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The invasive kelp *Undaria pinnatifida* hosts an epifaunal assemblage similar to native seaweeds with comparable morphologies

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ABSTRACT: Invasive seaweeds have the potential to disrupt ecosystem functioning if they are unsuitable hosts for the small mobile invertebrates (epifauna) that are an important trophic link between benthic primary producers and higher trophic levels. The Asian kelp *Undaria pinnatifida* has successfully invaded many coastal regions worldwide. We compared the epifaunal assemblage on *U. pinnatifida* with epifauna of 7 co-occurring, canopy-forming native brown seaweed species in southern New Zealand to help understand the effect of the invasive species on shallow subtidal ecosystems. The density, diversity and composition of epifauna across the 8 seaweeds were much more strongly related to host morphology than to the geographic origin of the host. *U. pinnatifida* and several native seaweeds with similarly simple morphologies supported relatively depauperate epifaunal assemblages dominated by copepods. More structurally complex native seaweeds supported more abundant and diverse epifaunal assemblages containing lower proportions of copepods and higher proportions of amphipods and other epifaunal groups. Our results indicate that abundances of epifauna at the ecosystem level will be reduced if *U. pinnatifida* displaces more structurally complex native seaweed species that host more diverse and dense epifaunal assemblages. The findings suggest that morphological complexity may be key to predicting the impacts of invasive seaweeds on epifaunal assemblages, and potentially on food webs, in other geographic regions.

KEY WORDS: *Undaria pinnatifida* · Epifaunal communities · Invasive seaweeds · Native seaweed · Morphological complexity · Fucales · Laminariales · Asian kelp

INTRODUCTION

Invasive species are an increasingly common feature of marine ecosystems worldwide (Molnar et al. 2008), so there is a pressing need to understand the impact of invaders on native flora and fauna. Alterations to seaweed communities are of particular concern, because they provide habitat and food for a wide range of faunal communities including abundant and diverse assemblages of small mobile invertebrates (epifauna) (e.g. Hay et al. 1987, Duffy & Hay 1991, Taylor & Steinberg 2005). Epifauna are key components of temperate rocky reef ecosystems. They contribute up to 80% of total secondary productivity on rocky reefs (Taylor 1998) and link benthic primary producers to higher trophic levels such as predatory fish (Edgar & Moore 1986, Taylor 1998). This link would be weakened if native seaweeds

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were displaced by invasive species that were less suitable hosts for epifauna.

Whether or not epifauna can successfully colonise an invasive seaweed depends on the nature of the epifauna–host relationship. Epifaunal species use their host as a platform to shelter from predators and/or wave action (Taylor 2015), and feed on either the host itself (Duffy 1990), epiphytic algae (Bamber & Davis 1982), detritus (Zimmerman et al. 1979), suspended matter (Caine 1974) or other animals (Roland 1978). Thus, the suitability of a potential new seaweed host will likely be determined by the degree of protection it affords from predation, the foraging opportunities and whether epifauna can attach to it securely. Typically, structurally complex (i.e. finely branched and filamentous) seaweeds support higher abundances of epifauna than structurally simple (i.e. foliose or leathery) species (e.g. Hacker & Steneck 1990, Gee & Warwick 1994, Taylor & Cole 1994, Zamzow et al. 2010). Strong host specificity, as might be driven by dietary specialisation (Hay et al. 1990) or microhabitat requirements (Sotka et al. 1999), could prevent native epifauna from colonising invasive species. In fact, the successful establishment of invasive species has been attributed to the absence of coevolved enemies (the 'enemy-release hypothesis') and to novel defences that deter generalists (the 'novel weapon hypothesis') (e.g. Wikström et al. 2006, Enge et al. 2012). Epifauna commonly prioritise refuge value over nutritional value (e.g. Duffy & Hay 1994, Jormalainen et al. 2001, Lasley-Rasher et al. 2011), but the specific morphological traits that best characterise such refuge value remain unclear. Morphological properties are not usually quantified, and studies examining these traits usually focus on structural aspects (e.g. surface area, branching; Chemello & Milazzo 2002, Schmidt & Scheibling 2006, 2007) rather than spatial properties (e.g. interstitial spaces; Hacker & Steneck 1990, Fukunaga et al. 2014).

A limited number of studies on the topic suggest that epifauna respond to host morphology regardless of whether the host is native or invasive, potentially enabling seaweed morphological traits to be used to predict impacts of invasive seaweeds on native epifaunal communities. Invasive seaweeds have been shown to host epifaunal communities similar to those of native seaweeds with similar morphologies (e.g. Viejo 1999, Gestoso et al. 2012, Fukunaga et al. 2014). Furthermore, the highly branched morphology of the invasive *Codium fragile* ssp. *tomentosoides* hosts more dense and diverse epifaunal assemblages than native kelps (Laminariales) that have relatively simple morphologies (Schmidt & Scheibling 2006). However, the relationship between epifaunal composition and host morphology remains poorly quantified and unclear, with results from some studies suggesting that variation in epifauna is unrelated to differences in host morphology (Cacabelos et al. 2010, Gestoso et al. 2010).

The Asian kelp *Undaria pinnatifida* has successfully invaded many parts of the world (e.g. Curiel et al. 1998, Valentine & Johnson 2003, Thornber et al. 2004, Casas et al. 2008), and it is likely to continue spreading, given its wide temperature tolerance (James et al. 2015). Once established in a new habitat, *U. pinnatifida* may reduce biodiversity by outcompeting native species (Casas et al. 2004, Farrell & Fletcher 2006), or it may have no apparent impacts on native seaweed communities (Valentine & Johnson 2003, 2004, Schiel & Thompson 2012, Thompson & Schiel 2012). Given its relatively simple morphology, consisting of a holdfast, stipe and a blade with a basal meristem and midrib, it is possible that *U. pinnatifida* will be a less suitable host for epifauna in invaded regions than native seaweed species. This was recently suggested by Arnold et al. (2016), who found that *U. pinnatifida* in the southern UK host depauperate epibiotic assemblages compared to some of the native kelps. However, the effect of morphology in driving the differences between the faunal assemblages was not explicitly examined in their study.

About 25 yr ago, *U. pinnatifida* invaded the rocky coast of Otago in the South Island of New Zealand (Hay & Villouta 1993), where rocky shores naturally contain a high diversity of canopy-forming brown seaweeds mostly belonging to the order Fucales and including *Carpophyllum* spp., *Cystophora* spp., *Marginariella* spp., *Sargassum sinclairii* and *Xiphophora gladiata* (Desmond et al. 2015, Jiménez et al. 2015a). *U. pinnatifida* is now common on many Otago rocky reefs (Russell et al. 2008), comprising up to 75% of the total seaweed density and percent cover in the first 3 m below the low tide mark (Jiménez et al. 2015a). Here, we studied the density, diversity and composition of the epifaunal communities present on *U. pinnatifida* and 7 co-occurring native brown seaweed species in relation to structural (i.e. surface area) and spatial (i.e. interstitial volume) morphological traits (Hacker & Steneck 1990), in order to evaluate the influence of seaweed structure on epifaunal communities. We hypothesised that the epifaunal community on *U. pinnatifida* would be different from those found on more complex native seaweeds, but similar to those on native seaweeds with comparable morphologies.

MATERIALS AND METHODS

Material collection

Five adult individuals (0.5–1.5 m length) of the invasive kelp *Undaria pinnatifida* (Laminariales) and the common native seaweeds *Marginariella urvilliana*, *M. boryana*, *Xiphophora gladiata*, *Desmarestia ligulata*, *Carpophyllum flexuosum*, *Cystophora scalaris* and *Sargassum sinclairii* (Fucales) were collected from 3 sites around the Otago coast, southern New Zealand. We focussed on canopy-forming brown seaweeds of similar size to *U. pinnatifida*, as we considered these to be the component of the seaweed community most at risk of displacement by *U. pinnatifida*. Collections were made in December 2011 and 2012 (following spring recruitment of *U. pinnatifida* and before summer senescence) and in March 2012 (following summer senescence of *U. pinnatifida*) (Aramoana: 170° 43′ S, 45° 46′ E; Harrington Point: 45° 47′ S, 170° 43′ E; and Mapoutahi: 170° 37′ E, 45° 44′ S). Not all species were present at all sites: *S. sinclairii* was only at Aramoana, *D. ligulata* and *M. boryana* were only at Mapoutahi, and *M. urvilliana* was only at Aramoana and Harrington Point. Not all sites could be sampled at all times, due to logistical constraints: Harrington Point was sampled only in December 2011, Aramoana in March and December 2012 and Mapoutahi in December 2012. *U. pinnatifida* was collected at all sites and times. Seaweeds were haphazardly selected underwater from 1.5–3 m depth as they were encountered while SCUBA diving. Each seaweed and its associated fauna was gently enclosed in a large plastic bag (120 × 65 cm; 100 µm thickness) and then detached from the substratum below the holdfast using a knife (Taylor & Cole 1994). Each bag had 100 µm mesh clamped into 1 corner to allow water to drain out without losing epifauna. The mouth of the bag was then sealed with a cord and transported inside an insulated bin to the laboratory.

Epifaunal communities

At the laboratory, each seaweed was washed vigorously in a plastic bucket containing 5 l of fresh water. Both the bucket and the bags were then washed twice onto 1 mm and 100 µm sieves to obtain size-fractionated epifaunal samples that simplified the processing. Animals retained on these sieves were then placed in individual 70 ml plastic jars containing ~40 ml of Shandon Glyo-Fixx preservative for later quantification and identification to the lowest taxonomic level possible. The density of each epifaunal taxon was recorded as the number of individuals per 100 g of seaweed wet weight. The Shannon-Wiener diversity index (H') of each sample was determined as follows:

$$H' = \sum_{i=1}^{S} Pi \ln Pi \quad (1)$$

where S is the number of taxa found and Pi is the proportion of the total epifaunal individuals found on a sample that belonged to the i^{th} taxon (Krebs 1989).

Seaweed morphology

The morphology or habitat architecture of seaweeds is defined by the quality and quantity of the fronds (structural components) and those of the spaces between the fronds (spatial component) (Hacker & Steneck 1990). While structural and spatial parameters represent different architectural traits, they are inter-related, since structural traits will define the spatial component. The space between the fronds of each seaweed species (n = 7 replicates species^{-1}) was analysed following the methods of Hacker & Steneck (1990). The interstitial volume (IV; volume in ml taken up by the spaces between the canopy of the seaweed) was quantified by subtracting the thallus volume (TV; volume in ml displaced by the seaweed), from the canopy volume (CV; volume in ml defined by the length, width, and height in cm that the seaweed occupied when submerged). A 5 l graduated flask filled with seawater was used for measurements of TV. Seaweeds were cut into sections if they were too large to fit inside the flask and volumes were summed to obtain a total TV. For measurements of CV, each seaweed was placed inside a 90 l clear plastic bucket containing freshwater with a 0.5 kg weight attached to its holdfast so the seaweed was vertical. The length, width and height of each submerged seaweed were then measured through the container using a tape. Seaweeds that were larger than the container were cut into 2 to 3 sections, and IV was obtained by adding up the length and considering the maximum height and width values measured. The measurement of the CV in the leathery/leafy/flattened seaweeds (*U. pinnatifida*, *X. gladiata*, *Marginariella* spp. and *D. ligulata*) was modified according to Hacker & Steneck (1990) so that it is not the same as the TV due to the 2-dimensional morphology of these species. CV was

defined as the thallus length × width × space around the thallus where epifauna are attached (Hacker & Steneck 1990). 'Space', representing the maximum volume that epifauna can occupy while attached to the fronds of seaweeds (Hacker & Steneck 1990), was obtained by adding the thickness of the frond (≤0.25 mm for *U. pinnatifida* and *D. ligulata*; ≤2 mm for *Marginariella* spp. and ≤5 mm for *X. gladiata*) to the dorsal–ventral thickness of the epifauna collected, which rarely exceeded 5 mm. The IV was standardised by the TV of each individual, and an individual IV:TV ratio was obtained for each seaweed by averaging the replicate ratios obtained.

The surface area (SA) of each seaweed species was quantified to get additional information on the structural component (i.e. branching) of its morphology. Replicates of the 2-dimensional seaweeds (*U. pinnatifida, M. urvilliana*, *M. boryana, X. gladiata*, *D. ligulata*) were cut into different sections and photographed over a white surface. The SA of 1 side of each section was obtained by using the software ImageJ and multiplied by 2. For the 3-dimensional seaweeds (*Cy. scalaris*, *Ca. flexuosum, S. sinclairii*), SA was estimated by subsampling within the individuals. All branches of each individual were weighed (W), and 5 (randomly chosen) branches were cut into small pieces (1–5 cm) to calculate SA as explained above. A relationship for SA:W was then established by regression analysis, and the SA values for the rest of the branches were calculated. If the stipe, or any other element, of any seaweed species was circular in cross-section, then the formula for a cylinder was applied to obtain the SA. The same principle was applied to any other geometrical form (e.g. sphere for the pneumatocysts).

Data analyses

The intention of the study was to focus on differences in epifaunal communities across seaweed species rather than on spatio-temporal variation. However, since epifauna communities can shift temporally, we first analysed the differences among months and seaweed species for Aramoana, which was sampled in March and December. This analysis demonstrated that differences among seaweed species and time existed, with an interaction between these factors (Supplement 1A; www.int-res.com/articles/supp/m582p045_supp.pdf). In further analyses of these data, each 1-way PERMANOVA per sampling time showed that the differences among seaweed species still existed when each time was examined independently (Supplement 1B,C). Since seaweed species were not collected at all sites and times (see above), we tested for differences in the epifaunal community across seaweed species using 1-way PERMANOVA on a subset of 5 randomly selected samples of each species from all sites and times. This procedure was repeated with a different subset of randomly selected samples in order to be confident of the validity of the selection procedure. Bonferroni adjustments were avoided for the pairwise comparisons, as they can increase Type II error (Cabin & Mitchell 2000). However, to minimize Type I errors in these multiple comparisons, we applied a more stringent p-value of 0.01. Differences in epifaunal assemblages across seaweed species were visualised by non-metric multidimensional scaling (nMDS) on the basis of Bray-Curtis similarity matrices constructed from square-root transformed density data.

The relationships between the morphological parameters (IV:TV ratio and SA) of the different seaweeds and the epifaunal communities were examined using the BIOENV test on the basis of Euclidean similarity matrices for density data using the Spearman correlation method. The IV:TV ratios of each seaweed species were related to their epifaunal density values in order to visualise the effect of the host's morphology.

All PERMANOVAs were conducted on the higher-level epifaunal taxa listed in Supplement 2 at www.int-res.com/articles/supp/m582p045_supp.pdf (2 phyla, 3 classes, 4 orders, 43 families). Pre-analyses indicated that members from all groups contributed to explaining the differences observed. All multivariate analyses run in this study were conducted using Primer v.6 and PERMANOVA (Primer-E).

The relationship between the means of the morphological parameters obtained from each native seaweed species and the total epifaunal density and diversity recorded on them were described with linear regressions using R v3.2.1. Upper and lower 95% confidence intervals on the regression lines were also calculated to determine whether epifauna on *U. pinnatifida* conformed to the epifaunal communities on native seaweeds. The contribution (%) of the main epifaunal groups (harpacticoid copepods, amphipods, miscellaneous) to the composition of the epifauna associated with each seaweed species was calculated. Similarly, the relationship between density of the groups and the morphological parameters was explored.

RESULTS

Fifty-four epifaunal taxa were identified, and common taxa (i.e. the amphipods *Aora typica*, *Protohyale rubra*) recorded on all native species were also common on *Undaria pinnatifida* (Table 1). The only taxa found solely on *U. pinnatifida* were single individuals of the shrimp *Hippolyte multicolorata* and the polychaete family Spionidae (Table 1).

Epifaunal composition differed among seaweed species (Fig. 1A; df = 7, $F = 6.74$, $p < 0.0001$), and this was supported by a second analysis using a different randomly selected data set (Supplements 1 & 3; www.int-res.com/articles/supp/m582p045_supp.pdf). Pairwise tests revealed differences in epifaunal composition between all seaweed species but not between *U. pinnatifida* and *Marginariella* spp. and *Xiphophora gladiata;* between the 2 *Marginariella* spp.; between *M. urvillana* and *X. gladiata;* between *X. gladiata* and *Desmarestia ligulata;* and among *Cystophora scalaris* with *Carpophyllum flexuosum* and *Sargassum sinclairii* (Supplement 3). This was clearly shown in the ordination analysis (nMDS). This revealed that the epifaunal community on *U. pinnatifida* tended to be more similar to those from *Marginariella* spp. and *X. gladiata* (around 40% similarity) than to those from *Ca. flexuosum*, *Cy. scalaris* and *S. sinclairii*, which were also more similar to each other than to any other seaweed species (Fig. 1A; stress loading 0.09). BIOENV showed that the spatial component IV:TV ratio was better than SA at explaining the differences observed in the epifaunal community (Rho = 0.502; significance level = 0.1%; Spearman correlations = 0.502 and 0.035, respectively). The nMDS bubble plots based on the values of IV:TV ratios assigned to each epifauna sample showed that the similarities between the groups of epifauna on seaweeds corresponded to similarities in the morphology index (Fig. 1B).

Linear relationships between the morphological parameters SA, SA:TV and SA:*W* ratios, and either epifaunal density or diversity were generally weak, with only density versus the SA:*W* ratio showing a significant linear association (Supplement 4; www.int-res.com/articles/supp/m582p045_supp.pdf). Linear regressions between epifaunal density and diversity and the IV:TV ratio of seaweeds were statistically significant and strongly positive (Supplement 4, Fig. 2A,B), with *U. pinnatifida*'s epifaunal density and diversity falling within the 95% confidence intervals for the regressions on epifauna from the native seaweeds (Fig. 2A,B). For the species *U. pinnatifida*, *Marginariella* spp., *X. gladiata* and *D. ligulata*, the log (IV:TV ratio) ranged from 0.25 to 1 ('structurally simple' species), epifaunal densities ranged from 118 to 490 ind. 100 g^{-1} blotted seaweeds, and epifaunal diversity (*H'*) ranged from 0.5 to 1.3. For the species *Cy. scalaris*, *Ca. flexuosum* and *S. sinclairii*, the log (IV:TV ratio) ranged from 2.0 to 2.3 ('structurally complex' species), epifaunal densities ranged from 750 to 1095 ind. 100 g^{-1} blotted seaweeds, and epifaunal diversity ranged from 1.14 to 1.7 (Fig. 2A,B).

Epifaunal communities were numerically dominated by harpacticoid copepods and amphipods (Fig. 2C). Harpacticoid copepods ranged from a maximum range of 73–79% of total epifauna recorded on *U. pinnatifida*, *M. urvilliana* and *D. ligulata*, to a minimum range of 32–55% recorded from *S. sinclairii*, *Cy. scalaris* and *Ca. flexuosum* (Table 1). In contrast, a minimum of 9–10% and a maximum of 32–39% of amphipods out of the total epifauna were recorded in epifaunal samples collected from *U. pinnatifida*, *M. urvilliana* and *D. ligulata*, and *S. sinclairii*, *Cy. scalaris* and *Ca. flexuosum*, respectively. Linear correlations with log (IV:TV ratio) were only statistically significant for amphipod density, which was positively correlated with this morphological variable (Supplement 3; Fig. 3). Amphipod densities recorded were below 100 ind. 100 g^{-1} blotted seaweed for the structurally simple species *U. pinnatifida*, *Marginariella* spp., *X. gladiata* and *D. ligulata*, whereas they ranged between 300 and 500 ind. 100 mg^{-1} blotted seaweed for the more structurally complex *Cy. scalaris*, *Ca. flexuosum* and *S. sinclairii* (Fig. 3A).

DISCUSSION

The invasive kelp *Undaria pinnatifida* hosted epifaunal assemblages similar to those of native seaweeds with similar simple morphologies, but a different epifaunal community than those on more complex native seaweeds. Morphological complexity based on the spatial traits (i.e. shelter volume offered) of the seaweed species, rather than structural properties (i.e. surface area offered), was most strongly correlated with variation in the epifaunal communities. *U. pinnatifida* along with other morphologically simple species, such as *Marginariella* spp. and *Xiphophora gladiata*, generally hosted low diversity and densities of epifauna, particularly gammarid amphipods, compared to the morphologically complex *Carpophyllum flexuosum*, *Cystophora scalaris* and *Sargassum sinclairii*. Thus, the effect that the invasive *U. pinnatifida* has on the abundance and

Table 1. Mean density values (ind. 100 g^{-1} blotted seaweed) for the epifaunal taxa found in the seaweed species collected. Seaweed species are *Undaria pinnatifida* (*U*), *Marginariella urvilliana* (Mu), *M. boryana* (Mb), *Xiphophora gladiata* (X), *Desmarestia ligulata* (De), *Carpophyllum flexuosum* (Ca), *Cystophora scalaris* (Cy) and *Sargassum sinclairii* (S). Epifaunal taxa include copepods (CO), caprellid amphipods (CA); gammarid amphipods (GA), isopods (I), gastropods (G,) bivalves (B), polychaetes (P), fish (F) and shrimps (S). (See Supplement 2 at www.int-res.com/articles/supp/m582p045_supp.pdf for specific information on taxa composition of orders and families)

Epifaunal taxa	Seaweed species							
	U	Mu	Mb	X	De	Ca	Cy	S
Order Tanaidacea	0.79	0.37	0.75	2.02	3.18	1.34	1.08	1.94
Class Ostracoda	4.73	2.30	2.28	1.69	1.44	13.04	4.11	31.55
Class Maxillopoda (CO)	**172.87**	**92.56**	**57.56**	**150.99**	**378.65**	**582.88**	**342.40**	**322.02**
Class Pycnogonida	0.04	0.02	0.05	0.15	0.66	1.15	0.02	0.00
Infraorder Brachyura	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00
Phylum Nematoda	0.45	0.25	0.34	0.65	0.00	0.23	0.24	0.09
Phylum Nemertea	0.06	0.25	0.06	0.19	0.00	0.03	0.04	0.07
Family Caprellidae (CA)	0.40	0.25	0.15	1.10	8.17	20.69	4.95	10.30
Family Aoridae (GA)	1.91	0.80	0.54	0.50	10.10	73.93	26.65	49.51
Family Podoceridae (GA)	0.60	0.01	0.53	1.21	1.85	17.41	27.49	4.47
Family Hyalidae (GA)	0.95	0.27	5.18	4.26	2.89	4.54	74.53	4.55
Family Stegocephalidae (GA)	0.15	0.06	0.26	0.07	1.33	0.02	0.25	0.27
Family Ischyroceridae (GA)	0.80	1.61	0.46	3.45	1.93	38.96	32.69	48.49
Family Isaeidae (GA)	0.31	0.06	1.44	1.50	0.51	3.27	18.39	3.06
Family Ampithoidae (GA)	0.22	1.61	0.02	0.07	0.00	2.26	0.00	0.00
Family Eusiridae (GA)	1.74	2.00	0.25	2.61	0.41	37.88	20.62	76.40
Family Corophiidae (GA)	0.00	0.00	0.05	0.02	0.00	0.80	0.12	0.00
Family Lysianassidae (GA)	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00
Family Amphilochidae (GA)	0.01	0.00	0.00	0.02	0.00	0.40	0.15	0.30
Family Gammaridae (GA)	0.20	0.12	0.03	0.32	0.06	2.98	0.04	0.13
Unidentified amphipods (GA)	6.96	3.65	9.22	11.37	28.81	172.28	88.56	255.74
Total amphipods	**14.26**	**10.44**	**18.19**	**26.50**	**56.06**	**375.42**	**294.43**	**453.22**
Family Idoteidae (I)	0.09	0.06	0.06	0.44	0.00	1.62	2.29	6.28
Family Limnoriidae (I)	0.97	0.23	2.28	3.12	0.16	0.34	0.08	0.16
Family Plakarthriidae (I)	0.01	0.72	0.07	0.13	0.00	0.28	0.03	1.13
Family Sphaeromatidae (I)	0.35	0.29	3.10	0.53	1.10	1.00	1.76	12.23
Family Paranthuridae (I)	0.02	0.06	0.10	0.00	0.00	0.00	0.00	0.00
Family Jaeropsidae (I)	0.47	1.19	0.76	0.19	0.48	0.20	0.23	0.34
Unidentified isopods (I)	0.22	0.01	0.30	0.10	0.00	0.15	0.37	0.00
Family Trochidae (G)	0.52	0.32	0.06	0.58	1.79	5.45	4.09	11.70
Family Scissurellidae (G)	1.94	0.50	0.93	2.96	0.00	13.30	24.94	20.39
Family Eatoniellidae (G)	0.42	0.32	3.84	2.10	5.03	4.87	5.22	13.62
Family Muricidae (G)	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Superfamily Seguenzioidea (G)	0.00	0.12	0.00	0.00	0.00	0.64	0.35	0.00
Family Rissoceae (G)	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00
Family Rosaea (G)	0.00	0.00	0.05	0.00	0.34	0.17	0.05	1.03
Unidentified gastropods (G)	1.93	0.82	3.72	2.32	14.14	18.67	13.09	75.12
Family Philobryidae (B)	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00
Family Mytilidae (B)	0.00	0.00	0.02	0.04	0.00	0.00	0.00	0.00
Unidentified Bivalvia (B)	0.00	0.02	0.04	0.02	0.00	0.00	0.00	0.00
Family Sabellidae (P)	2.05	0.29	10.53	0.59	1.26	1.20	0.12	0.29
Family Nereididae (P)	1.15	0.35	0.71	0.16	1.00	3.21	1.17	0.67
Family Syllidae (P)	0.58	0.17	0.46	0.07	0.13	0.13	0.05	0.00
Family Serpullidae (P)	0.10	0.09	0.00	0.02	0.00	5.74	0.01	0.38
Family Terebellidae (P)	0.25	0.11	0.15	0.00	0.17	0.00	0.02	0.06
Family Phyllodocidae (P)	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Family Eucinidae (P)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Family Spionidae (P)	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Family Maldanidae (P)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Family Hesionidae (P)	0.05	0.04	0.00	0.00	0.00	0.41	0.06	0.00
Unidentified Polychaetes (P)	1.96	0.43	1.60	1.24	0.48	5.87	1.12	0.57
Family Gobiesocidae (F)	0.00	0.08	0.00	0.09	0.55	0.00	0.00	0.00
Family Hippolytidae (S)	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Family Mysidae (S)	0.00	0.02	0.00	0.00	0.00	0.04	0.00	0.00
Family Ophiuridae	0.07	0.11	0.02	0.00	0.00	0.01	0.00	0.00
Miscellaneous	**19.20**	**9.37**	**32.28**	**19.25**	**31.88**	**79.08**	**60.50**	**177.56**
Total epifauna	**206.32**	**112.38**	**108.04**	**196.74**	**466.60**	**1037.38**	**697.33**	**952.80**

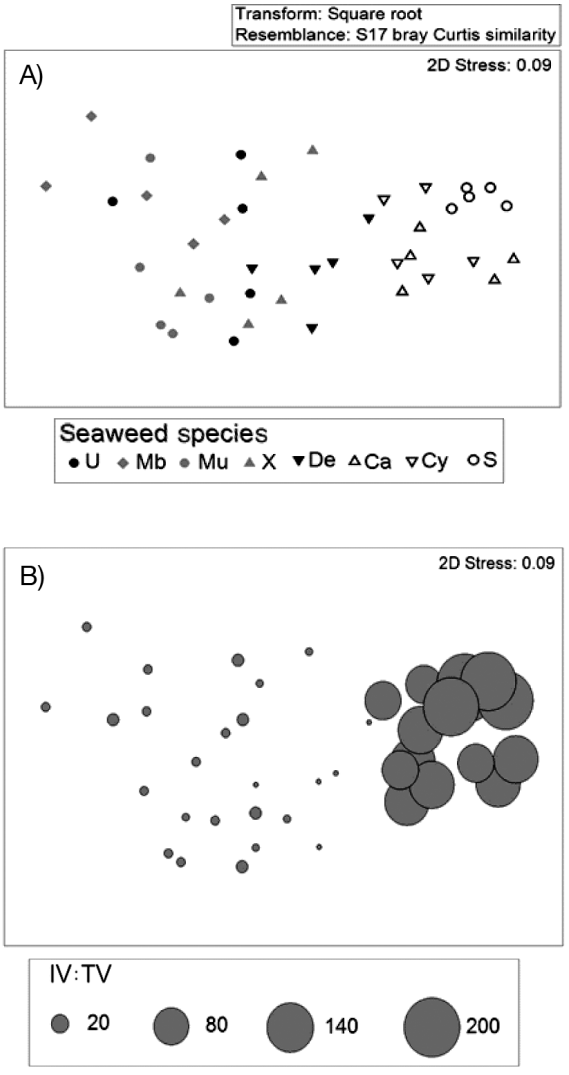

Fig. 1. Non-metric multidimensional scaling (nMDS) (A) on the epifaunal samples (subset 1) collected from *Undaria pinnatifida* (U), *Marginariella boryana* (Mb), *M. urvilliana* (Mu), *Xiphophora gladiata* (X), *Desmarestia ligulata* (De), *Cystophora scalaris* (Cy), *Carpophyllum flexuosum* (Ca) and *Sargassum sinclairii* (S); and (B) on a bubble plot showing the values of the interstitial volume to thallus volume (IV:TV) ratio values corresponding to each epifaunal sample. nMDS plots were created using Bray-Curtis dissimilarity matrices for density data that were square-root transformed

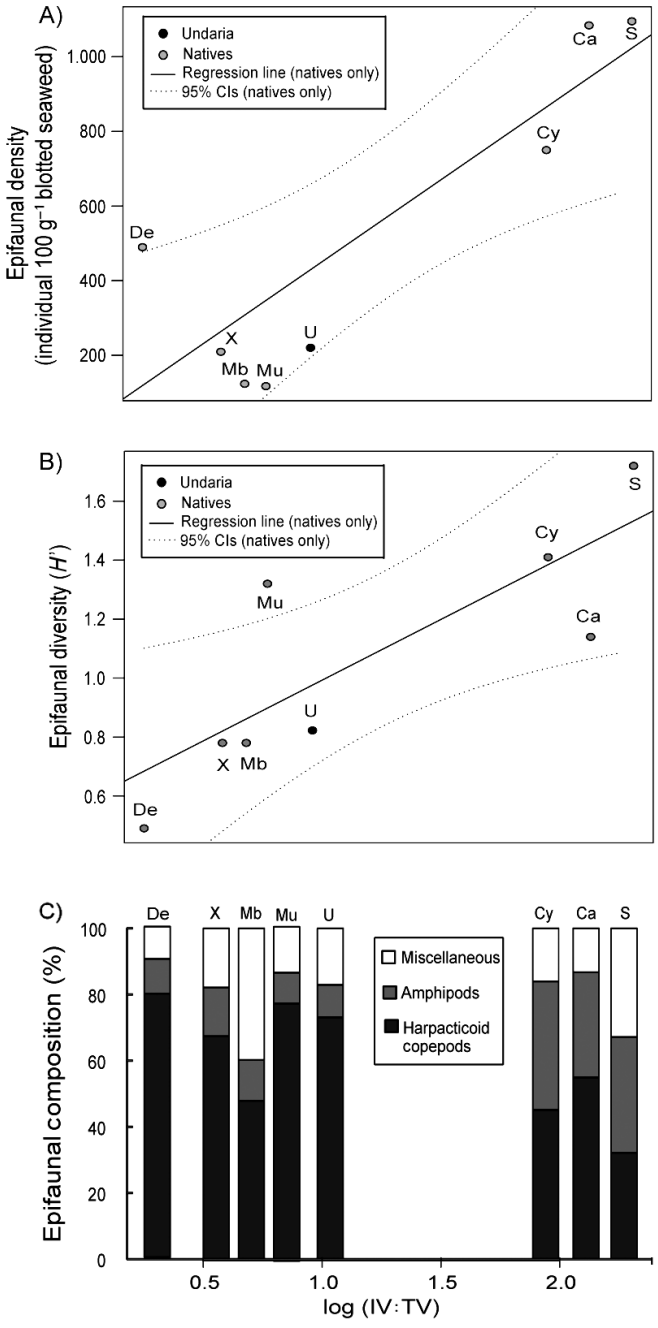

Fig. 2. (A) Relationship between log (interstitial volume to thallus volume, IV:TV ratio) and epifaunal density recorded on different seaweed species. (B) Relationship between log (IV:TV ratio) and epifaunal diversity recorded on different seaweed species. (C) Proportion of harpacticoid copepods (dark grey bars), amphipods (light grey bars) and miscellaneous (clear bars) to total epifaunal densities recorded on the different seaweeds ordinated according to their log (IV:TV ratio). The category 'amphipods' represents the order Amphipoda and includes the suborders Gammaridae, Caprellidae, unidentified and <1 mm amphipods. Diversity index (*H'*) was calculated following Krebs (1989) as explained in the 'Materials and methods'. Seaweed species are as defined in Fig. 1

composition of epifaunal assemblages appears to be due mainly to the morphological traits. The extent of its impacts will be determined by its relative abundance and whether or not it displaces native seaweeds.

Host morphology has often been suggested to drive patterns in epifaunal assemblages inhabiting seaweeds (e.g. Coull & Wells 1983, Hacker & Steneck 1990, Christie et al. 2007, Janiak & Whitlatch 2012), including comparisons between native and invasive species (e.g. Viejo 1999, Wernberg et al. 2004, Caca-

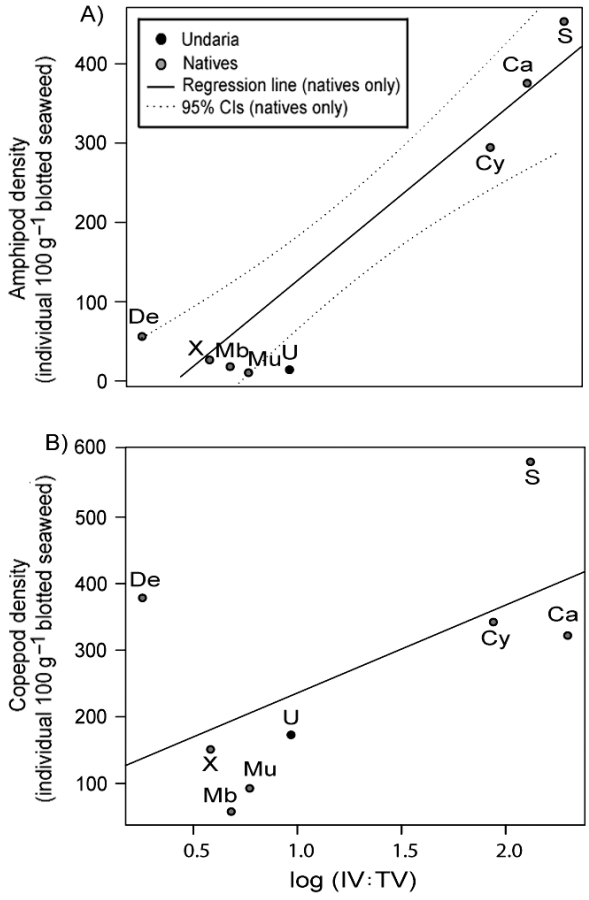

Fig. 3. Relationship between log (interstitial volume to thallus volume, IV:TV ratio) and the density of (A) amphipod and (B) copepod taxa on different seaweed species (defined as in Fig. 1)

belos et al. 2010, Tanner 2011, Gestoso et al. 2012), but the specific morphological features that drive such differences and their relationship with epifauna are poorly understood. Our results support those of Hacker & Steneck (1990) in showing that spatial components of seaweed morphology (space between fronds) are more important than structural components (traits of the fronds) in determining epifaunal assemblage structure on seaweed, although we recognise that those spatial traits are likely to be influenced by structural attributes. Our study also shows that for *U. pinnatifida*, this applies regardless of the geographic origin of the seaweeds (i.e. native vs. invasive), and that the TV:IV ratio can predict epifaunal composition, as suggested by Fukunaga et al. (2014). We support the suggestion of Arnold et al. (2016) that *U. pinnatifida* has a similar epifauna to structurally comparable native seaweed species, by using host morphological traits as explanatory variables in our analysis (rather than subjective comparisons), and by extending the generality of their results to a southern hemisphere location. The results here caution against inferring the absence of host morphological influences on epifauna based solely on structural components such as surface area (Cacabelos et al. 2010), although other structural properties such as degree of branching (not measured here) can sometimes directly influence epifauna (Chemello & Milazzo 2002).

Lower densities and diversities of epifauna recorded on *U. pinnatifida* and the morphologically simpler native species were generally expected since those host species provide a poorer refuge against predation or wave action (e.g. Gee & Warwick 1994, Christie et al. 2007, Zamzow et al. 2010, Taylor 2015). The diversity and total abundance of epifauna on *U. pinnatifida* were slightly lower than expected for the seaweed's morphology, based on regressions run on epifauna from the native seaweed species. This could be due simply to statistical error in the location of the regression lines, but the low epifaunal density and diversity observed on the invasive kelp may also have a biological basis. For example, epiphytes, which increase the refuge value of seaweeds and are important food sources (e.g. Hall & Bell 1988, Duffy 1990, Martin-Smith 1993, Pavia et al. 1999), were rarer on *U. pinnatifida* than on the other seaweeds (R. Suárez-Jiménez pers. obs.). Furthermore, *U. pinnatifida* can host dissimilar faunal assemblages to native kelps with similar life history and growth strategies (Arnold et al. 2016). In relation to this, our results provide some evidence to support the hypothesis that small grazers (mesograzers) inhabit seaweed species that provide shelter from predation rather than those that are the best food sources (e.g. Duffy & Hay 1994, Jormalainen et al. 2001, Lasley-Rasher et al. 2011). Despite preferentially consuming *U. pinnatifida* over more complex seaweeds (Jiménez et al. 2015b), lower abundances of the amphipod grazer *Aora typica* (see Table 1) were recorded on *U. pinnatifida.* In addition, the host's persistence through time affects habitat selection of some crustaceans (Duffy & Hay 1991, Wernberg et al. 2004, Gestoso et al. 2010), so the marked seasonality of *U. pinnatifida* relative to the native perennial species (Jiménez et al. 2015a) may make it a less stable habitat over time. In this sense, differences in the epifauna between *U. pinnatifida* and the native species were consistent across different months (Supplement 1A), suggesting that the invasive species will have a similar impact on algal epifauna throughout time when present.

The residual variation around our regressions of epifaunal density and diversity on host morphology suggests that the epifaunal communities we examined are also affected by factors other than morphology. Seaweed secondary metabolites have the potential to influence epifauna that graze on their host and/or use defended seaweeds as a refuge from larger consumers (Hay et al. 1987), and depauperate epifaunal communities on invasive seaweeds have been attributed to host chemical defences (e.g. Wikström et al. 2006). Evaluating the effects of secondary metabolites was beyond the scope of our study, but it is clear that chemical defences have the potential to modify the effects of morphological factors, and may therefore constrain the use of morphology to predict the suitability of an invasive seaweed as a host for local epifauna.

Results presented here suggest that epifauna on *U. pinnatifida* individuals are likely to contribute less to secondary productivity than epifauna on more structurally complex native seaweeds. Kelps usually host epifaunal communities that are less abundant than, and of different composition to, non-kelps whether native (Taylor & Cole 1994) or invasive (e.g. Schmidt & Scheibling 2006, Cacabelos et al. 2010, this study). Epifauna on kelps make a smaller contribution to secondary productivity than epifauna on morphologically complex seaweeds (Cowles et al. 2009). The nature of the contribution can also vary. *U. pinnatifida* hosted a very high proportion of harpacticoid copepods (73%) and a very low proportion of amphipods (9%, mostly *A. typica*; see Fig. 2C and Supplement 2), in contrast to more structurally complex species. Harpacticoid copepods are known to feed on fine particulate detritus or benthic microalgae (Coull 1999), while the amphipod *A. typica* is a grazer and suspension feeder (Taylor & Brown 2006, Jiménez et al. 2015b). High densities of harpacticoid copepods have been previously recorded on *U. pinnatifida* in both its native (e.g. Ho & Hong 1988, Park et al. 1990, Rho et al. 1993) and invasive range (Peteiro & Freire 2013). This suggests that *U. pinnatifida*'s biomass is likely to reach upper trophic levels (i.e. fish) through the detrital pathway (i.e. copepod consumption of detritus), in contrast to structurally complex seaweeds that likely reach upper trophic levels through direct consumption by the epifauna of the host or other algae. However, this has not yet been established, and the contribution of *U. pinnatifida* to higher trophic levels (Jiménez et al. 2015b) requires further research.

Based on seaweed structure, our results suggest that *U. pinnatifida* will most likely have a negative effect on the native epifaunal communities of regions that it colonises, supporting Arnold et al. (2016), who showed that the species provides a poor habitat for associated fauna in the UK. However, epifaunal communities will be compromised only if *U. pinnatifida* displaces native seaweeds that play a greater role in supporting them. The ability of *U. pinnatifida* to displace and/or alter seaweed communities remains unclear, and the impacts appear to be site-specific (e.g. Casas et al. 2004, Farrell & Fletcher 2006, Raffo et al. 2009, Thompson & Schiel 2012). Also, the effects of habitat-forming invasive species are known to be biomass dependent (Gribben et al. 2013), thus high abundances of *U. pinnatifida* (e.g. Curiel et al. 1998, Casas et al. 2004, Jiménez et al. 2015a) could be indicative of potential environmental change. In addition, the characteristics of the receiving environment, together with the invasion dynamics, are crucial to enable accurate predictions regarding impacts on the epifaunal community and beyond. For example, Irigoyen et al. (2011) showed that *U. pinnatifida* can provide a larger and more complex habitat compared to native species, which results in higher richness and diversity of benthic macrofaunal assemblages, further suggesting that relative morphological complexity is the driver of the differences.

In conclusion, our study suggests that the epifaunal community of *U. pinnatifida* is more affected by the morphology of its host than the host's recent geographical origin (i.e. whether it is native or invasive), and future research should investigate the generality of this result for other regions and other invasive seaweeds. The net impact of invasive seaweeds on epifauna at the scale of the reef will depend on whether the invasive seaweed is supplementing or displacing native seaweed, as well as its relative density and morphological complexity. We argue that the refuge value of host seaweeds, measured as spatial components, can be useful for predicting impacts of invasive seaweeds on epifaunal communities. The potential of invasive seaweeds such as *U. pinnatifida* to alter epifaunal communities, secondary productivity and ultimately ecosystem structure, should be a matter of concern.

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