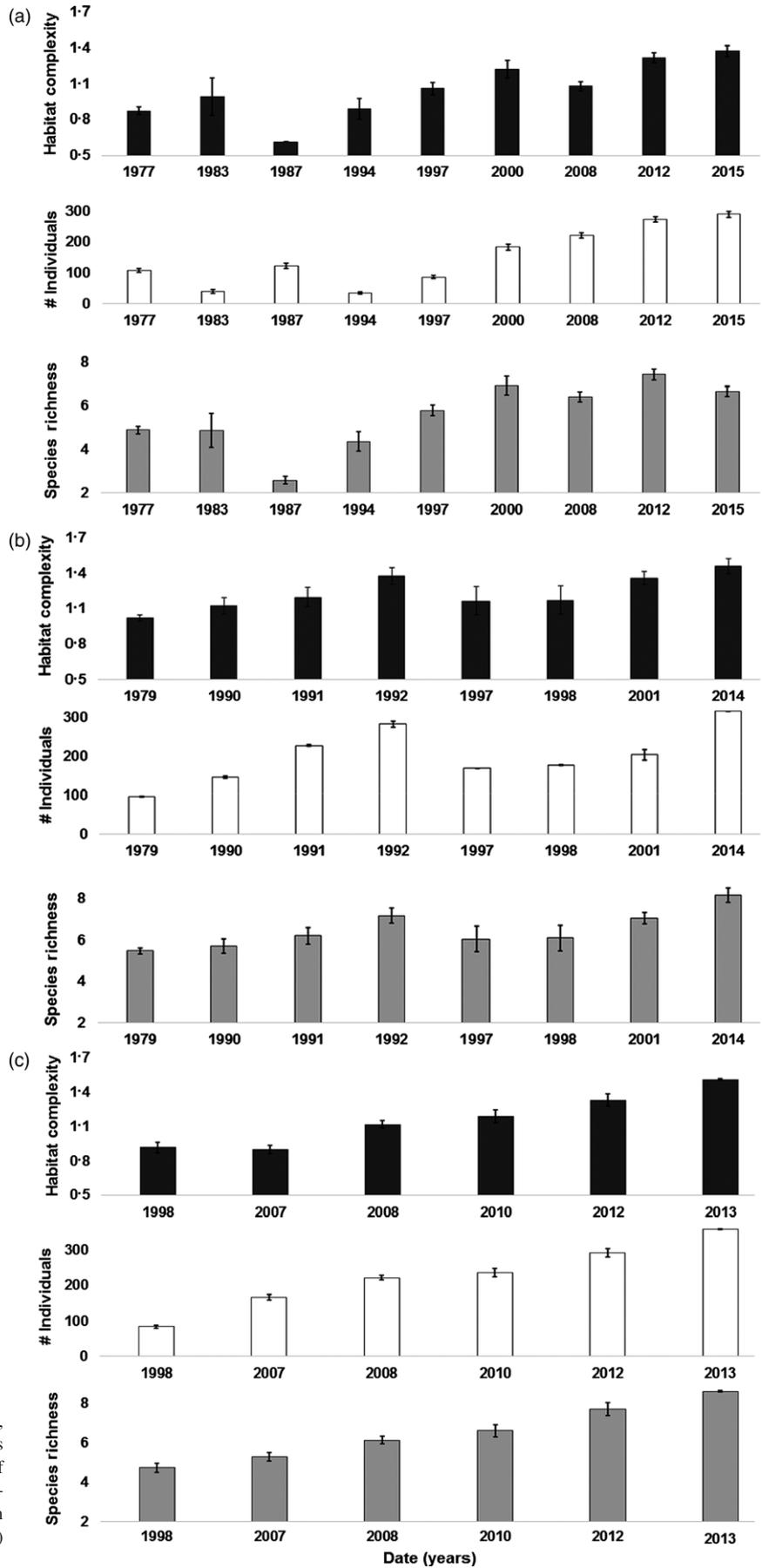


Fig. 5. Long-term trends in habitat complexity, mean-associated meso-invertebrate richness and abundance. Habitat complexity, number of associated meso-invertebrates and species significantly increased with time. Bars are mean values and error is SE. (a) Star Island, (b) Appledore Island, (c) White Island.

undergone a phase shift (adopted from Steneck 2002) over the past four decades from a kelp-dominated assemblage to a red filamentous seaweed assemblage that is predominantly composed of the invasive red filamentous alga, *D. japonica*. Around 50–90% of the bottom cover is now composed of introduced co-occurring red and green seaweeds that were not present or very rare in the pre-1980 kelp bed communities. Concurrent with our observed seaweed phase shift is a rise in the morphological complexity of these seaweed assemblages and a decline in canopy heights. Greater complexity in seaweed habitats occurs because of the limited morphological range of introduced species in our study combined with their greater densities. Highly complex foundation species, such as the introduced seaweeds observed in this study, also harbour greater numbers of associated individuals and species than those associated with less complex foundation species (Warfe & Barmuta 2004; Veiga, Rubal & Sousa-Pinto 2014). Overall, our study suggests that, in the Gulf of Maine, introduced seaweed species have increased habitat complexity that in turn has a positive effect on the biodiversity of meso-invertebrates.

Long-term (30+ years) shifts towards dominance of introduced seaweeds observed in this study may be due to temperature and/or herbivory. In the Gulf of Maine, Sea Surface Temperature (SST) has risen steadily since 2000 with annual yearly increases of 0.23°C, with highest temperatures on record occurring since 2004 (Mills *et al.* 2013; Pershing *et al.* 2015). Rising water temperature elicits stress responses in *S. latissima* and compromises the performance of their recruits (Wernberg *et al.* 2010; Heinrich *et al.* 2012; Simonson, Scheibling & Metaxas 2015), which may make them more vulnerable to decline. A recent study in western Australia documented a shift in community structure from kelp beds to turf-forming algae after a heat wave (Wernberg *et al.* 2013). Concurrent with this shift was an influx of tropical invertebrate (e.g. coral) and fish species (Wernberg *et al.* 2016). In the Mediterranean Sea and Japan, climate-mediated range expansions of herbivorous tropical fish species have facilitated a phase shift from dominance of kelp beds to barrens (Verges *et al.* 2014, 2016) and corals (Mezaki & Kubota 2012). While changes in fish abundance and distribution patterns have occurred in the Gulf of Maine, a large influx of herbivorous fish species such as those seen in the Mediterranean Sea and Japan have not been observed (Nye *et al.* 2009). Herbivory by invertebrates may reduce kelp beds. Grazing by gastropods such as *L. vincta* on kelp thalli and reproductive structures (O'Brien & Schiebling 2016), can reduce canopy area, particularly in the presence of *D. japonica* (Low *et al.* 2015). This facilitates kelp loss and lead to greater light availability to understory species (Johnson & Mann 1986; Chenelot & Konar 2007). *L. vincta* is a cold-water northern temperate species that experiences physiological stress at 25°C and mortality at 30°C (McMahon & Russell-Hunter 1977). While it is detrimental to kelp systems, its long-term effects on kelp beds remain unclear as warmer waters may restrict its abundance.

Other factors that may affect seaweed assemblages are eutrophication and ocean acidification. Eutrophication can

influence seaweed assemblages as rising nutrient levels tend to favour growth of green seaweeds. The Isles of Shoals is c. 10 km off the coast of New Hampshire and is uninhabited for most of the year. There are a few residents during the summer months and the Oceanic Hotel on Star Island and the Shoals Marine Laboratory are open. As the islands are little used, it is unlikely that the surrounding seaweed assemblages experience high levels of nutrient input compared to those in estuaries and bays. Ocean acidification has a negative effect on calcifying seaweeds and can favour dominance of fleshy seaweeds (Connell & Russell 2010; Porzio, Buia & Hall-Spencer 2011; Dudgeon & Kubler 2015). However, the relationship between CO₂ concentrations and the composition of fleshy seaweed assemblages is still unclear as studies report species-specific and regional specific responses (reviewed in Koch *et al.* 2013). The relative number of open niches in the Gulf of Maine, due to low species richness, may also facilitate the establishment of introduced species (Stachowicz, Whitlatch & Osman 1999).

Regardless of the cause in long-term changes in seaweed composition, the greater densities of filamentous red seaweeds has axiomatically altered the biogenic structure and the biodiversity of lower trophic level groups that occur in these temperate reef ecosystems. Our results indicate that introduced and native species that have similar morphological forms (e.g. filamentous, blade) have similar complexity values and support similar levels of meso-invertebrate biodiversity. Morphological complexity has been shown to be positively correlated with the number of meso-invertebrates (Holmlund, Peterson & Hay 1990; Warfe, Barmuta & Wotherspoon 2008; Veiga, Rubal & Sousa-Pinto 2014; Torres *et al.* 2015, this study). By incorporating percent cover into our calculations of complexity, we found that greater densities of introduced filamentous forms led to a more biogenically complex seaweed habitat that could support two and three times the richness and abundance of lower trophic-level species compared to the native seaweed assemblage (Fig. 4). In contrast to observed greater morphological complexity, our results suggest that canopy height of the habitat has declined due to the overall decline in kelp beds (Fig. 2). This is in contrast to terrestrial systems in which introduced species have led to greater canopy height and little light reaching the understory resulting in fewer understory plant species (Asner *et al.* 2008). While introduced seaweeds are shorter than native ones in this study, they form dense mats that may, due to their densities limit the availability of light that reaches the seafloor which may inhibit recruitment and establishment of newly settled seaweeds and other species.

Meso-invertebrates inhabiting the host species exhibit trade-offs in their host plant choice between nutritional value of the seaweed, the value of the seaweed as a shelter from intense predation, and the availability of palatable seaweed in the environment (Duffy & Hay 1991; Lasley-Rasher *et al.* 2011). They are important members of seaweed assemblages as they can affect ecological processes such as recruitment potential, biofouling, and fish behaviour (Enge, Nylund & Pavia 2013;

Wright *et al.* 2014). Our results indicate that amphipods were the dominant group of species in our samples with the highest percentages found on native and introduced filamentous seaweeds and the native branched seaweed, *C. crispus* (Table 1). Amphipods consume seaweeds and they are important prey for fish species (Ning 1973; Holmlund, Peterson & Hay 1990). As such, they may be deleterious for seaweeds that are the least chemically defended (e.g. *Ulva* spp. or *S. latissima*). Duffy & Hay (1991) demonstrated that herbivores enhanced the growth of red seaweeds while reducing growth of neighbouring brown seaweeds through increased consumption. Enge, Nylund & Pavia (2013) demonstrated that the introduced species, *B. hamifera*, provided a better refuge against fish predation than native seaweeds and suggested it was due to greater toxicity levels in the tissues. The relationship between other herbivorous species such as isopods and grazing on introduced vs. native species is still unclear as studies report increased grazing of native seaweeds in the presence of introduced seaweeds (*B. hamifera*, Enge, Nylund & Pavia 2013) and equal grazing among introduced (*D. japonica*) and native seaweeds (Low *et al.* 2015). Introduced seaweeds may also exert pressure on fish distribution patterns as many fish species tend to consume meso-invertebrates associated with these species (Lazzari & Stone 2006; Severns & Warren 2008). However, lack of a canopy species such as kelp could reduce the complexity of the habitat as perceived by fish and consequently limit their abundance in these habitats. Limited fish abundance may alter trophic interactions by reducing the role of the next trophic level. The observed shift in seaweed composition towards a dominance of complex introduced species can therefore have important consequences for ecosystem function. This is especially true for the Gulf of Maine, a region of relatively low diversity in which additional species may have a larger impact on ecosystem function in this region compared to systems with high species richness. Together these studies, along with ours, suggest that introduced seaweeds have the potential to affect trophic-level interactions as the structure of habitats is a driving force for the networks of feeding interactions (Wonham, O'Conner & Harley 2005; Severns & Warren 2008).

Marine and terrestrial systems are undergoing rapid human-mediated changes in species composition that reflect replacements, additions or losses of habitat-forming species such as kelp whose physical structure provides essential ecosystem services (Hoegh-Guldberg & Bruno 2010). While many variables such as ocean warming, pollution and land development among others can alter the assemblage of species, the introduction of species will directly affect the biogenic structure of the habitat. Such shifts in habitat structure can propagate not only to lower trophic-level species as shown in this study but also to higher level species that utilize these seaweed assemblages and the organisms they support as refuge or for feeding. This is particularly true for benthic marine systems that are thought to have the strongest trophic cascades in nature (Shurin, Borer & Seabloom 2002). In cases where the seaweed assemblage has changed, as has occurred in many rocky subtidal ecosystems around the globe (e.g. Graham 2004;

Connell *et al.* 2008; Wernberg *et al.* 2013), they are likely to result in indirect effects on the structure of food webs.

Authors' contributions

J.A.D. and L.G.H. conceived the idea; J.A.D., K.M., A.L. and C. Ware analysed the data and performed statistical analyses; J.A.D., L.G.H., A.L., K.M. and C.W. collected the data. J.A.D. led the writing with substantial contributions from all authors.

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Data accessibility

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.2kpf51> (Dijkstra 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Long-term (30+ years) survey sites (1979 to 2015) of seaweed assemblages.

Appendix S2. Literature used to obtain and verify supplemental and quadrat data.

Appendix S3. Height sources for Fig. 2.

Appendix S4. Nonparametric test to determine differences in complexity values of seaweeds collected from different sites and their associated meso-invertebrate.

Appendix S5. Nonparametric comparison of complexity values among seaweed species.

Appendix S6. Lunging Island.