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Inconspicuous impacts: Widespread marine invader causes subtle but significant changes in native macroalgal assemblages

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Abstract. Invasive species are a major cause of global biodiversity decline; however, under certain environmental settings, some invaders can co-exist with native species with little detectable impact. Even so, in many cases the realized impact of invasive species may be underestimated due to procedural or temporal constraints related to observation or experimentation. The invasive kelp, *Undaria pinnatifida*, is considered to have limited impact on macroalgal assemblages on rocky reefs of the northeast Atlantic, although this is largely based on correlative or observational findings. Here, a high intensity press-removal manipulation was maintained for two years at a heavily invaded, *Undaria* dominated study site to improve current understanding of the potential impacts of *Undaria* on native macroalgal assemblages. Population and community effects as well as organismal performance effects (biochemical measures of condition and stress) were examined to investigate the potential for cryptic impacts. Where *Undaria* was removed, there was no difference in understory macroalgal assemblages; however, for three native kelp species, significant increases in abundance, biomass, and condition were recorded. The two perennial native kelps (*Laminaria digitata* and *Saccharina latissima*) exhibited small and inconsistent increases in all impact metrics where *Undaria* was removed, and therefore, the overall effects of *Undaria* on their populations are likely to be negligible. However, the native annual kelp, *Saccorhiza polyschides*, was consistently and significantly higher (3–6 times when compared to controls) in abundance and biomass under reduced competition from *Undaria* and exhibited significant changes in organismal-level responses which indicated improved condition of sporophytes. Whether the potential replacement of this native species could alter ecosystem functioning requires further investigation. Targeted long-term manipulative experiments can identify previously undetected impacts of invasive species in coastal ecosystems. Caution must be used when broadly classifying invasive species as having limited ecological impacts on recipient communities. Subtle impacts manifesting at the organism, population, and community levels should be considered before robust management prioritizations can be made.

Key words: impact; invasion ecology; invasive; kelp; macroalgae; non-native; *Undaria pinnatifida*;.

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Introduction

Human-mediated introductions of species into areas outside of their native range have caused, and continue to cause, irreversible changes to the natural environment (McKinney and Lockwood 1999, Gallardo et al. 2016). The magnitude of impact that these invasive species have on recipient ecosystems can vary greatly (Ricciardi et al. 2013, Simberloff et al. 2013). There is

considerable evidence that invasive species can outcompete native flora and fauna (Simberloff et al. 2013), alter nutrient pathways (Cloern 1996, Simberloff 2011, Gallardo et al. 2016), change habitat structure (Crooks 2002, Simberloff 2011, Dijkstra et al. 2017), and disrupt trophic interactions (Dijkstra et al. 2013, Salvaterra et al. 2013), even leading to regional and global species extinctions (Gurevitch and Padilla 2004, Simberloff et al. 2013). In contrast, many invasive species do not drive ecosystem change and some can co-exist with native species with little detectable impact (Williamson and Fitter 1996, Parker et al. 1999, Ricciardi and Cohen 2007, Simberloff 2011, Schlaepfer et al. 2012). It can, however, be argued that all species introductions must have some impact on recipient communities simply by their presence—reducing the availability of space, food, water, or other resources for co-occurring species (Simberloff et al. 2013, Russell and Blackburn 2017).

Various unifying frameworks have been developed to better measure and compare invasive species impact; such approaches generally consider measures of abundance, range, and per capita effect (Parker et al. 1999, Thomsen et al. 2011, Ricciardi et al. 2013). Quantifying the per capita effect of an invasive species across a given ecosystem is highly challenging because (1) perceived impacts vary across both space (between sites and habitat types) and time (between seasons and years); (2) perceived impacts vary between studies conducted within the same area due to different methodological approaches or chosen response variables (Thiele et al. 2010, Hulme et al. 2013, Thomsen et al. 2014). The potential for the effects of invasive species to manifest themselves across multiple levels of biological organization adds further complexities to measuring overall impact (Hulme et al. 2013, Simberloff et al. 2013). Where invasive species cause widespread mortality or facilitation of native species, impact can be relatively easily identified and (to a certain extent) quantified, by examining population-level changes through manipulative or before–after control-impact (BACI) studies (Byers et al. 2002, Forrest and Taylor 2002, Thomsen et al. 2014). Conversely, more subtle sub-lethal effects of invasive species on native species, such as changes in physiology, fecundity, growth, and behavior, are more difficult to measure and are therefore rarely quantified (Hulme et al. 2013, Thomsen et al. 2014). Even so, persistent and prolonged effects at the organism level could translate to population- and community-level changes; thus, considering a range of invasive species impacts across biological scales is important for developing evidence-based approaches to conservation and management.

The invasive kelp, *Undaria pinnatifida*, which originates from the northeast Pacific (hereafter referred to as *Undaria*), is a global invader, prevalent in many parts of the northeast and southwest Atlantic, southwest and east Pacific, and the Tasman Sea (Epstein and Smale 2017*b*). As *Undaria* has been present in parts of its non-native range for over 40 yr, there have been a relatively high number of studies on its ecological impact. These range from fully quantitative methods such as BACI, control-impact, or long-term invader exclusion manipulations, to more qualitative studies using observational, correlative, or pulse disturbance techniques (Epstein and Smale 2017*b*; and references therein). The majority of research has been conducted within Australasia, with some manipulative impact assessments also undertaken in Argentina (Epstein and Smale 2017*b*; and references therein). Within the northeast Atlantic, *Undaria* has been considered to have limited impact on rocky reef communities due to (1) being found more commonly or in higher abundance where the native canopy is limited; (2) being less competitive than long-lived natives due to its annual and opportunistic life-history characteristics; and (3) being facilitated by disturbance to canopies (Castric-Fey et al. 1993, Floc'h et al. 1996, Farrell 2003, Cremades et al. 2006, Heiser et al. 2014, De Leij et al. 2017, Epstein and Smale 2017*b*). These conclusions are, however, variable and context specific, and based largely on observational or correlative results; therefore, the effects of *Undaria* on recipient communities within this ecoregion could be greatly underestimated (Epstein and Smale 2017*b* and references therein).

The overall aim of this study was to improve current understanding of the potential impacts of *Undaria* on native macroalgal assemblages in southwest England (UK) through a long-term experimental manipulation. A high intensity

manipulation was established at a heavily invaded, *Undaria* dominated study site. Experimentation was constrained within areas of highest *Undaria* density, therefore targeting the highest potential for impact. Over two years, *Undaria* was manipulated within experimental patches of low intertidal rocky reef to yield three treatment intensities (0%, 50%, and 100% removal) in order to ascertain overall impact on native macroalgal communities and identify any density-dependent effects. Responses were recorded at the organism, population, and community levels to elucidate potential impact across multiple biological scales.

Methods

Study site

Undaria was first recorded within Plymouth Sound (southwest UK) in a marina in 2003 and has since spread to natural rocky habitats (Heiser et al. 2014, Epstein and Smale 2017*a*). Kelp-dominated communities on rocky substrates within Plymouth Sound are a designated conservation feature of the Special Area of Conservation and a number of Sites of Special Scientific Interest (Langston et al. 2003). As *Undaria* is now a major component of macroalgal assemblages in many locations within these protected sites (Epstein and Smale 2017*a*), it is important to better understand the potential for impact on designated features. The *Undaria* dominated study site was to the west of the Plymouth waterfront at Devil's Point (Fig. 1). For further information on the study site, see Appendix S1.

Set-up and maintenance

In September 2016, 15 circular treatment plots of 3 m diameter were established along ~120 m of shoreline on stable bedrock (Fig. 1). Plots were each separated by at least 4 m and positioned within the lower tidal zone on the shore (i.e., 0.2–0.7 m above chart datum). Each plot was assigned to one of three treatments: 0%, 50%, and 100% press removal of *Undaria*. A randomized block design accounted for spatial variation across the study site, with five blocks each containing three plots randomly assigned to one of each treatment. Although the study site was largely homogenous, a randomized block design was considered appropriate due to the plots being spaced across a long narrow band of shoreline, potentially leading to a gradient in abiotic conditions (such as wave exposure or light intensity). The *Undaria* press removal was maintained regularly throughout the 2-yr manipulation period, typically monthly but occasionally once every two months dependent on tidal constraints (18 times in total). During each visit, *Undaria* was removed from 50% treatment plots (maintaining density and canopy cover at around half of that found in the 0% plots for each block, respectively) and 100% treatments plots (all *Undaria* removed). Sporophytes were removed by gently prising the holdfast from the substrate once of sufficient size for conclusive identification to species in situ (generally >10 cm in total length). During each maintenance period, all plots were visited by a surveyor thus ensuring that all plots, including those assigned to the 0% removal treatment, had similar trampling disturbance. The total number of *Undaria* sporophytes present in, and removed from, each plot was recorded during most (but not all due to time constraints) maintenance visits.

Ecological responses

Macroalgae cover and density were surveyed at the start of the experiment and a further six times during the manipulation (January, April, August, and October 2017; February and August 2018). During each survey, data were obtained by haphazardly placing three 0.25-m^2 quadrats within each plot during periods of emersion, avoiding the outer 20 cm to reduce any edge effects (Fig. 1). For canopy-forming brown macroalgae, the abundance counts and percent cover of each species were estimated visually by a single observer. Additionally, in all but one survey period (missed due to tidal time constraints), the understory macroalgal assemblage was quantified. Within each 0.25-m^2 quadrat, canopy formers were first moved to one side to reveal the understory assemblage before three smaller 0.01-m^2 quadrats were haphazardly placed on the exposed bedrock; therefore, a total of nine understory quadrats were collected per plot. Each smaller quadrat was then photographed using a Panasonic Lumix FT5 digital camera. These smaller quadrats measured a subsample of the whole understory community but were of sufficient size to capture a representative

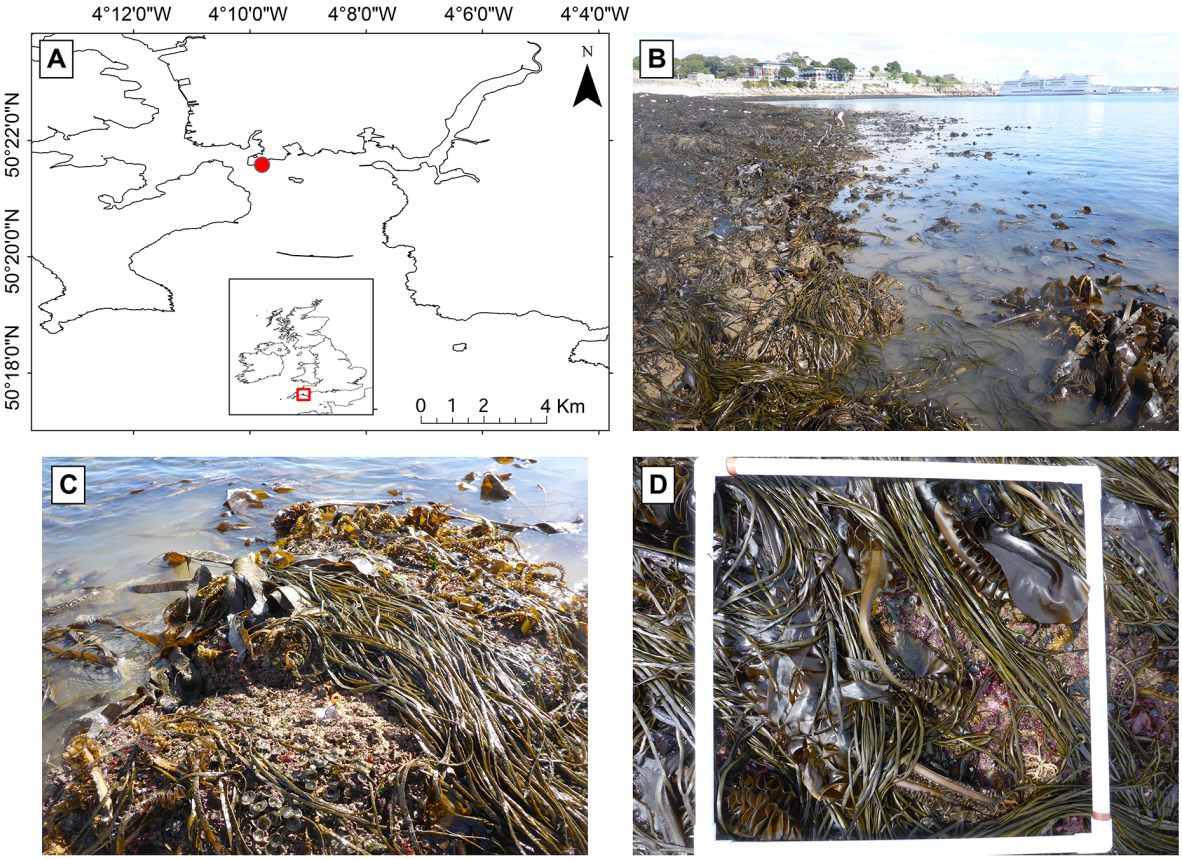

Fig. 1. (A) Study site (red circle) shown in the context of Plymouth Sound. Location of Plymouth Sound within the UK shown by red box on inset map. (B) The study site, known as Devil's Point. (C) An example experimental plot. (D) An example monitoring quadrat used for recording canopy-forming algae.

understory assemblage. For subsequent analysis, subsample quadrats were gridded (into 25 cells of 2 × 2 cm) before quantifying (1) the total number of *Himanthalia elongata* buttons and (2) the number of cells containing erect red, brown, and green macroalgae (which were then converted to a percentage of total cells within each quadrat and used as a proxy for percent cover). The values were averaged across the three subsample quadrats and used to estimate the total abundance of *Himanthalia elongata*, and percent understory cover of red, brown, and green macroalgae within each larger 0.25-m^2 quadrat.

In September 2018, at the end of the manipulation period, the macroalgal assemblage was destructively sampled by haphazardly placing four 0.25-m^2 quadrats within each plot, avoiding the outer 20 cm to reduce edge effects. Canopy-forming brown macroalgae were removed from all quadrats, while understory macroalgae were removed from three. Samples were returned to the laboratory for identification and counting; all macroalgae were identified to species-level, except for *Ceramium* spp. and *Corallina* spp. which were identified to genus and green macroalgae which were treated as one taxonomic group due to being taxonomically complex (Burrows 1991) and present at very low biomass/cover (see *Results*). All species were immediately weighed (fresh weight biomass), and the density of each canopy-forming brown macroalga species was also recorded for each quadrat.

Biochemical responses

Investigation of organism-level responses (i.e., concentration of indicator compounds which act

as proxies for macroalga condition, stress, and defense) was confined to the native co-occurring kelps *Laminaria digitata, Saccharina latissima,* and *Saccorhiza polyschides* (which, although not a true kelp (Laminariales), is an important canopy former that performs a similar ecological function and is referred to as a kelp hereafter). During the destructive sampling in September 2018, three individuals of each species were haphazardly selected within each of the 15 plots (*L. digitata* was not found in four plots, and *S. polyschides* was absent from three plots, leading to reduced replication for these two species). Two sections of tissue (~20 g fresh weight) were removed from the middle of the blade of each sporophyte and immediately placed on ice (leading to 228 samples in total). Following collection, each section was cleaned to remove any epiphytes before being frozen at −18°C for subsequent analysis.

Each sample was freeze-dried (Lablyo Freeze-drier, Frozen in Time) for at least 48 h, ground to a fine powder, passed through a 0.25-μm sieve, and stored in a dehumidified −18°C freezer. Calculation of semi-quantitative relative concentrations of laminarin, mannitol, phenols, lipids and total Polysaccharides (hereafter referred to as Polysaccharides) was carried out using Fourier transform infrared spectroscopy and an attenuated total reflection (ATR) method on dried powder material (Mayers et al. 2013, Meng et al. 2014), while the relative C:N ration was calculated using an Elemental Microanalysis CHN Analyser. Further details of these analyses can be found in Appendix S1.

Data analysis

All ecological data were analyzed using multivariate generalized linear models (GLMs) using the *mvabund* package (Wang et al. 2018; for detail see Warton et al. 2011, 2017) in R (R Core Team 2017). Abundance data were modeled using negative binomial GLMs (due to overdispersion from the Poisson distribution), while percent cover and biomass data used Tweedie GLMs (with a variance power of 1.5 to account for a compound Poisson distribution of non-negative values with mass at zero). *Undaria* was removed from the dataset prior to analyses as it was the manipulated species, while *Laminaria ochroleuca* was removed due to very low abundance/cover values (only nine occurrences were recorded across the entire study) and consequently insufficient replication between blocks and sampling months. Canopy-forming macroalgae and understory macroalgae datasets were analyzed separately. All data were analyzed in three steps; firstly, the initial pre-treatment survey data were analyzed to determine whether any differences between treatment plots were evident prior to the long-term manipulation; secondly, all non-destructive survey data were analyzed to examine the effects of treatments over the timespan of the manipulation; and finally, data generated from the destructive end point sampling were analyzed to assess treatment effects following two years of manipulation. For both start and end point datasets, the multivariate response was modeled as a function of Treatment (categorical; three levels), with restricted bootstrap resampling within Block (five levels) to account for the randomized block design. For the non-destructive temporal sampling, data were modeled as a function of Treatment and Month (categorical; six levels—indicating the number of months since the initial manipulation), with their interaction. Restricted bootstrap resampling was again constrained to Block; however, individual Plot ID (15 levels) was also applied as an additional grouping factor to account for temporally repeated measures.

Where multivariate analyses indicated a significant treatment effect, univariate post hoc test statistics and *P*-values were calculated for each species separately, and for those species found to have a significant treatment effects, pairwise differences between treatment levels (and months where appropriate) were assessed using univariate generalized linear mixed models (GLMMs)—for further information on these analyses, see Appendix S1. Lastly, for end point sampling data, unconstrained ordination using latent variable models (negative binomial and Tweedie distributions for abundance and biomass data, respectively) was used to visualize multivariate dissimilarities between plots, using the boral package (Hui 2016).

Organism-level responses were analyzed using multivariate linear techniques, with the six different biochemical metrics treated as a multivariate response. For each kelp species separately, multivariate dissimilarity between plots was visualized using principal component analysis (PCA)

using the prcomp function from base R (R Core Team 2017). Differences in biochemistry between press-removal treatments were then statistically tested with multivariate linear models (LMs) using the manylm command from the mvabund package in R (Wang et al. 2018). Model structure, bootstrapping, validation, and post hoc testing followed the same procedure as ecological end point sampling as explained above or within Appendix S1. For those univariate responses found to have a significant treatment effects, pairwise differences between treatment levels were assessed using univariate linear mixed models (LMMs; with Block as a random factor), using the lme4 (Bates et al. 2015) and multcomp (Hothorn et al. 2008) packages.

All statistics were implemented in R 3.4.3 (R Core Team 2017), data manipulation used the dplyr and reshape2 packages (Wickham 2007, Wickham and Francois 2015), graphs were created using ggplot2 (Wickham 2009), and maps (Fig. 1) were made within ArcMap 10.3.1. Where relevant, all data are shown ±standard error.

Results

Population- and community-level responses

At the start of the study, prior to the first manipulation, the abundance of *Undaria* (mean 35.9 ± 5.3 inds. per 7.1 m^2), the abundance and percent cover of native canopy-forming macroalgae and the percent cover of understory macroalgae did not differ between treatments (negative binomial GLMM for *Undaria* abundance $-\chi^2 = 2.21$, $P = 0.331$; Table 1; Fig. 2; Appendix S2: Fig. S1). Over the course of the two-year manipulation, >1630 and >500 individual *Undaria* sporophytes were removed from 100% and 50% treatments, respectively (Appendix S2: Fig. S1). *Undaria* was recorded at the study site year-round, with some individuals removed in each of the 18 maintenance events, although maximum abundance, cover, and removal density occurred in Spring (i.e., March–May; Appendix S2: Fig. S1).

Throughout the experiment, the surveys revealed high variation in the abundance and cover of native canopy-forming and understory macroalgae, both between plots and sampling months (Fig. 2). A significant overall treatment and sampling month effect was detected for both the abundance and cover of native canopy-forming macroalgae, whereas the interaction between treatment and month was non-significant (Table 1, Fig. 2). Univariate tests indicated that the significant treatment effect was primarily due to differences in the abundance and cover of *S. polyschides*, and the abundance of *L. digitata* (Table 2). For *S. polyschides* abundance, pairwise tests identified significant differences between all treatments with abundance in 100% removal plots >50% > 0%, whereas *S. polyschides* canopy cover was significantly higher in the 100% removal plots compared with both 50% and 0% treatments (Appendix S2: Table S1). For *L digitata* abundance, however, pairwise tests indicated no significant differences between treatments (Appendix S2: Table S1). For understory macroalgae, the non-destructive surveys detected no significant treatment effect on the cover of the assemblage, although it did differ significantly between sampling months (Table 1, Fig. 2).

End point destructive sampling also identified a significant treatment effect on abundance and biomass of native canopy-forming algae, but no effect on understory macroalgae (Table 1, Fig. 3; Appendix S2: Figs. S2, S3). For canopy species biomass and abundance, ordination of multivariate community data showed some partitioning of 100% removal plots when compared to 50% and 0% treatment plots (Fig. 3); there was, however, no clear separation in understory communities between treatments (Appendix S2: Fig. S3). Univariate test statistics highlighted that the significant treatment effect in canopy-forming community was primarily due to differences in abundance and biomass of *S. polyschides*, and abundance of *S. latissima* (Table 2). In all cases, pairwise tests identified that the effect was due to higher abundance/biomass values in 100% removal plots compared with both 50% and 0% removal plots (Appendix S2: Table S1).

Organism-level responses

Visualization of multivariate biochemical response data showed some partitioning between press-removal treatments for *L. digitata* and *S. polyschides* (Appendix S2: Fig. S4), but there was no indication of separation between treatments for *S. latissima* (Appendix S2: Fig. S4). Multivariate linear models identified significant differences between treatments for *S. polyschides* ($F_{2,33} = 22.61$, $P = 0.015$) and *S. latissima* ($F_{2,42} = 11.67$, $P =$

Table 1. Multivariate generalized linear models testing for the effect of treatment and sampling month on native canopy formers and understory macroalgal assemblages.

Coefficient	Canopy cover/biomass†			Canopy abundance			Understory cover/biomass‡		
	df	LR	*P*	df	LR	*P*	df	LR	*P*
Start									
Treatment	2	49.77	0.588	2	2.60	0.952	2	11.96	0.307
Temporal monitoring									
Month	**5**	**1512.50**	**<0.001**	**5**	**107.97**	**<0.001**	**5**	**187.04**	**<0.001**
Treatment	**2**	**361.18**	**<0.001**	**2**	**65.89**	**<0.001**	2	10.02	0.419
Month*Treatment	10	89.71	0.993	10	18.88	0.884	10	42.97	0.336
End point									
Treatment	**2**	**1199.10**	**0.003**	**2**	**27.76**	**0.002**	2	291.98	0.141

Notes: Start sampling and temporal monitoring quantified the abundance (inds. 0.25 m^{-2}) and canopy cover (%) of canopy-forming macroalgae, and cover (%) of understory macroalgae. End point sampling quantified the abundance (inds. 0.25 m^{-2}) of canopy-forming macroalgae, and the biomass (g 0.25 m^{-2}) of canopy-forming and understory macroalgae. Significant coefficients shown in bold ($\alpha = 0.05$). LR = sum of likelihood-ratio test statistic.

† Canopy cover for start and temporal monitoring; canopy biomass for end point sampling.

‡ Understory cover for start and temporal monitoring; understory biomass for end point sampling.

0.030), but not for *L. digitata* ($F_{2,30} = 9.652$, $P = 0.127$). Post hoc univariate test statistics highlighted that the significant treatment effects were primarily due to differences in lipids and laminarin for *S. polyschides*, and mannitol for *S. latissima* (Table 3). In general, pairwise tests identified that the significant treatment effects were due to lower concentrations in *Undaria* press-removal treatments when compared with control plots (Appendix S2: Table S2; Fig. 4). Univariate visualization of all biochemical response measures showed marginal differences in most contrasts (Fig. 4). There was a reasonably consistent negative trend in most compounds with reducing competition from *Undaria* in 50% and 100% removal treatments; however, changes in relative concentration were small and in most cases not statistically significant (Fig. 4). This pattern was not apparent for C:N ratios which marginally increased or was unchanged in press-removal treatments (Fig. 4). Overall, these trends were particularly apparent for *S. polyschides* but could also be identified in *S. latissima* and *L. digitata* (Fig. 4).

Discussion

Identifying ecological impact

This study is the first empirical evidence that the proliferation of *Undaria* is having an impact on native macroalgal assemblages on rocky reefs in the northeast Atlantic, at least under certain environmental conditions. Globally, this is only the second region, along with the coastlines of Argentina, where *Undaria* has been considered to be driving a detectable level of ecological change within natural rocky coastal environments (Casas et al. 2004, Irigoyen et al. 2010, 2011, Epstein and Smale 2017*b*). Overall, our study demonstrates that caution must be used when broadly classifying an invasive species as having limited ecological impacts on recipient communities. Prioritizing species for targeted management, based on impact and management feasibility, is crucial, especially in the marine environment where control methods are costly and often ineffective (Thresher and Kuris 2004, McGeoch et al. 2016, Booy et al. 2017, Epstein 2017). However, where possible, complex manipulative studies which consider conspicuous population and community-level impacts as well as subtle sub-lethal or ecophysiological impacts on individuals within recipient communities should be considered before such prioritization is made.

The experimental design used in the current study was specifically constructed to identify the potential for impact rather than quantify broader impacts across different habitats and the wider ecosystem. Manipulation was constrained to a heavily invaded, wave-sheltered site within the most favorable habitat for *Undaria* establishment. A high intensity manipulation and sampling regime enabled identification of any cryptic impacts. As such, to determine the impact of

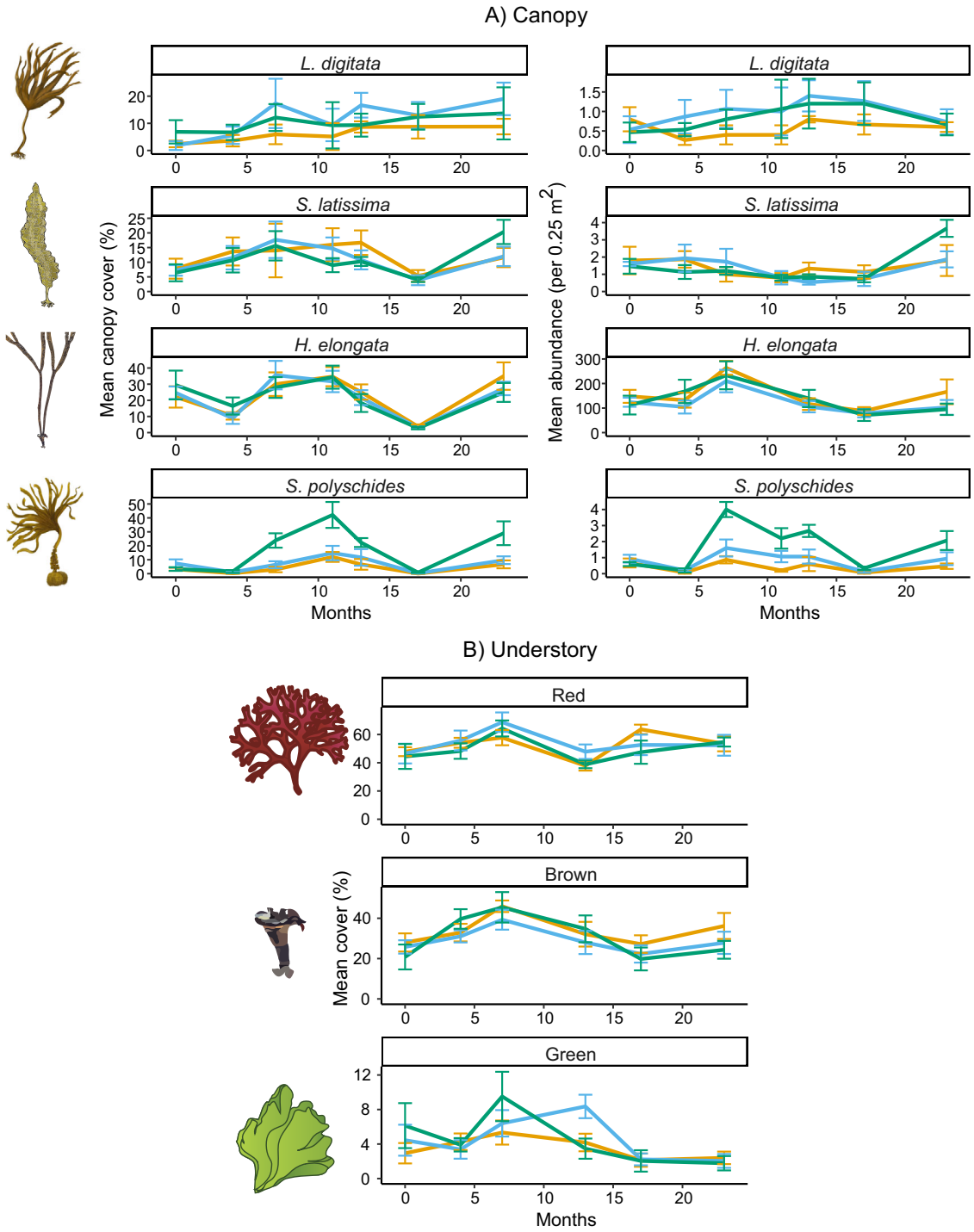

Fig. 2. Temporal monitoring of native canopy formers (A) and understory macroalgal assemblages (B) within the three different *Undaria* press-removal treatments (0% = orange, 50% = blue, and 100% = green). Mean abundance (inds. 0.25 m^{-2}; canopy only) and cover (%; canopy and understory) were estimated for each species/taxonomic unit in situ for 23 months. Macroalgae drawings courtesy of Jack Sewell and the Integration and Application Network (ian.umces.edu/symbols/).

Table 2. Univariate post hoc test statistics from multivariate generalized linear models testing for the effect of treatment (df = 2) on native canopy-forming macroalgae.

	Temporal monitoring				End point			
	Cover		Abundance		Biomass		Abundance	
Species	LR	*P*	LR	*P*	LR	*P*	LR	*P*
Saccorhiza polyschides	**294.10**	**<0.001**	**55.08**	**<0.001**	**628.51**	**0.007**	**15.14**	**0.003**
Saccharina latissima	2.81	0.733	0.19	0.895	121.74	0.012	**7.50**	**0.036**
Laminaria digitata	294	0.012	**10.62**	**0.002**	322.15	0.050	2.29	0.329
Himanthalia elongata	2.44	0.633	2.97	0.316	126.67	0.196	2.83	0.329

Notes: Temporal monitoring quantified the abundance (inds. 0.25 m^{-2}) and canopy cover (%), while end point sampling quantified the abundance (inds. 0.25 m^{-2}) and biomass (g 0.25 m^{-2}). Significant treatment effects shown in bold ($\alpha = 0.05$ for abundance; $\alpha = 0.01$ for cover/biomass due to unadjusted *P*-values). LR = likelihood-ratio test statistic.

Undaria on native assemblages at wider spatial scales, similar manipulations should be conducted across a range of habitat types (e.g., in subtidal or more wave-exposed sites) and ecological contexts (e.g., different recipient communities or population density of *Undaria*). Even so, this study highlights how highly targeted and long-term manipulative experiments can identify previously undetected impacts of invasive species in coastal ecosystems.

Competition and ecosystem functioning

This study recorded statistically significant effects of the presence of *Undaria* on the populations of three co-occurring native kelp species: *L. digitata*, *S. latissima,* and *S. polyschides*. The results, however, were only consistent across time, response metrics, and statistical analyses for *S. polyschides*. Both *Undaria* and *S. polyschides* are annual species that exhibit marked seasonality in recruitment, maturation, growth, and senescence at similar times of year. Typically, sporophytes of both species recruit during early spring, grow throughout summer, and senesce in autumn (Norton and Burrows 1969, Fletcher and Farrell 1999, Epstein and Smale 2018). Spatially, they occupy a similar niche in the subtidal fringe and are both considered relatively opportunistic species (Norton and Burrows 1969, Castric-Fey et al. 1993, Fletcher and Farrell 1999, Epstein and Smale 2017*a*). Previous studies have suggested, therefore, that these species may directly compete for space or other resources, although the strength and direction of such competition have not been quantified (Castric-Fey et al. 1993, Fletcher and Farrell 1999, Epstein and Smale 2017*a*). The results of this study indicate that under certain conditions *Undaria* is able to suppress and displace, but not exclude *S. polyschides* in invaded communities.

There was some indication of a density-dependent effect of *Undaria* within the temporal monitoring data; the effect size on *S. polyschides* density was significantly different between all treatment levels. *S. polyschides* abundance showed a 5.4 ± 1.2 fold increase in 100% treatments and 2.7 ± 0.6 fold increase in 50% treatments when compared to the 0% removal controls. Although this pattern was similar for canopy cover data (5.9 ± 1.4 and 2.7 ± 0.4 fold increases for 100% and 50% treatments, respectively), only the 100% treatment was statistically different from the control. At the end of the experiment, no density-dependent effects of *Undaria* were identified; abundance and biomass of *S. polyschides* were highly similar between 50% treatments and controls. In contrast, 100% treatments had a statistically significant 5.3- and 3.6-fold increase in abundance and biomass of *S. polyschides*, respectively. Overall, that *S. polyschides* did not increase significantly in the 50% removal treatments suggests that *Undaria* exerts a relatively strong suppressive effect on this native species even at relatively low densities and cover.

It is important to consider how this displacement of a native species may alter ecosystem functioning. There is evidence that these two species attract similar epifaunal and epifloral assemblages, so substitution may have minimal community-level impacts (Arnold et al. 2016). Additionally, *Undaria* is far less tolerant of wave action than *S. polyschides*, which can become the dominant canopy former under wave-exposed

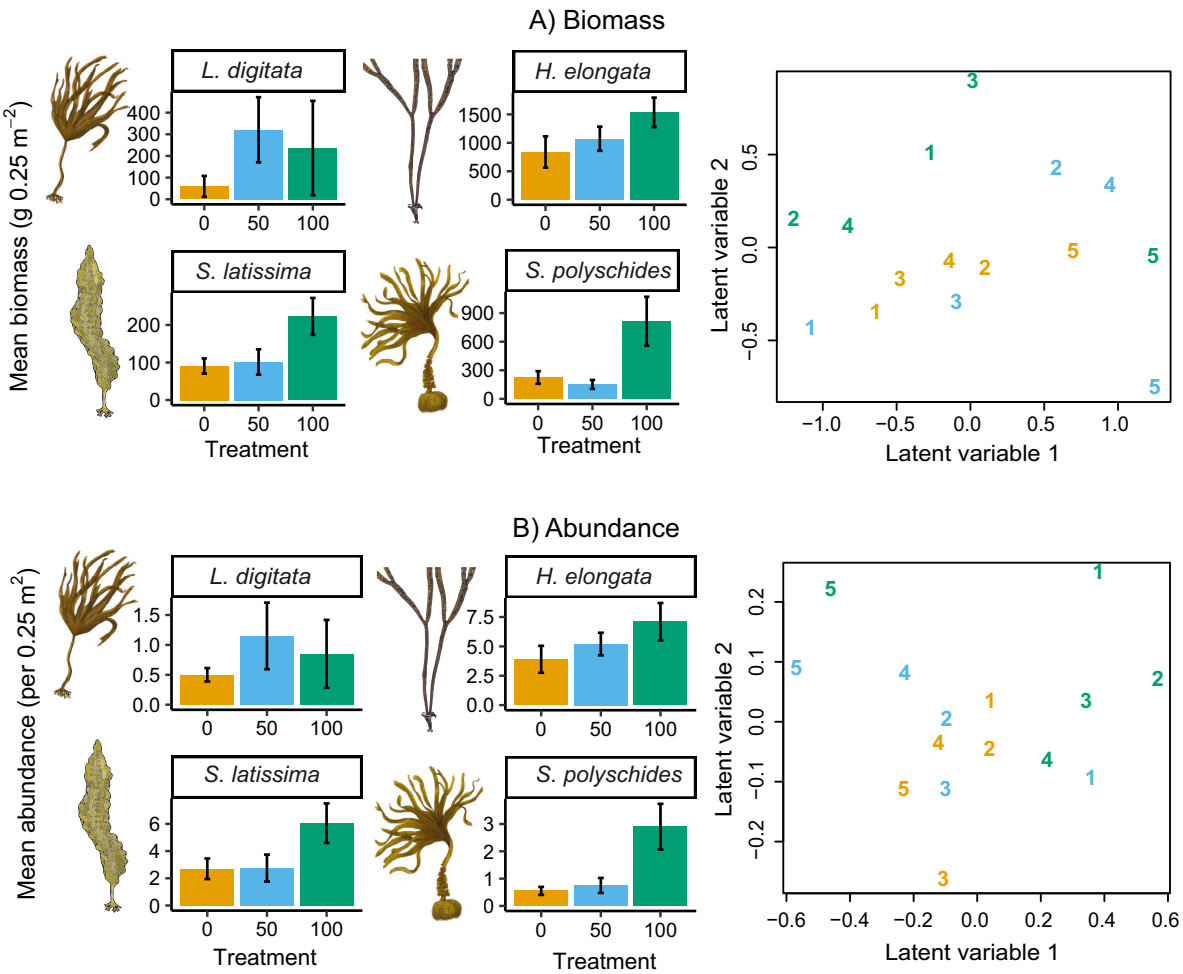

Fig. 3. End point sampling of native canopy-forming macroalgal assemblage within the three different *Undaria* press-removal treatments (0% = orange, 50% = blue, and 100% = green). (A) Mean biomass (g 0.25 m^{-2}) and (B) abundance (inds. 0.25 m^{-2}) were quantified by destructive sampling at the end of the manipulation after 24 months. Data illustrated as univariate species responses (bar plots; ±SE between plots) and multivariate community data (ordination plots of treatment plot averages). Numbers on ordination plots indicate each experimental block. Macroalgae symbols courtesy of Jack Sewell.

conditions (Burrows 2012, Epstein and Smale 2017*a*). This would suggest that competitive exclusion might only occur at wave-sheltered sites; thus, wider regional displacement of *S. polyschides* is unlikely. Moreover, anecdotal evidence suggests that, regionally, *S. polyschides* may have increased in density and extent over recent decades, perhaps due to increased sea temperatures or changes in canopy disturbance and structure (Birchenough and Bremner 2010, Smale et al. 2013). As such, any localized suppression by *Undaria* may be offset by wider trends on wave-exposed open coastlines. However, due to the complex and convoluted coastline of the UK (and wider northeast Atlantic) there are many wave-sheltered habitats where these species co-occur, and therefore, localized alterations in ecosystem function, due to the displacement of *S. polyschides*, could occur in numerous localities. Clearly, the drivers of change are complex, and further research is needed to determine wider ecological consequences of species substitutions, such as on trophic provision to grazers, habitat provision to

Table 3. Univariate post hoc test statistics from multivariate LMs testing for the effect of treatment (df = 2) on biochemistry of native kelps.

Biochemical response	*Saccharina latissima*		*Saccorhiza polyschides*	
	F	*P*	*F*	*P*
C:N	0.64	0.649	0.17	0.854
Lipids	0.74	0.649	**4.60**	**0.043**
Phenols	1.97	0.314	4.07	0.062
Polysaccharides	2.38	0.212	3.69	0.070
Mannitol	**4.08**	**0.043**	3.77	0.068
Laminarin	1.87	0.314	**6.31**	**0.019**

Note: Significant treatment effects shown in bold ($\alpha = 0.05$).

mobile species, primary production, and carbon cycling (Smale et al. 2013).

Although other species were identified in this study as suffering a potential ecological impact from the proliferation of *Undaria* (*L. digitata* and *S. latissima*), the effect size was inconsistent and relatively small. The impact of these interactions on ecosystem functioning, even at the local level, is therefore likely to be negligible, particularly as this study was designed to identify the highest likelihood of effect.

Organism-level impacts

Subtle yet persistent ecophysiological effects of invasive species have the ability to induce population and community-level changes to native species (Hulme et al. 2013, Thomsen et al. 2014, DeAmicis and Foggo 2015). In this study, although changes in native kelp biochemistry were marginal and inconsistent, there were some significant differences between press-removal treatments. Polysaccharides (predominantly in the form of mannitol and laminarin) and lipids are the primary storage compounds in kelp species (Black 1950, Guschina and Harwood 2006, Schiener et al. 2015). During periods of limited growth, these compounds increase in concentration within the kelp blade, acting as long-term energy stores for growth under preferential environmental conditions (Black 1950, Maschek and Baker 2008, Schiener et al. 2015). The concentration of these compounds is therefore often negatively correlated with growth rates (Black 1950, Zimmerman and Kremer 1986, Schiener et al. 2015). The native kelps investigated in this study (*L. digitata*, *S. latissima,* and *S. polyschides*) all had a small, and in some cases significant (*S. latissima* and *S. polyschides*),

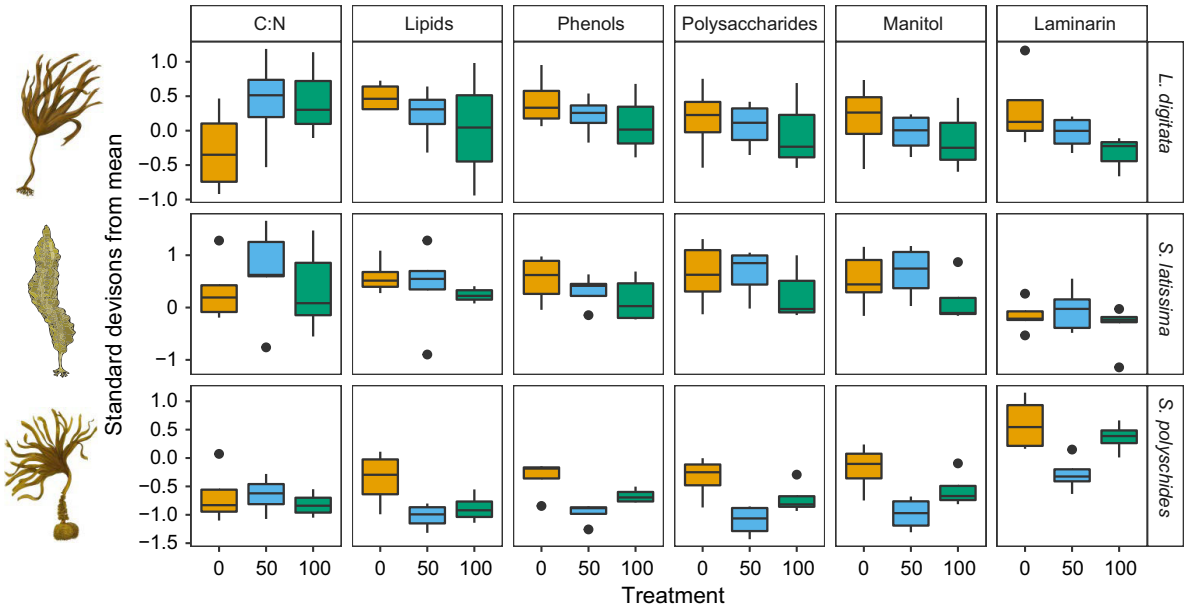

Fig. 4. Boxplots indicating the relative values of biochemical response metrics for *Laminaria digitata, Saccharina latissima,* and *Saccorhiza polyschides* within each *Undaria* press-removal treatment. All measures have been standardized [$(x - \mu)/\sigma$] and therefore are on the same unitless scale.

decrease in these compounds within *Undaria* press-removal treatments. Although further investigation would be needed, this may indicate that the growth rate of native kelps increases in the absence of competition from *Undaria*. The changes in C:N ratios also indicate the potential for competitive inhibition from *Undaria* on native kelps. C:N ratios generally correlate to nutrient availability, with decreased C:N in nutrient-replete settings (Harrison and Druehl 1982). This can be due to changes in external nutrient availability or nutrient uptake-driven by competition, changes in water movement or other abiotic factors (Gerard 1982, Harrison and Druehl 1982, Kregting et al. 2016). The small increase in C:N ratios recorded within *Undaria* press-removal treatments for *L. digitata* and *S. latissima* may have been due to increased water motion and therefore higher nutrient uptake in the native kelps. Finally, phenolic compounds primarily function as defensive or stress response compounds in kelps (Arnold and Targett 2003, Maschek and Baker 2008). In this study, the reduction or exclusion of *Undaria* generally reduced the concentration of phenols in native kelps, potentially indicating a reduction in stress or defense responses.

Overall, the analyses of biochemical responses to the *Undaria* press-removal treatments indicate that some native kelp species in the region may exhibit ecophysiological responses when persisting within *Undaria* stands. As with the ecological response variables, the largest effect size was identified in the functionally similar annual kelp *S. polyschides;* however, some marginal effects were also identified in *S. latissima* and *L. digitata* (although changes in the latter were not statistically significant). Further investigations would be needed to identify how these biochemical changes reflect the physiology, growth, or reproduction of native kelps, and therefore the ecosystem function of kelp communities. It should be noted, however, that many of these biochemical responses were marginal and inconsistent, and as such, the overall impacts could be deemed negligible, particularly in relation to the perennial species *S. latissima* and *L. digitata*.

Contrast to previous studies

Although variable and context specific, previous studies have considered *Undaria* to have limited impact on rocky reef macroalgal communities within the northeast Atlantic (Castric-Fey et al. 1993, Floc'h et al. 1996, Cremades et al. 2006, Heiser et al. 2014, Arnold et al. 2016, De Leij et al. 2017, Epstein and Smale 2017*a*). These studies largely used observational or correlative data to make predictions on the potential impact from *Undaria*. Using these techniques does allow some estimation of the extent of community or ecosystem-level impact, however, when compared to this study, the contrasting results highlight that using correlative data alone is unlikely to identify all levels of potential impact. It should be noted that the results of this study do not directly contradict previous results, as significant population declines were only identified in one functionally similar native species. As previously stated, the overall impact on ecosystem functioning may still be limited when considering macroalgal assemblages and rocky reef communities as a whole.

Conclusion

The impact of *Undaria* on recipient communities can vary greatly across its non-native range (Epstein and Smale 2017*b*; references therein). This study identified that in the northeast Atlantic, the presence of *Undaria* has the potential to displace but not exclude the native kelp *S. polyschides* and may cause ecophysiological impacts on three native co-occurring kelp species. Whether these effects are sufficient to prioritize the implementation of targeted management measures is unclear, and would require complex cost-benefit and risk analyses (Booy et al. 2017, Courtois et al. 2018). Under certain environmental settings, *Undaria* is now an established part of the flora of the northeast Atlantic, found at high abundance and cover across a variety of habitats and locations (Epstein and Smale 2017*b*). It seems unlikely that *Undaria* can be excluded or controlled in areas where it has already proliferated (Hewitt et al. 2005, Forrest and Hopkins 2013, Epstein et al. 2018); however, this study suggests that limiting its further spread may be justified.

Finally, although the impact invasive species have on recipient communities can vary greatly (Ricciardi et al. 2013, Simberloff et al. 2013), with some being passengers rather than drivers of ecosystem change (MacDougall and Turkington 2005), it is important to remember that all species

introductions are highly likely to have some impact on recipient communities simply by their presence (Simberloff et al. 2013, Russell and Blackburn 2017). Complex targeted manipulations or long-term monitoring techniques that consider responses across biological scales are likely to uncover many previously undetected impacts of species introductions.

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