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Life history interactions between the red algae *Chondrus crispus* (Gigartinales) and *Grateloupia turuturu* (Halymeniales) in a changing global environment

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ABSTRACT: The invasive rhodophyte *Grateloupia turuturu* is a large perennial alga, discovered first in Narragansett Bay (Rhode Island) in 1994 and subsequently in the Long Island Sound estuary. The alga's low intertidal to shallow subtidal distribution overlaps that of the native *Chondrus crispus*. Our field measurements suggest that physical disturbance may promote increased substrate cover by *G. turuturu*. Molecular quantification of spore abundance suggests *G. turuturu* produces fewer spores, which also disperse shorter distances than spores of *C. crispus*. However, sporelings of *G. turuturu* grew faster than those of *C. crispus* at all environmentally relevant light levels, salinities and temperatures tested. In addition, the temperature tolerance of *G. turuturu* sporelings was broader; *C. crispus* sporelings died just after germination at 30°C; whereas, those of *G. turuturu* survived. The results have implications for community shifts as coastal waters continue to warm into the future.

KEY WORDS: Disturbance, Growth, Nonindigenous species, Reproductive output, Spore, Temperature

INTRODUCTION

Introductions of nonindigenous marine species have increased exponentially as transportation systems have become faster and trade has expanded globally (e.g. Williams *et al.* 2013; Bailey 2015). Human activities, demography (i.e. human population density) and economic factors help explain successful introductions of a diverse group of taxa (Pyšek *et al.* 2010; Zabin *et al.* 2014). These factors are, in fact, proxies for propagule pressure, which determines the number of individuals released into a new habitat (Brawley *et al.* 2009) as well as the reproductive output of new introductions that enable population spread. It is important to note that only a small portion of the introduced species become an invasive species; whereas, most of them are highly restricted in a small area, such as ports or artificial substrata. If the invasion was successful, the introductions pose significant direct threats to biodiversity and may indirectly alter local community composition and influence ecosystem performance and can result in significant economic costs (e.g. Grosholz 2002; White & Shurin 2011; Marbuah *et al.* 2014).

Coastal zones are subject to the highest invasion pressures and concomitant nonnative species loads (e.g. Ruiz & Carlton 2003; Brawley *et al.* 2009). The New England coastline of North America is particularly vulnerable to the introduction of exotic marine species (Kim *et al.* 2016). Its many marine ports and high volume of commercial and

recreational ship traffic elevate the risk for successful introductions of nonnatives. In addition, two biogeographic regimes abut at Cape Cod: the colder Boreal Province occurs to the north of the boundary and the warmer Virginian Province to the south (Lüning 1990). Adjacent to the Cape Cod biogeographic boundary, many species are at the limits of their distributional ranges and are likely susceptible to challenges of competition by newly introduced species.

Many seaweeds have life history characteristics that facilitate successful invasions. For example, seaweeds can grow on surfaces moved by humans (e.g. ships, shellfish), develop through a heteromorphic life history that commonly includes cryptic stages that may tolerate suboptimal conditions, disperse by asexual fragments or numerous asexual or sexual spores, and grow rapidly (e.g. Johnson 2008; Engelen & Santos 2009; Zhang *et al.* 2016). Invasive marine macroalgae can have serious ecological and economic impacts. For example, *Sargassum muticum* (Yendo) Fensholt, a phaeophyte introduced from Japan, drove significant changes in autotroph community structure along the shores of Western Europe (Salvaterra *et al.* 2013; Davidson *et al.* 2015). Indirect effects included declines in native urchin populations (Britton-Simmons 2004). A diet rich in the invasive *Caulerpa cylindracea* Sonder altered muscle fatty acid composition in the culturally valuable white sea bream (*Diplodus sargus* Linnaeus; Felling *et al.* 2014).

Recent work has suggested that certain life history characteristics can help explain why some introduced species rapidly spread and flourish while others do not (Nettleton *et al.* 2013). For example, the invasive seaweed *Gracilaria vermiculophylla* (Ohmi) Papenfuss has a broad temperature (5°C–34°C) and salinity (5–30 psu) tolerance; whereas, the

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native *G. tikvahiae* cannot withstand prolonged exposures to salinities of ≤ 20 psu and temperatures of $\leq 10^{\circ}\text{C}$ or $\geq 34^{\circ}\text{C}$ (Kim *et al.* 2016). Generally speaking, broad tolerance of environmental variability may enable nonnatives to successfully invade environmental refuges from competition by natives (Salvaterra *et al.* 2013).

The rhodophyte *Grateloupia turuturu* Yamada (formally *Grateloupia doryphora*) is a large perennial red alga, native to the Pacific but introduced with imported oysters onto the coast of France in the 1960s (Gavio & Fredericq 2002) and extended to neighbouring countries, the United Kingdom (Hardy & Guiry 2003), Spain (Araújo *et al.* 2003), Portugal (Araújo *et al.* 2003), Italy (Sordo *et al.* 2011) and the Netherlands (Stegenga *et al.* 2007). The first record of *G. turuturu* in the northwestern Atlantic came from Narragansett Bay in 1994 (Villalard-Bohnsack & Harlin 1997, 2001). The seaweed spread subsequently south into Long Island Sound; in September 2004, it was discovered at Millstone Point, Waterford, Connecticut (John Swenarton, personal communication). In October 2014, *G. turuturu* was reported in Greenwich, Connecticut, at the New York border (Roger Bowen & M. Van Patten, personal communication).

Grateloupia turuturu has the potential to grow to large size; individual thalli of 3000 cm² have been reported (Villalard-Bohnsack & Harlin 2001; cf. <http://www.algae.uconn.edu>). This species flourishes under eutrophic conditions and under a range of wave exposures and salinities, making it a nonindigenous species of concern (Simon *et al.* 1999). Observations on the coasts of the northeastern United States, France, the British Isles and northeastern Taiwan describe a zonation pattern with *G. turuturu* present in the upper subtidal to low intertidal zones (e.g. Simon *et al.* 2001; D'Archino *et al.* 2007). *Grateloupia turuturu* co-occurs with Irish moss (*Chondrus crispus* Stackhouse) in the lower intertidal zone of protected to moderately exposed rocky shores. Morphologically, these potential competitors differ, with *C. crispus* more structurally complex than the simple foliose *G. turuturu*. Hu & Juan (2014) reported that *G. turuturu* alters interspecific competition and habitat complexity, and transforms biogeochemical cycles and estuarine food webs in ways that can be both positive and negative. Though Maggi *et al.* (2015) concluded generally that negative effects of nonnative seaweeds are likely most pronounced within the same trophic level, Janiak & Whitlatch (2012) reported negative effects on mesoepifaunal invertebrates, and Hu & Juan (2014) reported avoidance of *G. turuturu* by invertebrate grazers.

Periodic or exceptional disturbance can alter interactions among competitors. Major disturbance to intertidal seaweed communities occurs when storm-generated waves overturn substrate (e.g. Sousa 1979; Scrosati & Heaven 2008; Scheibling *et al.* 2009). This mortality frees up resources and can allow competitively inferior species to persist (e.g. Dayton 1971). In addition to competition for resources (attachment space, light and nutrients), reproductive output will also mediate long-term competitive outcomes. Spore release and dispersal is one mechanism for the spread of a nonnative species like *G. turuturu*. Many marine macroalgae have dispersal ranges estimated to be hundreds of meters [e.g. *Laminaria hyperborea* (Gunnerus) Foslie spore dispersal ≥ 200 m; Fredriksen *et al.* 1995; Gaylord *et al.* 2006].

However, like those of other rhodophytes, spores of *G. turuturu* lack flagella. This lack of motility could limit spore dispersal. Red algae such as *Gracilaria gracilis* (Stackhouse) M. Steentoft, L.M.Irvine & W.F.Farnham and *Gracilaria longissima* (S.G.Gmelin) M.Steentoft, L.M.Irvine & W.F.Farnham have directly measured spore dispersal ranges of only 1–3 m (Kinlan & Gaines 2003).

The goal of this project was to describe potential interactions of *G. turuturu* with *C. crispus* at two sites in Long Island Sound – Waterford and Groton, Connecticut – where *C. crispus* is a dominant species in the lower intertidal and upper subtidal zones. The *Chondrus*-dominated habitats have a poor algal species richness; although, the total macroalgal biomass was high (Garbary *et al.* 2011; Janiak & Whitlatch 2012). The specific objectives were to compare the substrate cover of *G. turuturu* and *C. crispus* on stable and unstable substrates, to compare spore output by *G. turuturu* and its native competitor *C. crispus*, to measure spore dispersion to gauge the general capacity for the spread of the *G. turuturu* and to determine the abilities of *G. turuturu* and *C. crispus* sporelings to grow under light, temperature and salinity regimes characteristic of estuarine conditions.

MATERIAL AND METHODS

Permanent quadrats were established on stable rock platforms in the lower intertidal zone of two sites: Millstone Point, Waterford, Connecticut ($n = 20$; site MP-P; $41^{\circ}18'21''\text{N}$, $72^{\circ}09'41''\text{W}$), and the University of Connecticut–Avery Point Marine Sciences campus, Groton, Connecticut (site AP-P; $41^{\circ}18'56''\text{N}$, $72^{\circ}03'45''\text{W}$). The MP-P site is characterised by water temperatures that are *c.* 2°C higher than AP-P due to the discharge of cooling water from the Dominion Resources nuclear power plant (M. Keser, personal communication). Thermal discharge from power plants may act as a gateway for the successful introduction of aquatic invasive species (Hyytiäinen *et al.* 2013). At the MP-P site, 20 quadrats (0.25 m²) were sampled from January to April 2007 and 18 from April 2007 through June 2008. At the AP-P site, eight quadrats were sampled from April to September 2007 and 25 quadrats from October 2007 to March 2008. On each date, the percent cover of *G. turuturu* and *C. crispus* was assessed visually by the same field technician. The technician estimated the percent of the 0.25-m² quadrat covered by each of the two species. In addition, over the course of the study, this technician collected samples of the diverse visible macroalgae for identification in the laboratory.

The role of physical disturbance and substrate instability was evaluated using quadrats placed in the lower intertidal area dominated by cobble-size substrate at MP ($n = 24$). The quadrat location along the cobble beach was randomly assigned each month. Quadrats (0.25 m²) were used to estimate percent cover from July 2006 to June 2008 at the MP-C site.

The extent of the spore cloud released by the two rhodophytes was assessed from 1-litre water samples obtained monthly at MP during the outgoing tide at 0.1, 1, 10 and 100 m where *G. turuturu* and *C. crispus* co-occur

Table 1. Primers used in the study to quantify the density of *Grateloupia turuturu* and *Chondrus crispus* spores.

Primer name	Sequence (5'–3')	Application
18SCOMF ¹	TGCATGGCCGTTCTTAGTTGGTGG	PCR of 18S–28S
com28SR1 ²	TCACGCATAGTTCACCATCTTTTCG	PCR of 18S–28S
com28SR2 ²	TTAGACTCCTTGGTCCGTGTTT	PCR of 18S–28S
G_turF1 ³	GATGGGTGGAGGAGTCTAAGTG	qPCR
G_turF2 ³	GAGTCTAAGTGCTTCTCGTATTGTC	qPCR
G_turR1 ³	ACTGCAATGAAAAAAGTGTAAAAAAACTC	qPCR
G_turR2 ³	TCCAGTCGCAATCCTTCTAACC	qPCR
C_crispusF1 ³	GCTTTGTATGGGGATGTTGTTCTTG	qPCR
C_crispusF2 ³	GCAGAGCGGTTGTGGAAGG	qPCR
C_crispus1 ³	CAATGAAGACCCGTCTTTTCCTTTC	qPCR
C_crispusR2 ³	ATGTTATAGTGGTTTATGTTACAATGAAGAC	qPCR

¹ Zhang & Lin (2002).² Wang *et al.* (2014).³ This study.

along the shoreline (one 1-litre sample at each distance on each date). Water samples were filtered to isolate the 3–200- μ m size fraction. DNA extracted from macroalgal samples of each species was subjected to polymerase chain reaction (PCR) following methods of Zhang & Lin (2002). Species-specific primers for these two species were developed in ITS2 based on a multialignment of ITS1–5.8S–ITS2 regions of *G. turuturu* with those from *C. crispus* and other algae and more than 100 phytoplankton species available from GenBank. We chose the ITS2 region because it offers sufficient variation to allow distinction of even very closely related species (see Wang *et al.* 2014 and the references therein). The primers designed were first blasted against the GenBank database to confirm their specificity, then tested against more than 50 phytoplankton DNA samples in our lab (e.g. Zhang *et al.* 2007). The PCR products resulting from samples were directly sequenced to confirm species identity of the DNA sample. If polymorphism was detected, indicating the presence of multiple species, the PCR products were cloned, and 10 clones from each sample were randomly chosen for sequencing. The abundance of spores was quantified via a real-time quantitative PCR (qPCR) assay (Zhang & Lin 2005) using the species-specific primers and an enumerated culture sample of *G. turuturu* or *C. crispus* spores as a standard. Primers used in this study are shown in Table 1.

The responses of *G. turuturu* and *C. crispus* to the primary determinants of early growth (light, temperature and salinity) were evaluated through the early germling state. Tetraspores of each species were seeded at constant density (c. 50 spores cm^{-2}) onto glass slides, which were then cultured in environmentally controlled growth chambers at the University of Connecticut–Stamford using filtered, autoclaved seawater enriched with Von Stosch culture medium (Yarish & Edwards 1982). After spore germination, cell division generated circular crusts (e.g. Adharini & Kim 2014). Early growth of germlings was evaluated at six temperatures (5°C, 10°C, 15°C, 20°C, 25°C and 30°C), all under 50 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ and 27 psu. Additionally, growth was measured as a function of light intensity (25, 50 and 100 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) at 20°C and 35 psu and as a function of salinity (10, 15, 20, 25 and 30 psu) at 50 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ and 20°C. These values of light, temperature and salinity span a typical estuarine range. Three to five replicate slides were grown in separate vessels for each

treatment combination. Measurements of the size (largest dimension) of 30 haphazardly selected germlings per slide (out of 900–1000) were made via microscopy at $\times 40$ after 1, 2, 4, 8 and 16 days' growth.

The method of analysis of the population data was influenced by data variability and sampling method. The variances of both the randomly collected (unstable cobble) and the repeated samples (stable platform) data sets were not constant among samples from the same date, nor were variances of *C. crispus* and *G. turuturu* percent cover similar. Additionally, monthly estimates of cover were nonnormally distributed. This heteroscedasticity and nonnormality could not be rectified via transformation. Therefore, nonparametric statistics were applied to evaluate differences in *C. crispus* and *G. turuturu* cover and differences between the two sites.

Because our interests centred on the interaction of populations of *C. crispus* and *G. turuturu* at these sites, we analysed data pooled across the duration of the study. Mann–Whitney rank sum tests compared *C. crispus* and *G. turuturu* cover within the randomly sampled quadrats on the unstable cobble substrate at MP. Wilcoxon signed rank tests compared *C. crispus* and *G. turuturu* cover at each stable platform site. The Wilcoxon test also compared the MP and AP sites for each species. Data from the stable platform and unstable cobble substrates at the MP site could not be compared statistically due to different sampling protocols (random sampling for cobble substrate, repeated sampling for platform).

The water samples collected for determination of spore abundance were not replicated on each sampling date. We examined the dispersal of spores by standardising the abundance at 1, 10 and 100 m to the abundance at 0.1 m (the source) for each species. These relative abundances were regressed on ln-transformed distance from the source. Similarly, the relative abundance of spores of the two species was assessed as a ratio (*Chondrus:Grateloupia*) at each distance from the shoreline source.

To determine the effects of temperature, salinity and irradiance on germling growth, the sizes of the 30 germlings measured on each replicate slide were averaged and plotted against elapsed time (days). These data ($n = 3$ measurements per date) were fit to an exponential growth curve

$$S = a \cdot e^{(\text{GR} \cdot \text{ET})}$$

Table 2. Macroalgal species recorded within sample quadrats at Millstone Point and Avery Point sites during the estimation of the *Grateloupia turuturu* and *Chondrus crispus* population levels (July 2006–May 2007).

Species	Taxonomic group	Unstable cobble	Stable rock platform
<i>Grateloupia turuturu</i> Yamada	Rhodophyta	•	•
<i>Chondrus crispus</i> Stackhouse	Rhodophyta	•	•
<i>Neosiphonia harveyi</i> (J.W.Bailey) M.-S.Kim, H.-G.Choi, Guiry et G.W.Saunders in H.-G.Choi	Rhodophyta	•	•
<i>Ceramium virgatum</i> Roth	Rhodophyta	•	•
<i>Dasya baillouviana</i> (S.G.Gmelin) Montagne	Rhodophyta	•	•
<i>Agardhiella subulata</i> (C.Agardh) Kraft et M.J.Wynne	Rhodophyta	•	•
<i>Hypnea musciformis</i> (Wulfen) J.V.Lamouroux	Rhodophyta	•	•
<i>Corallina officinalis</i> Linnaeus	Rhodophyta		•
<i>Pyropia leucosticta</i> (Thuret) Neefus & J.Brodie	Rhodophyta		•
<i>Antithamnion pectinatum</i> (Montagne) J.Brauner	Rhodophyta		•
<i>Ulva lactuca</i> Linnaeus	Chlorophyta	•	•
<i>Ulva intestinalis</i> Linnaeus	Chlorophyta	•	•
<i>Ulva linza</i> Linnaeus	Chlorophyta		•
<i>Chaetomorpha melagonium</i> (F.Weber & D.Mohr) Kützing	Chlorophyta		•
<i>Codium fragile</i> Suringar	Chlorophyta		•
<i>Sargassum filipendula</i> C.Agardh	Phaeophyta	•	•
<i>Petalonia fascia</i> (O.F.Müller) Kuntze	Phaeophyta	•	•
<i>Fucus vesiculosus</i> Linnaeus	Phaeophyta		•
<i>Scytosiphon lomentaria</i> (Lyngbye) Link	Phaeophyta		•

where S represents the germling size, *a* is a constant, GR is the growth rate (day⁻¹) and ET = elapsed time (days). *R*² values for all regressions averaged 0.97. Growth rate data (i.e. the exponent GR) met assumptions for analysis of variance and were compared across species and each environmental factor.

RESULTS

Field population data

Nineteen macroalgal species were identified at the stable rock platform site (Table 2). Species richness was about 40% lower at the unstable cobble sites, where only 11 species were recorded. The abundance of both *G. turuturu* and *C. crispus* on the unstable cobble substrate varied greatly over the course of 2 years at the MP unstable cobble site (Fig. 1, upper panel). The effects of the passage of Hurricane Barry (on-site 4 June 2007) are visible in the reduction of the combined cover of *G. turuturu* and *C. crispus* from 35% before the storm in May to < 1% 4 days after. During the 4 months after this disturbance, the cover of *G. turuturu* increased greatly. *Chondrus crispus*, however, did not recover to prestorm levels for about 6 months. Averaged over the entire sampling period, *G. turuturu* occupied c. 8% of the unstable cobble substrate; whereas, *C. crispus* occupied c. 10% of the substrate. The percent cover of *C. crispus* and *G. turuturu* did not differ significantly (data pooled over the course of the study; Mann–Whitney *U* = 82,760, *n* = 408, *P* = 0.88; Fig. 2; Table 3).

The temporal pattern of percent cover on the two substrate types at the AP stable platform site differed (Fig. 1; Table 3). In general, *G. turuturu* and *C. crispus* cover on the unstable cobble substrate (uppermost panel) showed much greater intra- and intermonth variability compared with the stable rock platform (middle panel).

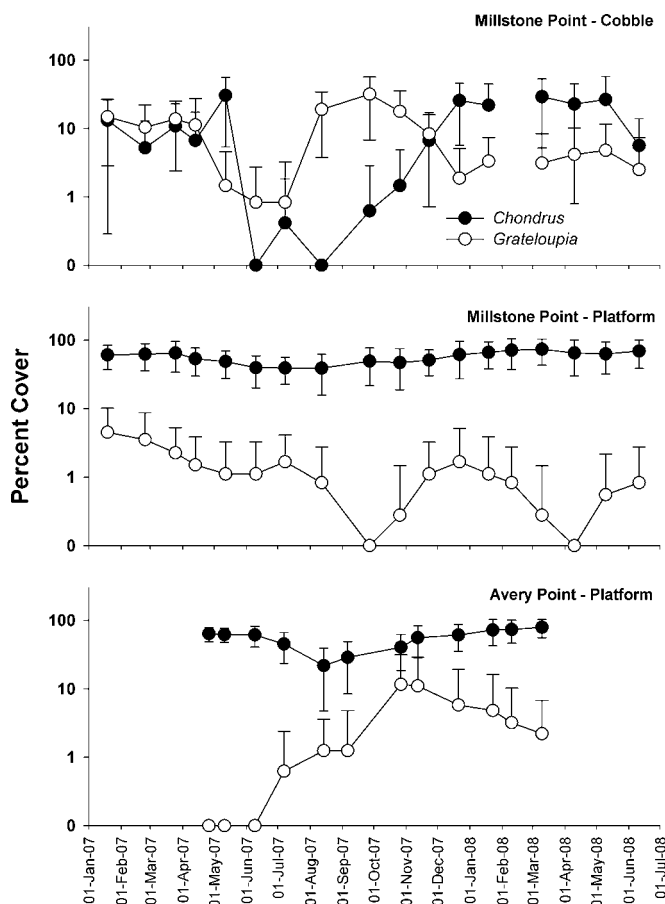


Fig. 1. Percent cover for the native *Chondrus crispus* and nonnative *Grateloupia turuturu* obtained from quadrats at the Millstone Point cobble beach (unstable; MP-C; *n* = 24), Millstone Point rocky platform (stable; MP-P; *n* = 20) and Avery Point rock platform (stable; AP-P; *n* = 8–25) sites. Values represent averages drawn from 20 replicate quadrats. Symbols on the horizontal axis represent true averages of 0% cover.

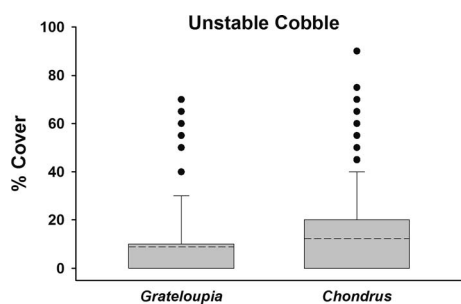


Fig. 2. Box-and-whisker plot of percent cover data pooled over the course of the study at the Millstone Point unstable cobble site. Dashed line represents the median value, and black circles represent those data outside of the 5th and 95th percentiles. Percent cover of *Chondrus crispus* and *Grateloupia turuturu* did not differ significantly at this site.

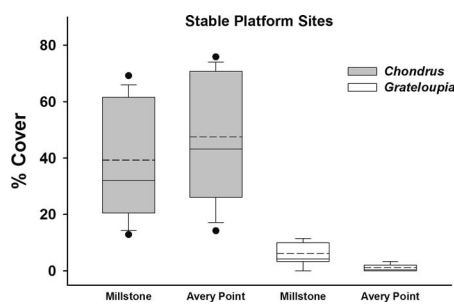


Fig. 3. Box-and-whisker plot of percent cover data pooled over the course of the study at the stable rock platform sites at Millstone Point and Avery Point. Dashed line represents the median value, solid line represents those within the box represents the mean value and black circles represent those data outside of the 5th and 95th percentiles. See the text for the results of interspecific and intersite comparisons.

Substrate cover of *G. turuturu* at both stable platform sites (Fig. 1, middle and lower panels) was generally more variable than that of *C. crispus*. Cover of the native (*C. crispus*) declined slightly into the summer months at both the Millstone and the AP stable platform sites (note the log scaling). The percent cover of *C. crispus* was significantly greater than that of *G. turuturu* at both stable platform sites (Z values for both sites = 3.72, $P < 0.001$; Table 3). Cover of *C. crispus* was significantly greater at the AP stable platform site than at the MP platform site (median values 32% and 43%, respectively; $Z = 3.296$; $P < 0.001$); whereas, *G. turuturu* was more abundant at the MP stable platform site (median values 4.3% and 0.4%, respectively; $Z = 3.063$, $P < 0.001$). The impact of Hurricane Barry (4 June) was not apparent for either species at either stable platform site (Fig. 1). Stable substrate appeared to favor *C. crispus*; over the common sampling period (April 2007–March 2008), the native rhodophyte occupied 57% and 55% of the substrate at the MP and AP sites, respectively. Over the same period, *G. turuturu* covered only 1.3% and 3.5% at the same sites.

Spore abundance

Spores of *G. turuturu* were relatively more abundant at three points during the study: October, January and May (Fig. 4, upper panel). *Chondrus crispus* revealed only a mid-September peak (Fig. 4, lower panel). On several occasions, the spore densities of both species were higher at 1 and 10 m than adjacent to the bed (0.1 m). Spores of *C. crispus* were more abundant at all distances from the source algal beds than those of *G. turuturu* (Fig. 5); the average abundance of spores of *C. crispus* at 0.1 m from the algal bed was 61 times greater than that of *G. turuturu*; whereas, the disparity increased to 680-fold greater at 100 m distant.

The relative abundances of spores of the two species differed moving away from the shoreline. Although the density of spores of both species was, on average, greatest at 0.1-m distance from the intertidal zone, *C. crispus* spores appeared to disperse farther than those of *G. turuturu* (Fig. 6). The decline in spore density with increasing distance was more rapid for *G. turuturu* than for *C. crispus*; the log-linear regression model predicted a 75% drop in spore density of *C. crispus* at about 85 m from the shore; whereas, the same reduction for *G. turuturu* occurred within only 11 m of the longshore algal bed (Fig. 6). Consequently, the relative abundance of spores of *C. crispus*, compared with *G. turuturu*, increased with distance from the intertidal algal beds (Fig. 5).

Germling growth

Temperature had a significant effect on the growth of crusts of both species ($F_{4,27} = 251$, $P < 0.001$; Fig. 7; Table 4). On average, growth rates were highest at 20°C. *Grateloupia turuturu* germlings grew significantly faster than those of *C. crispus* at 15°C–30°C though not at 5°C and 10°C. The rates of postgermination growth of *G. turuturu* were 44%, 62% and 98% greater at 15°C, 20°C and 25°C, respectively, than those of *C. crispus*. Germlings of *C. crispus* died within 2 days at 30°C; whereas, *G. turuturu* continued to grow at 30°C at rates similar to those at 15°C. Neither irradiance nor salinity had a significant main effect on germling growth ($F_{2,11} = 1.76$, $P = 0.22$, and $F_{4,20} = 1.77$, $P = 0.17$, respectively). However, early germling growth of *G. turuturu* was significantly faster than that of *C. crispus* at all salinities ($F_{1,20} = 55.9$, $P < 0.001$) and light levels ($F_{1,11} = 419$, $P < 0.001$) tested (Fig. 7; Table 4). On average in the salinity experiment, *G. turuturu* grew 50% faster than *C. crispus*; whereas the invasive species also outgrew the native by an average of 70% across the three light levels.

Table 3. Results of statistical analyses of population (percent cover) data. Data pooled over the course of the study.

Millstone Point unstable cobble substrate	<i>Chondrus crispus</i> vs <i>Grateloupia turuturu</i>	<i>Chondrus</i> > <i>Grateloupia</i> ; $P = 0.88$
Millstone Point stable platform substrate	<i>C. crispus</i> vs <i>G. turuturu</i>	<i>Chondrus</i> > <i>Grateloupia</i> ; $P < 0.001$
Avery Point stable platform substrate	<i>C. crispus</i> vs <i>G. turuturu</i>	<i>Chondrus</i> > <i>Grateloupia</i> ; $P < 0.001$
<i>Chondrus crispus</i>	Millstone Point vs Avery Point (stable substrate)	Avery > Millstone; $P < 0.001$
<i>Grateloupia turuturu</i>	Millstone Point vs Avery Point (stable substrate)	Millstone > Avery; $P < 0.001$

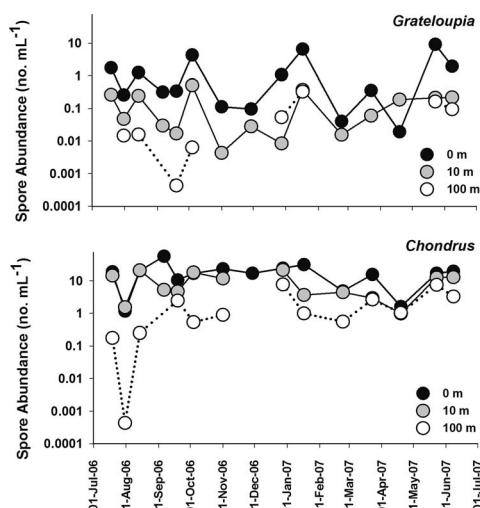


Fig. 4. Spore density of the native *Chondrus crispus* and nonnative *Grateloupia turuturu* as a function of distance from a mixed *C. crispus*-*G. turuturu* bed along the coast at the Millstone Point site.

DISCUSSION

Classical ecological theory argues that primary producers with overlapping distributions, like *G. turuturu* and *C. crispus*, compete for resources (Elton 1958). For a wide variety of organisms, the outcome of competitive interactions is now understood to be context dependent (i.e. mediated by environmental conditions; Olson & Lubchenco 1990; Stachowicz & Hay 1999; Chamberlain *et al.* 2014). The role played by substrate stability in influencing seaweed communities has been reported previously (Richardson 1979; Davis & Wilce 1987; Scheibling *et al.* 2009; Sangil *et al.* 2015). The population monitoring at the MP cobble and MP platform sites supported this idea of context dependence; substrate stability strongly influenced space occupancy, with *C. crispus* dominating the stable rock platforms at both the MP and the AP site and *G. turuturu* having variable but slightly greater success during the study on the unstable cobble (Fig. 1). The effects of physical disturbance in the present study were also apparent at the community level, with the number of macroscopic algal taxa recorded at the unstable cobble site only 58% of that recorded at the adjacent stable platform. Harlin & Villalard-Bohnsack (2001) suggested that lower percent cover by *G. turuturu* at a site with smaller cobble was the result of more frequent and/or severe disturbances, in general agreement with the conclusion by Britton-Simmons & Abbott (2008) that the invasion success of *S. muticum* was determined by the clearing of substratum by disturbance, in combination with the degree of propagule pressure. The periodic, wave-driven overturning of cobbles is a disturbance causing mortality of organisms and clearly created opportunity for *G. turuturu*. This was evident on the cobble substrate for the 4 months following the passage of the remnants of Hurricane Barry (Fig. 1). Valentine *et al.* (2007) examined the literature for clues to successful invasion by nonnative seaweeds and report that physical disturbance facilitates establishment and spread of some species. Bertocci *et al.* (2015) reported that high-intensity disturbance enabled *c.* 20 times greater

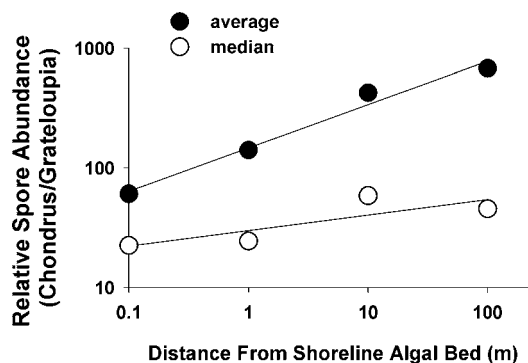


Fig. 5. *Chondrus crispus* spore abundance divided by *Grateloupia turuturu* spore abundance as a function of distance from source algal bed.

substrate cover by *G. turuturu* compared with the control. The unstable cobble substrate in the present study lent itself to physical disturbance that facilitates greater success of *G. turuturu*.

The degree of seasonality evident in the space occupied by *G. turuturu* in Narragansett Bay, Rhode Island (Harlin & Villalard-Bohnsack 2001), was not seen in our study. Though the substrate was similar to that of the present study (cobbles, boulders and bedrock), Harlin & Villalard-Bohnsack (2001) reported up to 70% substrate covered by *G. turuturu*. Given the embayment location of those sites, the degree of physical disturbance was likely less than at either of our more wave-exposed sites. This lends further support to the idea that the success of *G. turuturu* on the northeastern US coast is dependent on the environmental context.

The global increase in temperature has also influenced interactions among species and driven changes in species ranges (Sagarin *et al.* 1999; Johnson *et al.* 2011). Seaweed species are shifting poleward, though not at the same rate, and community compositions have changed (e.g. Wernberg *et al.* 2011; Harley *et al.* 2012). The waters of Long Island Sound have warmed by *c.* 0.4°C decade⁻¹ from 1979 to 2002 (though the January–March rate of increase was 0.6°C decade⁻¹; Keser *et al.* 2005), making temperature-driven changes in the primary producer community a likely future trend. A 10-year study by Schiel *et al.* (2004), for example,

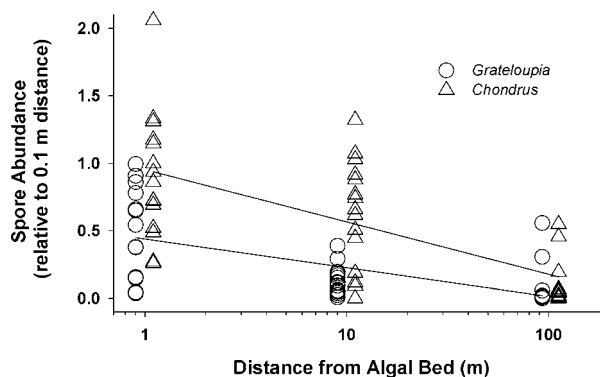


Fig. 6. Spore density of each species as a proportion of the species' spore DNA abundance at 0.1 m from the longshore source algal bed on the same day.

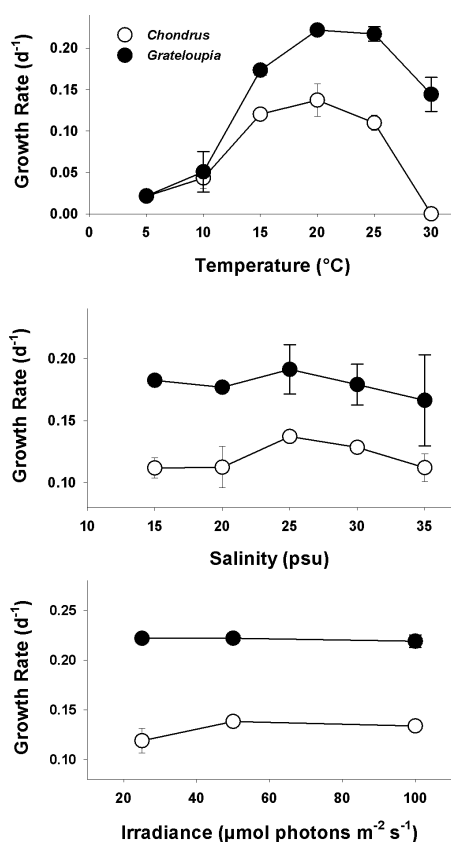


Fig. 7. Rate of growth of sporelings over the 16-day postgermination period as a function of temperature (top panel), salinity (middle) and irradiance (bottom). $n = 3-5$ replicates per treatment. Error bars (s) often smaller than symbol (e.g., *Grateloupia turuturu* grown at 15°C, 20°C and 25°C). All *Chondrus crispus* sporelings died within 2 days after germination at 30°C.

reported decline in abundance of less than half of the intertidal plant and animal taxa. The AP-P and MP-P sites provide a qualitatively similar comparison, with the MP site *c.* 2°C warmer than the nearby AP site. During the period of sampling overlap at the two sites (April 2007–March 2008), the substrate covered by *G. turuturu* at the warmer MP site (0.96% on average) was only about one-third of cover at the cooler AP site (3.5%). However, though separated by less than 10 km, we cannot be sure that both sites were invaded by *G. turuturu* contemporaneously.

Spore dispersal and eventual recruitment onto hard substrate is required for the maintenance as well as the spread of a population of an introduced alga (Bobadilla & Santelices 2005). Based on Mathieson’s (1982) results, our spore data likely represent a combination of tetraspore and carpospore release, with the late summer peak probably carposporic. Spore dispersal from reproductively mature *G. turuturu* thalli is an important part of the life cycle, and understanding the spread of this nonnative species requires more knowledge of dispersal dynamics. The density of the algal stand (Santelices 1990), the numbers of spores produced by individual thalli, the spore sinking rate (a function of spore diameter) and water motion (Brennan *et al.* 2014) will all influence the movement of the spore shadow (also known as the spore cloud).

Table 4. Results of statistical analyses of germling growth rates.

Outcome			
Source	ν	F	P
Response of germling growth rate to temperature			
Temperature	4	251	$P < 0.001$
Species	1	158	$P < 0.001$
Temperature \times species	4	26.4	$P < 0.001$
Residual	27		
Total	36		
	<i>Chondrus crispus</i>	<i>Grateloupia turuturu</i>	
Comparisons via Fisher LSD test (mean growth rates; % day ⁻¹)			
5°C	2.1	2.2	$P = 0.97$
10°C	4.3	5.1	$P = 0.40$
15°C	12.0	17.4	$P < 0.001$
20°C	13.7	22.2	$P < 0.001$
25°C	11.0	21.7	$P < 0.001$
30°C*	0	14.4	$P < 0.001$
* One-sample <i>t</i> test of <i>G. turuturu</i> average growth rate vs 0.			
Source	ν	F	P
Response of germling growth rate to light			
Light	2	1.76	$P = 0.22$
Species	1	419	$P < 0.001$
Light \times species	2	2.33	$P = 0.14$
Residual	11		
Total	16		
	<i>C. crispus</i>	<i>G. turuturu</i>	P
Comparisons via Fisher LSD test (mean growth rates; % day ⁻¹)			
25 $\mu\text{mol m}^{-1} \text{s}^{-1}$	11.9	22.2	$P < 0.001$
50 $\mu\text{mol m}^{-1} \text{s}^{-1}$	13.8	22.2	$P < 0.001$
100 $\mu\text{mol m}^{-1} \text{s}^{-1}$	13.3	21.9	$P < 0.001$
Source	ν	F	P
Response of germling growth rate to salinity			
Salinity	4	1.77	$P = 0.17$
Species	1	55.9	$P < 0.001$
Salinity \times species	4	0.24	$P = 0.91$
Residual	20		
Total	29		
	<i>C. crispus</i>	<i>G. turuturu</i>	P
Comparisons via Fisher LSD test (mean growth rates; % day ⁻¹)			
15 psu	11.2	18.2	$P < 0.001$
20 psu	11.2	17.7	$P < 0.001$
25 psu	13.7	19.1	$P < 0.001$
30 psu	13.0	17.9	$P < 0.001$
35 psu	11.1	16.6	$P < 0.001$

This reproductive output has contributed to the spread of *G. turuturu* in the northwestern Atlantic (average rate *c.* 21 km year⁻¹; Lyons & Scheibling 2009). By 2007, 11 years after its discovery in Narragansett Bay (Villalard-Bohnsack & Harlin 1997), *G. turuturu* was reported near Boston, its range expansion probably also facilitated by hull-attached thalli moving with coastal ship traffic (Mathieson *et al.* 2008). By 2013, *G. turuturu* was reported from surveys along the southern coast of Maine (Mathieson, personal communication). In 2014, *G. turuturu* was reported in Greenwich, Connecticut (R. Bowgen & M. Van Patten, personal communication), about 120 km from the MP study site. This range extension within Long Island Sound occurred over roughly 6 years, close to that predicted by the average rate reported by Lyons & Scheibling (2009). Though spore dispersal contributed to the observed spread, the relative importance of ‘jump’ dispersal cannot be ruled out, especially since the possibility of recreational boating as a vector remains unexplored for this species (Kinlan & Gaines

2003; Wilson *et al.* 2009; Clarke Murray *et al.* 2011, 2014; Zabin *et al.* 2014).

The spread and eventual impact of *G. turuturu* will be determined by the interactions among life history characteristics (e.g. magnitude and periodicity of spore production), environment and roles of animals, including grazing by herbivores and facilitation of the spread by humans. The recruitment of spores from the water column, followed by germination and growth of perennating crusts, promotes the spread. Macroalgal species differ with respect to dispersal (Lyons & Scheibling 2009), with reports of spore dispersal distances quite variable; Santelices (1990) estimated 40 m for spores of *Macrocystis pyrifera*, Kinlan & Gaines (2003) suggested a range of 1–1000 m for macroalgae in general, and Amsler & Searles (1980) reported ‘*Enteromorpha*’ (now *Ulva*) spores 35 km from the nearest source. The presence of more spore DNA at 1 and 10 m than adjacent to the bed (0.1 m) suggests suspended spores derived from other locations and/or prior days.

The presence of *G. turuturu* in tide pools (e.g. Simon *et al.* 2001) as well as subtidally is evidence for broad salinity, temperature and light tolerances. Measurements of the rates of photosynthesis and respiration support this. Dudgeon *et al.* (1995) reported the temperature dependence of net photosynthesis for *C. crispus* that is qualitatively similar to our patterns of sporeling growth. Simon *et al.* (1999) found photosynthesis:respiration ratios highest at 34 psu, with significant rates of the net photosynthetic rate (P_{net}) at both 22 and 12 psu. Mathieson (1982) reported very similar growth from 15 to 40 psu at lower temperatures (3°C and 11°C). Our data showing similar sporeling growth rates from 15 to 35 psu support this. We are unsure why culture irradiance did not produce a strong influence on growth in our experiments since others have reported stimulation of postgermination growth at irradiances of 30–90 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (Mathieson 1982; Wei *et al.* 2013).

Physical disturbance also appeared important in determining success. We found strong differences between *G. turuturu* and *C. crispus* in early sporeling growth, with the former outgrowing the latter under most tested conditions of temperature, salinity and irradiance. A question unanswered by the current study is why *G. turuturu* has not outcompeted *C. crispus* under field conditions, requiring instead physical disturbance to enable occupancy of more than a few percent of the substrate. The substrate structure (e.g. boulder size) may be a key for a population change (Garbary *et al.* 2012). Smaller boulders are too mobile; whereas, larger ones develop longer-lived perennials. The continued dominance of *C. crispus* may be due to different growth kinetics of adult thalli, grazer preference for the nonnative (i.e. the inverse of Monteiro *et al.* 2009) and/or greater propagule pressure and more effective dispersal. The latter is supported by a conclusion by Mathieson (1982) that sustained output of spores, both tetra- and carpospores, describes the successful reproductive strategy of *C. crispus*. In the absence of an altered disturbance regime, the negative impacts of *G. turuturu* may, therefore, be limited to small-scale (m^2) patches where the invader has been able to obtain a foothold.

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REFERENCES

- ADHARINI R.I. & KIM H.G. 2014. Developmental pattern of crust into upright thalli of *Grateloupia asiatica* (Halymeniaceae, Rhodophyta). *Journal of Applied Phycology* 26: 1911–1918.
- AMSLER C.D. & SEARLES R.B. 1980. Vertical distribution of seaweed spores in a water column offshore of North Carolina. *Journal of Phycology* 16: 617–619.
- ARAÚJO R., BÁRBARA I., SANTOS G., RANGEL M. & SOUSA PINTO I. 2003. Fragmenta Chorologica Occidentalia, Algae, 8572–8640. *Anales del Jardín Botánico de Madrid* 60: 405–409.
- BAILEY S.A. 2015. An overview of thirty years of research on ballast water as a vector for aquatic invasive species to freshwater and marine environments. *Aquatic Ecosystem Health & Management* 18: 261–268.
- BERTOCCI I., GODINO J.D., FREITAS C., INCERA M., ARAÚJO R., BIO A., ARENAS F., SOUSA-PINTO I., REIS P.A. & DOMÍNGUEZ R. 2015. The regime of climate-related disturbance and nutrient enrichment modulate macroalgal invasions in rock pools. *Biological Invasions* 17: 133–147.
- BOBADILLA M. & SANTELICES B. 2005. Variations in the dispersal curves of macroalgal propagules from a source. *Journal of Experimental Marine Biology and Ecology* 327: 47–57.
- BRAWLEY S.H., COYER J.A., BLAKESLEE A.M., HOARAU G., JOHNSON L.E., BYERS J.E., STAM W.T. & OLSEN J.L. 2009. Historical invasions of the intertidal zone of Atlantic North America associated with distinctive patterns of trade and emigration. *Proceedings of the National Academy of Sciences* 106: 8239–8244.
- BRENNAN G., KREGTING L., BEATTY G.E., COLE C., ELSÄER B., SAVIDGE G. & PROVAN J. 2014. Understanding macroalgal dispersal in a complex hydrodynamic environment: a combined population genetic and physical modelling approach. *Journal of the Royal Society Interface* 11: 20140197.
- BRITTON-SIMMONS K.H. 2004. Direct and indirect effects of the introduced alga *Sargassum muticum* on benthic, subtidal communities of Washington State, USA. *Marine Ecology Progress Series* 277: 61–78.
- BRITTON-SIMMONS K.H. & ABBOTT K.C. 2008. Short-and long-term effects of disturbance and propagule pressure on a biological invasion. *Journal of Ecology* 96: 68–77.
- CHAMBERLAIN S.A., BRONSTEIN J.L. & RUDGERS J.A. 2014. How context dependent are species interactions? *Ecology Letters* 17: 881–890.
- CLARKE MURRAY C., PAKHOMOV E.A. & THERRIAULT T.W. 2011. Recreational boating: a large unregulated vector transporting marine invasive species. *Diversity and Distribution* 17: 1161–1172.
- CLARKE MURRAY C., GARTNER H., GREGR E.J., CHAN K., PAKHOMOV E. & THERRIAULT T.W. 2014. Spatial distribution of marine invasive species: environmental, demographic and vector drivers. *Diversity and Distribution* 20: 824–836.
- D’ARCHINO R., NELSON W.A. & ZUCCARELLO G.C. 2007. Invasive marine red alga introduced to New Zealand waters: first record of *Grateloupia turuturu* (Halymeniaceae, Rhodophyta). *New Zealand Journal of Marine and Freshwater Research* 41: 35–42.
- DAVIDSON A.D., CAMPBELL M.L., HEWITT C.L. & SCHAFFELKE B. 2015. Assessing the impacts of nonindigenous marine macroalgae: an update of current knowledge. *Botanica Marina* 58: 55–79.

- DAVIS A.N. & WILCE R.T. 1987. Floristics, phenology, and ecology of the sublittoral marine algae in an unstable cobble habitat (Plum Cove, Cape Ann, Massachusetts, USA). *Phycologia* 26: 23–34.
- DAYTON P.K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* 41: 351–389.
- DUDGEON S.R., KÜBLER J.E., VADAS R. & DAVISON I.R. 1995. Physiological responses to environmental variation in intertidal red algae: does thallus morphology matter? *Marine Ecology Progress Series* 117: 193–206.
- ELTON C.S. 1958. *The ecology of invasions by animals and plants*. University of Chicago Press, Chicago. 181 pp.
- ENGELEN A. & SANTOS R. 2009. Which demographic traits determine population growth in the invasive brown seaweed *Sargassum muticum*? *Journal of Ecology* 97: 675–684.
- FELLINE S., MOLLO E., FERRAMOSCA A., ZARA V., REGOLI F., GORBI S. & TERLIZZI A. 2014. Can a marine pest reduce the nutritional value of Mediterranean fish flesh? *Marine Biology* 161: 1275–1283.
- FREDRIKSEN S., SJØTUN K., LEIN T.E. & RUENESS J. 1995. Spore dispersal in *Laminaria hyperborea* (Laminariales, Phaeophyceae). *Sarsia* 80: 47–53.
- GARBARY D.J., TOMPKINS E., WHITE K.L., COREY P. & KIM J.K. 2011. Temporal and spatial variation in the distribution of life history phases of *Chondrus crispus* (Gigartinales, Rhodophyta). *Algae* 26: 61–71.
- GARBARY D.J., BEVERIDGE L.F., FLYNN A.D. & WHITE K.L. 2012. Population ecology of *Palmaria palmata* (Palmariales, Rhodophyta) from harvested and non-harvested shores on Digby Neck, Nova Scotia, Canada. *Algae* 27: 33–42.
- GAVIO B. & FREDERICQ S. 2002. *Grateloupia turuturu* (Halymeniaceae, Rhodophyta) is the correct name of the non-native species in the Atlantic known as *Grateloupia doryphora*. *European Journal of Phycology* 37: 349–359.
- GAYLORD B., REED D.C., RAIMONDI P.T. & WASHBURN L. 2006. Macroalgal spore dispersal in coastal environments: mechanistic insights revealed by theory and experiment. *Ecological Monographs* 76: 481–502.
- GROSHOLZ E. 2002. Ecological and evolutionary consequences of coastal invasions. *Trends in Ecology and Evolution* 17: 22–27.
- HARDY F.G. & GUIRY M.D. 2003. *A check-list and atlas of the seaweeds of Britain and Ireland*. British Phycological Society, London. 435 pp.
- HARLEY C.D., ANDERSON K.M., DEMES K.W., JORVE J.P., KORDAS R.L., COYLE T.A. & GRAHAM M.H. 2012. Effects of climate change on global seaweed communities. *Journal of Phycology* 48: 1064–1078.
- HARLIN M.M. & VILLALARD-BOHNSACK M. 2001. Seasonal dynamics and recruitment strategies of the invasive seaweed *Grateloupia doryphora* (Halymeniaceae, Rhodophyta) in Narragansett Bay and Rhode Island Sound, Rhode Island, USA. *Phycologia* 40: 468–474.
- HU Z.M. & JUAN L.B. 2014. Adaptation mechanisms and ecological consequences of seaweed invasions: a review case of agarophyte *Gracilaria vermiculophylla*. *Biological Invasions* 16: 967–976.
- HYTTIÄINEN K., LEHTINIEMI M., NIEMI J.K. & TIKKA K. 2013. An optimization framework for addressing aquatic invasive species. *Ecological Economics* 91: 69–79.
- JANIÁK D. & WHITLATCH R.B. 2012. Epifaunal and algal assemblages associated with the native *Chondrus crispus* (Stackhouse) and the non-native *Grateloupia turuturu* (Yamada) in eastern Long Island Sound. *Journal of Experimental Marine Biology and Ecology* 413: 38–44.
- JOHNSON C. [Ed.] 2008. *Seaweed invasions: a synthesis of ecological, economic and legal imperatives*. Walter de Gruyter, Berlin. 144 pp.
- JOHNSON C.R., BANKS S.C., BARRETT N.S., CAZASSUS F., DUNSTAN P.K., EDGAR G.J., FRUSHER S.D., GARDNER C., HADDON M., HELIDONIOTIS F., HILL K.L., HOLBROOK N.J., HOSIE G.W., LAST P.R., LING S.D., MELBOURNE-THOMAS J., MILLER K., PECL G.T., RICHARDSON A.J., RIDGWAY K.R., RINTOUL S.R., RITZ D.A., ROSS D.J., SANDERSON C.J., SHEPHERD S.A., SLOTWINSKI A., SWADLING K.M. & TAW N. 2011. Climate change cascades: shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. *Journal of Experimental Marine Biology and Ecology* 400: 17–32.
- KESER M., SWENARTON J.T. & FOERTCH J.F. 2005. Effects of thermal input and climate change on growth of *Ascophyllum nodosum* (Fucales, Phaeophyceae) in eastern Long Island Sound (USA). *Journal of Sea Research* 54: 211–220.
- KIM J.K., YARISH C. & PEREIRA R. 2016. Tolerances to hypo-osmotic and temperature stresses in native and invasive *Gracilaria* species. *Phycologia* 55: 257–264.
- KINLAN B.P. & GAINES S.D. 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* 84: 2007–2020.
- LÜNING K. 1990. *Seaweeds: Their environment, biogeography, and ecophysiology*. John Wiley & Sons, San Francisco. 527 pp.
- LYONS D.A. & SCHEIBLING R.E. 2009. Range expansion by invasive marine algae: rates and patterns of spread at a regional scale. *Diversity and Distribution* 15: 762–775.
- MAGGI E., BENEDETTI-CECCHI L., CASTELLI A., CHATZINIKOLAOU E., CROWE T.P., GHEDINI G., KOTTA J., LYONS D.A., RAVAGLIOLI C., RILOV G., RINDI L. & BULLERI F. 2015. Ecological impacts of invading seaweeds: a meta-analysis of their effects at different trophic levels. *Diversity and Distribution* 21: 1–12.
- MARBUAH G., GREN I.M. & MCKIE B. 2014. Economics of harmful invasive species: a review. *Diversity* 6: 500–523.
- MATHIESON A.C. 1982. Reproductive phenology and sporeling ecology of *Chondrus crispus* Stackhouse. In: *Proceedings of Republic of China-United States cooperative science seminar on cultivation and utilization of economic algae* (Ed. by R.T. Tsuda & Y.-M. Chiang), pp. 33–40. University of Guam Marine Laboratory, Mangilao.
- MATHIESON A.C., DAWES C.J., PEDERSON J., GLADYCH R.A. & CARLTON J.T. 2008. The Asian red seaweed *Grateloupia turuturu* (Rhodophyta) invades the Gulf of Maine. *Biological Invasions* 10: 985–988.
- MONTEIRO C.A., ENGELEN A.H. & SANTOS R.O. 2009. Macro- and mesoherbivores prefer native seaweeds over the invasive brown seaweed *Sargassum muticum*: a potential regulating role on invasions. *Marine Biology* 156: 2505–2515.
- NETTLETON J.C., MATHIESON A.C., THORNER C., NEEFUS C.D. & YARISH C. 2013. Introduction of *Gracilaria vermiculophylla* (Rhodophyta, Gracilariales) to New England, USA: estimated arrival times and current distribution. *Rhodora* 115: 28–41.
- OLSON A.M. & LUBCHENCO J. 1990. Competition in seaweeds: linking plant traits to competitive outcomes. *Journal of Phycology* 26: 1–6.
- PYŠEK P., JAROŠÍK V., HULME P.E., KÜHN I., WILD J., ARIANOUTSOU M., BACHER S., CHIRON F., DIDŽIULIS V., ESSL F. & GENOVESI P. 2010. Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proceedings of Richardson M.G. 1979. The distribution of marine Antarctic macro-algae related to depth and substrate. British Antarctic Survey Bulletin* 49: 1–13.
- RICHARDSON M.G. 1979. The distribution of Antarctic marine macroalgae related to depth and substrate. *British Antarctic Survey Bulletin* 49: 1–13.
- RUIZ G.M. & CARLTON J.T. 2003. Invasion vectors: a conceptual framework for management. In *Invasive species: Vectors and management strategies* (Ed. by G.M. Ruiz & J.T. Carlton), pp. 459–504. Island Press, Washington DC.
- SAGARIN R.D., BARRY J.P., GILMAN S.E. & BAXTER C.H. 1999. Climate-related change in an intertidal community over short and long time scales. *Ecological Monographs* 69: 465–490.
- SALVATERRA T., GREEN D.S., CROWE T.P. & O'GORMAN E.J. 2013. Impacts of the invasive alga *Sargassum muticum* on ecosystem functioning and food web structure. *Biological Invasions* 15: 2563–2576.
- SANGIL C., SANSÓN M. & AFONSO-CARRILLO J. 2015. Spatio-temporal variations and recruitment of *Sargassum flavifolium* Kützinger in sublittoral cobble bottoms: relationships with environmental variables. *Journal of Applied Phycology* 27: 455–467.
- SANTELICES B. 1990. Patterns of reproduction, dispersal and recruitment in seaweeds. *Oceanography and Marine Biology Annual Review* 28: 177–276.

- SCHIEBLING R.E., KELLY N.E. & RAYMOND B.G. 2009. Physical disturbance and community organization on a subtidal cobble bed. *Journal of Experimental Marine Biology and Ecology* 368: 94–100.
- SCHIEL D.R., STEINBECK J.R. & FOSTER M.S. 2004. Ten years of induced ocean warming causes comprehensive changes in marine benthic communities. *Ecology* 85: 1833–1839.
- SCROSATI R. & HEAVEN C. 2008. Trends in abundance of rocky intertidal seaweeds and filter feeders across gradients of elevation, wave exposure, and ice scour in eastern Canada. *Hydrobiologia* 603: 1–14.
- SIMON C., GALL E.A., LEVAVASSEUR G. & DESLANDES E. 1999. Effects of short-term variations of salinity and temperature on the photosynthetic response of the red alga *Grateloupia doryphora* from Brittany (France). *Botanica Marina* 42: 437–440.
- SIMON C., GALL E.A. & DESLANDES E. 2001. Expansion of the red alga *Grateloupia doryphora* along the coasts of Brittany (France). *Hydrobiologia* 443: 23–29.
- SORDO L., FOURNIER J., DE OLIVEIRA V.M., GERN F., DE CASTRO PANIZZA A. & DA CUNHA LANA L. 2011. Temporal variations in morphology and biomass of vulnerable *Halodule wrightii* meadows at their southernmost distribution limit in the southwestern Atlantic. *Botanica Marina* 54: 13–21.
- SOUSA W.P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* 60: 1225–1239.
- STACHOWICZ J.J. & HAY M.E. 1999. Mutualism and coral persistence: the role of herbivore resistance to algal chemical defense. *Ecology* 80: 2085–2101.
- STEGENGA H., KARREMANS M. & SIMONS J. 2007. Zeewieren van de voormalige oesterputten bij Yerseke. *Gorteria* 32: 125–143.
- VALENTINE J.P., MAGIEROWSKI, R.H. & JOHNSON C.R. 2007. Mechanisms of invasion: establishment, spread and persistence of introduced seaweed populations. *Botanica Marina* 50: 351–360.
- VILLALARD-BOHNSACK M. & HARLIN M.M. 1997. The appearance of *Grateloupia doryphora* (Halymeniaceae, Rhodophyta) on the northeast coast of North America. *Phycologia* 36: 324–328.
- VILLALARD-BOHNSACK M. & HARLIN M.M. 2001. *Grateloupia doryphora* (Halymeniaceae, Rhodophyta) in Rhode Island waters (USA): geographical expansion, morphological variations and associated algae. *Phycologia* 40: 372–380.
- WANG L., ZHUANG Y., ZHANG H., LIN X. & LIN S. 2014. DNA barcoding species in *Alexandrium tamarense* complex using ITS and proposing designation of five species. *Harmful Algae* 31: 100–113.
- WEI X., SHUAI L., LU B., WANG S., CHEN J. & WANG G. 2013. Effects of temperature and irradiance on filament development of *Grateloupia turuturu* (Halymeniaceae, Rhodophyta). *Journal of Applied Phycology* 25: 1881–1886.
- WERNBERG T., RUSSELL B.D., THOMSEN M.S., FREDERICO C., GURDEL D., BRADSHAW C.J.A., POLOCZANSKA E.S. & CONNELL SD. 2011. Seaweed communities in retreat from ocean warming. *Current Biology* 21: 1828–1832.
- WHITE L.F. & SHURIN J.B. 2011. Density dependent effects of an exotic marine macroalga on native community diversity. *Journal of Experimental Marine Biology and Ecology* 405: 111–119.
- WILLIAMS S.L., DAVIDSON I.C., PASARI J.R., ASHTON G.V., CARLTON J.T., CRAFTON R.E., FONTANA R.E., GROSHOLZ E.D., MILLER A.W., RUIZ G.M. & ZABIN C.J. 2013. Managing multiple vectors for marine invasions in an increasingly connected world. *BioScience* 63: 952–966.
- WILSON J.R., DORMONTT E.E., PRENTIS P.J., LOWE A.J. & RICHARDSON D.M. 2009. Something in the way you move: dispersal pathways affect invasion success. *Trends in Ecology & Evolution* 24: 136–144.
- YARISH C. & EDWARDS P. 1982. Field and cultural studies on the seasonal and horizontal distribution of estuarine red algae of New Jersey. *Phycologia* 21: 112–124.
- ZABIN C.J., ASHTON G.V., BROWN C.W., DAVIDSON I.C., SYTSMAN M.D. & RUIZ G.M. 2014. Small boats provide connectivity for nonindigenous marine species between a highly invaded international port and nearby coastal harbors. *Management of Biological Invasions* 5: 97–112.
- ZHANG H. & LIN S. 2002. Detection and quantification of *Pfiesteria piscicida* by using the mitochondrial cytochrome *b* gene. *Applied Environmental Microbiology* 68: 989–994.
- ZHANG H. & LIN S. 2005. Development of a cob-18S rDNA real-time PCR assay for quantifying *Pfiesteria shumwayae* in the natural environment. *Applied Environmental Microbiology* 71: 7053–7063.
- ZHANG H., BHATTACHARYA D. & LIN S. 2007. A three-gene dinoflagellate phylogeny suggests reconciliation of *Exuviaella* with *Prorocentrum* and a basal position for *Amphidinium* and *Heterocapsa*. *Journal of Molecular Evolution* 65: 463–474.
- ZHANG J., KIM J.K., YARISH C. & HE P. 2016. The expansion of *Ulva prolifera* O.F. Müller macroalgal blooms in the Yellow Sea, PR China, through asexual reproduction. *Marine Pollution Bulletin* 104: 101–106.

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