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Between-habitat variability in the population dynamics of a global marine invader may drive management uncertainty

Graham Epstein[a,b,*], Dan A. Smale[a]

[a] Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK
[b] Ocean and Earth Science, University of Southampton, National Oceanography Centre Southampton, Waterfront Campus, European Way, Southampton SO14 3ZH, UK

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ABSTRACT

Understanding population dynamics of established invasive species is important for designing effective management measures and predicting factors such as invasiveness and ecological impact. The kelp *Undaria pinnatifida* has spread to most temperate regions of the world, however a basic understanding of population dynamics is lacking for many regions. Here, *Undaria* was monitored for 2 years, at 9 sites, across 3 habitats to investigate habitat-related variation in population structure, reproductive capacity and morphology. Populations on marina pontoons were distinct from those in reef habitats, with extended recruitment periods and higher abundance, biomass, maturation rates and fecundity; potentially driven by lower inter-specific and higher intra-specific competition within marinas. This suggests that artificial habitats are likely to facilitate the spread, proliferation and reproductive fitness of *Undaria* across its non-native range. More broadly, generalising population dynamics of invasive species across habitat types is problematic, thus adding high complexity to management options.

1. Introduction

The spread of invasive non-native species (INNS) is recognised as a major threat to global biodiversity and the provision of ecological goods and services. As well as ecological impacts, INNS have major socio-economic implications, causing losses of $120 billion per year in the USA alone (Early et al., 2016; Pimentel et al., 2005; Williams et al., 2010). Biosecurity measures are of principle importance in preventing the establishment and subsequent impacts of invasive non-native species. However, as no combination of biosecurity measures is entirely effective, active management of INNS within their non-native range is often needed (Early et al., 2016; McGeoch et al., 2016; Seebens et al., 2017; Simberloff et al., 2013). At the outset of an invasion process, an INNS will generally have a limited geographical range, relatively low propagule pressure, and have completed few reproduction cycles. It is therefore widely accepted that rapid response greatly increases the likelihood of eradication or containment (Beric and MacIsaac, 2015; Early et al., 2016). Rapid response measures require decisive action but relatively minimal understanding of the biology or ecology of an INNS (Simberloff, 2003). If an INNS is not removed, it is likely to increase its geographical range, population size and propagule pressure over time. Where this occurs, management activities may be constrained to limiting the size of populations or reducing their spread (Fraser et al., 2006; Hulme, 2006; Simberloff et al., 2013). In these situations, information on the biology and ecology of an INNS is critical for effectively designing and implementing management measures (Sakai et al., 2001; Simberloff, 2003).

Information on the population dynamics of INNS is also important to improve the wider understanding of general ecological processes, and to achieve a more holistic view of INNS management (Sakai et al., 2001). Differing life-history and morphological traits can exert a strong influence on a species' invasiveness, spread and ecological impact within recipient communities (Bauer, 2012; Duyck et al., 2007; Kolar and Lodge, 2001; Ricciardi and Cohen, 2007; Williamson and Fitter, 1996). In some cases, information on the traits or behaviours of an INNS may be available from within its native range, which can be useful in determining management options. However, as INNS often exhibit high phenotypic or genetic plasticity, traits and attributes recorded in the native range may differ from those exhibited within a non-native range (Kolar and Lodge, 2001; Williamson and Fitter, 1996; Zenni et al., 2014). INNS can also be found in differing habitat types in their non-native range, where they are often associated with modified or anthropogenic habitats, rather than natural habitats which may be more suitable in their native range (Airoldi et al., 2015; Glasby et al., 2007). As such, predicting an invader's traits based on its native ecology is problematic, and highlights the need for site-specific studies. Determining how the population biology of an INNS varies across regions or habitats should improve our understanding of potential impacts and,

* Corresponding author at: Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK.
E-mail address: graeps@mba.ac.uk (G. Epstein).

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consequently, inform management decisions and design of efficient and effective control methods.

The invasive kelp, *Undaria pinnatifida* (hereafter referred to as *Undaria*), is one of the most widespread marine invaders, and can now be found in many parts of the northeast and southwest Atlantic, southwest and east Pacific, and the Tasman Sea (Epstein and Smale, 2017b). In its non-native range *Undaria* is predominantly recorded on artificial substrates, particularly floating structures within ports, marinas and aquaculture sites (Cremades et al., 2006; Epstein and Smale, 2017a; Fletcher and Manfredi, 1995; Floc'h et al., 1996; Kaplanis et al., 2016; Veiga et al., 2014). However, *Undaria* is also found in natural habitats throughout much of its non-native range, predominantly within shallow rocky reef habitats that are sheltered or moderately exposed to wave action (Dellatorre et al., 2014; Epstein and Smale, 2017a; Fletcher and Farrell, 1999; James and Shears, 2016b; Russell et al., 2008).

In its native range, *Undaria* is an over-wintering annual species found on rocky substrates from the low intertidal to 18 m depth (Saito, 1975). It is also a major mariculture species, primarily grown on seeded ropes held at shallow depths (Yamanaka and Akiyama, 1993). Due to its importance in mariculture, a considerable volume of research has been conducted on native populations to examine reproduction, morphology, physiology, chemical properties and population dynamics in both natural and artificial habitats (e.g. Choi et al., 2007; Matsuyama, 1983; Nanba et al., 2011; Shibneva et al., 2013; Skriptsova et al., 2004; Watanabe et al., 2014). In its non-native range, several population studies have been conducted – primarily in Australasia but also in the USA and Argentina – either in natural or artificial habitats, but not both (Casas et al., 2008; James and Shears, 2016a; Primo et al., 2010; Schaffelke et al., 2005; Schiel and Thompson, 2012; Thornber et al., 2004). In the northeast Atlantic, where *Undaria* has been present since the early 1980s, understanding of its population dynamics remains severely limited (Castric-Fey et al., 1999a; Cremades et al., 2006; Murphy et al., 2016; Murphy et al., 2017). Furthermore, as *Undaria* is known to exhibit a relatively plastic life-history and morphology (James et al., 2015; James and Shears, 2016a; Nanba et al., 2011; Schiel and Thompson, 2012; Shibneva et al., 2013), formal examinations of population-level variability between habitats types and environmental settings are needed to better understand its non-native biology and potential role within invaded systems. Any dissimilarity in population dynamics between habitats could mediate its impacts upon native flora and fauna and have important implications for management decisions.

Undaria was first recorded in the UK in 1994, attached to floating marina pontoons in Port Hamble (Fletcher and Manfredi, 1995), but can now be found across much of the UK, predominantly on artificial structures such as marina and harbour pontoons (Epstein and Smale, 2017a; Fletcher and Farrell, 1999; Heiser et al., 2014; Kraan, 2016; Minchin and Nunn, 2014). In some areas *Undaria* has also been recorded on natural rocky substrates (Arnold et al., 2016; De Leij et al., 2017; Epstein and Smale, 2017a; Fletcher and Farrell, 1999; Heiser et al., 2014). Although *Undaria* has been present in the UK for almost 15 years, there remains a dearth of information regarding its population dynamics, even though it is listed as a priority species for monitoring and surveillance as part of obligations to the Marine Strategy Framework Directive (Stebbing et al., 2015). In this study, we examined spatiotemporal variability in population structure, reproductive activity and morphology of *Undaria* over 2 years at 9 sites, representing 3 habitat types: subtidal rocky reef, intertidal rocky reef and marina pontoons. The aim was to: 1) characterise spatiotemporal variability in the population structure of *Undaria* in its non-native range; 2) determine the influence of habitat-type on the population dynamics and morphology of *Undaria*; and 3) consider how variability patterns may affect potential management. The over-arching objective was to adopt *Undaria* as a case study to examine how environmental setting may mediate population dynamics of marine INNS in general and, in turn, influence approaches to management.

2. Materials & methods

2.1. Site selection

Plymouth Sound is one of few areas in the UK where *Undaria* is widespread in both artificial and natural habitats (Epstein and Smale, 2017a). It was first recorded in 2003 within marinas and in 2011 on natural substrates (NBN, 2017). Due to the widespread distribution of *Undaria* (Arnold et al., 2016; De Leij et al., 2017; Epstein and Smale, 2017a; Heiser et al., 2014), the extensive areas of intertidal and subtidal rocky-reef, as well as numerous marinas (Knights et al., 2016), Plymouth Sound is an ideal location to conduct long-term studies on *Undaria* populations.

Selection of 9 long-term study sites (3 each of intertidal reef, subtidal reef and marinas) was carried out between 10th March and 5th April 2016. Sites were chosen based on the following criteria: 1) available safe access points; 2) approval to conduct scientific work; 3) widespread occurrence of *Undaria* (based on previous information or in-situ sightings); 4) limited human disturbance; 5) similar substrate type within habitats; and 6) extensive suitable substrate ($\geq 40\,m^2$ in marinas, $\geq 100\,m^2$ reef sites). During the site selection process, visual searches of the low intertidal zone were conducted across the Plymouth waterfront and at Mount Batten (Fig. 1); subtidal searches were conducted at 7 sites across the same area by SCUBA; while site visits and discussions for permissions to work at marinas were conducted at 4 locations (Fig. 1). Further local knowledge on suitability of sites and *Undaria* status were gained for both rocky-reef (Smale, pers. comm.) and marinas (Wood, pers. comm.). Three marina and reef sites were selected across the Plymouth waterfront, with subtidal reef sites deeper and adjacent to intertidal reef sites (Fig. 1).

The intertidal and subtidal rocky reef sites were all sheltered to moderately-sheltered from wave action and were characterised by extensive bedrock platforms interspersed with areas of larger boulders and compacted cobbles. The marina sites were distributed along the Plymouth waterfront all within sheltered, non-drying harbours, with similar concrete pontoon constructions (Fig. 1). At reef sites, in order to aid relocation, permanent markers were placed at each site; a stainless steel screw and coloured markers were fixed to the shore at intertidal sites, and a large clump-weight with a sub-surface marker buoy was placed at each subtidal site. A light and temperature sensor (HOBO Temperature/Light weather-proof Pendant Data Logger 16k, Onset) was also deployed for the duration of the study, recording temperature (in degrees Celsius) and illuminance (lux) at 30 min intervals. The loggers were attached to permanent markers at reef sites, or adjacent to the pontoons at marinas.

2.2. Sampling & population structure

Sampling of *Undaria* populations was carried out every 3 months (March, June, September, December) from March 2016 to December 2017, with all 9 sites sampled within a 2-week period during each sampling event. As *Undaria* is predominantly found in the low intertidal to shallow subtidal zone of rocky-reefs (Fletcher and Farrell, 1999; Heiser et al., 2014; Saito, 1975), subtidal sites were restricted to depths of 0.5–1.2 m below chart datum and intertidal sites to 0.3–1 m above chart datum. At each sampling event $10 \times 0.25\,m^2$ haphazard quadrats (stratified to rocky substrate) were placed within an area of approximately $100\,m^2$ around the permanent marker at each site. Due to the large size of the sampling area it is highly unlikely that quadrats would have been placed in directly the same location over the 8 sampling events. All subtidal sites were sampled using SCUBA, and when the tidal range allowed intertidal sites were sampled on low-spring tides, otherwise all sampling was carried out by SCUBA.

Sampling within marinas was carried out on the vertical sides of floating pontoons, with the entire area being fully immersed at all times; the depth of the sampling area was therefore 0–0.4 m below the

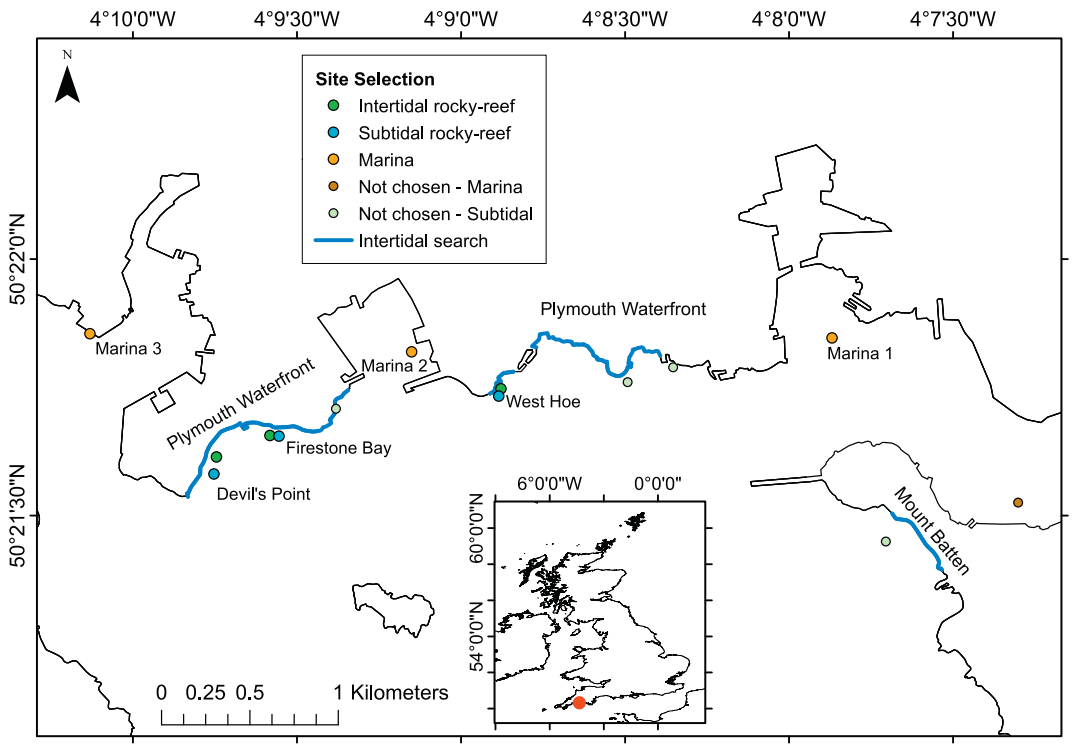

Fig. 1. Study sites in Plymouth Sound (location of Plymouth within the UK shown as red point on inset map). Selection of 9 long-term study sites, 3 each of intertidal rocky-reef (large green points) subtidal rocky-reef (large blue points) and marinas (large orange points), was carried out in March–April 2016. This included visual searches of the low intertidal zone (blue line), subtidal searches (green points) and marina site visits (brown points). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

surface. During each sampling event, 10 × 0.25 m^2 haphazardly placed quadrats were positioned blindly against the pontoon surface. Sampling was restricted to approximately 40 m^2 of pontoon surface in the outer section of the marina based on substrate suitability, interactions with vessels and human disturbance. Due to the relatively limited area available for sampling, a note of the position of each quadrat was taken to avoid overlapping quadrat samples during the study.

All visible *Undaria* sporophytes were removed from each quadrat by gently prising the holdfast from the substrate, and were placed into collection bags and returned to the laboratory for further analysis. Most individuals could be identified to species by eye, however when needed, confirmation of the species as *Undaria* was carried out using light-microscopy and the presence of Yendo cells (Castric-Fey et al., 1999b, Fig. 2). For each quadrat the *Undaria* sporophytes were sorted into developmental stages (Fig. 2, Table 1), based on a categorical classification system numbered from 0 to 5 (adapted from Casas et al., 2008). The abundance and biomass of *Undaria* sporophytes categorised to each developmental stage was recorded for each quadrat separately.

2.3. Morphology

To quantify spatiotemporal variability in *Undaria* sporophyte morphology, up to 10 random sporophytes representing each developmental stage were randomly selected and retained from each sites, during every sampling event. Attributes measured to the nearest 0.1 cm were: Stipe width (SW), stipe length (SL), lamina width (LW), lamina length (LL), sporophyll width (SPW) and sporophyll length (SPL) (Fig. 4). Dependent on the developmental stage, different morphological attributes were recorded based on their presence and appropriateness for describing the morphology (developmental stages 0 & 1 = SW, SL, LW, LL; developmental stages 2, 3 & 4 = SL, LW, LL, SPW, SPL; developmental stage 5 = SW, SL, SPW, SPL).

2.4. Reproductive activity

Reproductive activity of *Undaria* populations was assessed using a standardised spore release method from a sample of mature sporophytes (method adapted from Schaffelke et al., 2005). At each sampling event up to 10 random mature sporophytes (developmental stage 2 or 3, and SPW > 2 cm) were selected from each site. Due to the seasonality of *Undaria* populations, 10 mature sporophytes were not always found across the 10 quadrats. Therefore, where mature sporophytes were found, the average sample size for each site was 7.7 sporophytes (ranging from 3 to 10 dependent on the sampling event). Where no reproductive sporophylls were found reproductive activity was assumed to be zero. As different parts of the sporophyll mature at different rates (Schaffelke et al., 2005), 3 sub-samples of sporophyll tissue were taken from each sporophyte. Discs of 0.6 cm in diameter were punched from each sporophyll, one towards the top of the sporophyll, one from the middle and one from towards the bottom. Each disc was taken from the centre of the sporophyll lobe, and the total biomass of the three discs was recorded to the nearest 0.01 g. The remainder of the sporophyll was removed from the stipe and also weighed to the nearest 0.01 g. As a procedural control, 3 random samples of 0.6 cm diameter discs of non-reproductive blade tissue were also selected at each sampling event and site. All discs were wiped clean and patted dry using absorbent paper. They were then placed in individually labelled 2 ml Eppendorf tubes and incubated overnight at 4 °C in complete darkness. Following the incubation, 0.96 ml of room temperature 30 kDa filtered seawater was added to each tube to induce spore release, and was left for 1 h. To end the spore release 0.04 ml of 10% formalin (diluted in filtered seawater) was then added to each tube and the sporophyll disc was removed using sterile forceps.

The number of spores within the 1 ml solution in each Eppendorf was estimated using a BD Accuri C6© flow cytometer, using a 20 mW 488 nm solid state blue laser. *Undaria* zoospores are generally spherical, measuring approximately 4 μm in diameter upon release (Petrone et al.,

Fig. 2. Developmental stages of *Undaria pinnatifida* sporophytes (adapted from Casas et al., 2008). Early-Mid-Late indicates growth towards the next developmental stage for comparative purposes; however this distinction was not recorded. Each box shows a single sporophyte with a magnified image of the sporophyll/stipe, except 'Stage 0 — Early' which shows two sporophytes and a magnified section of the outer part of the blade indicating the presence of Yendo cells (see Castric-Fey et al., 1999b). Table 1 describes each stage.

Table 1
Description of *Undaria pinnatifida* developmental stages as shown in Fig. 2.
Classification adapted from Casas et al. (2008).

Developmental stage	Developmental category	Description
Stage 0	Recruit	No defined midrib or pinnate blade divisions. Identified as *Undaria* due to presence of Yendo cells (as shown in first image of Fig. 2)
Stage 1	Recruit	Defined midrib and pinnate blade divisions, no sporophyll
Stage 2	Mature	As stage 1 but with ruffled sporophyll which does not surround the stipe
Stage 3	Mature	As stage 1 but with ruffled sporophyll surrounding the stipe
Stage 4	Senescing	Decaying sporophyte identified by dark colouration of blade and sporophyll, and distinct morphology of blade
Stage 5	Senescing	Blade completely lost; with or without sporophyll

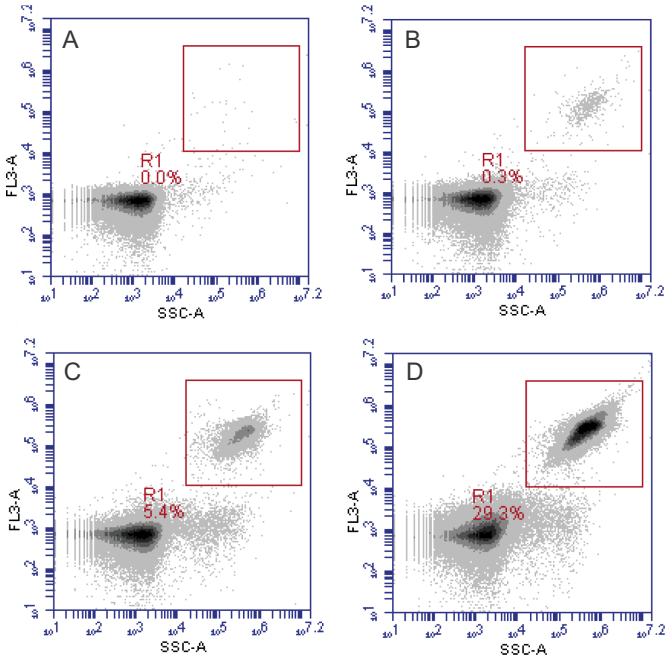

Fig. 3. An example of flow cytometry density plots from a procedural control (A) and three sporophytes with varying reproductive activity (B–D). Side scatter (SSC-A; light scattered by particles at 90° to the direction of the laser beam, recording a proxy of particle size) is plotted against red fluorescence (FL3-A; wavelength > 670 nm). A single square electronic gate (red box) was drawn on the density plots around the point cloud to select the occurrence of spores; its position was the same within each set of samples. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

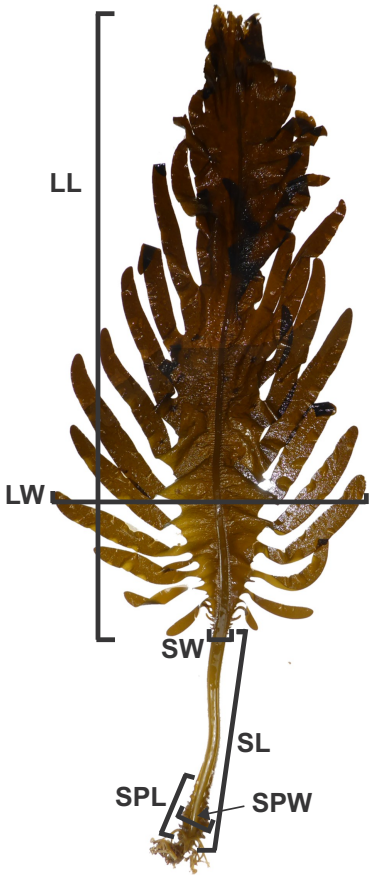

Fig. 4. Morphological attributes measured for *Undaria pinnatifida* sporophytes (example shown is developmental stage 2). Attributes measured to the nearest 0.1 cm were: Stipe width (SW), stipe length (SL), lamina width (LW), lamina length (LL), sporophyll width (SPW) and sporophyll length (SPL).

2011). Therefore, acquisition thresholds of forward light scatter (FSC; light scattered by particles at narrow angles in the same direction as the laser beam, recording a proxy of particle size) was set at 2000, and red fluorescence (FL3; wavelength > 670 nm) was set at 900. Based on previous experience these thresholds are considered appropriate for capturing autofluorescent picoplankton and small nanoplankton such as *Undaria* spores (van der Merwe et al., 2014). A 30 µl subsample was analysed from each Eppendorf at a flow rate of 66 µl/min and a core size of 22 µm. For each particle passing the laser, FL3 and side scatter (SSC; light scattered by particles at 90° to the direction of the laser beam, recording a proxy of particle size) values were recorded on logarithmic density plots generated using the BD Accuri CFlow© Plus software. These plots allowed for optimal distinction between instrument or water sample background noise and *Undaria* spores. Where spore release had occurred, a distinct "point cloud" could be identified on the density plots at values > 10^4 FL3 and SSC (Fig. 3), which is characteristic of autofluorescent phytoplankton of the size of *Undaria* spores (van der Merwe et al., 2014). For each set of samples a single square electronic gate was drawn on the density plots around the point cloud to select the occurrence of spores. The number of particles within the gated region was then enumerated using the software. In order to remove further procedural noise, the average number of particles (rounded to the nearest whole spore) counted in the gated region of the three non-reproductive procedural control samples was subtracted from the count for each sporophyll sample (if the mean procedural count was greater than the number counted for a sample, the value was set as zero, not a negative value). Overall, this gave an estimate of the number of spores present in 30 µl of the solution in each Eppendorf. Values were averaged for the 3 sub-samples of each sporophyll, and multiplied to gain two metrics of reproductive activity — number of spores released per cm^2 of sporophyll tissue, and total number of spores per sporophyll based on the percentage biomass of the 3 sporophyll discs from total sporophyll biomass.

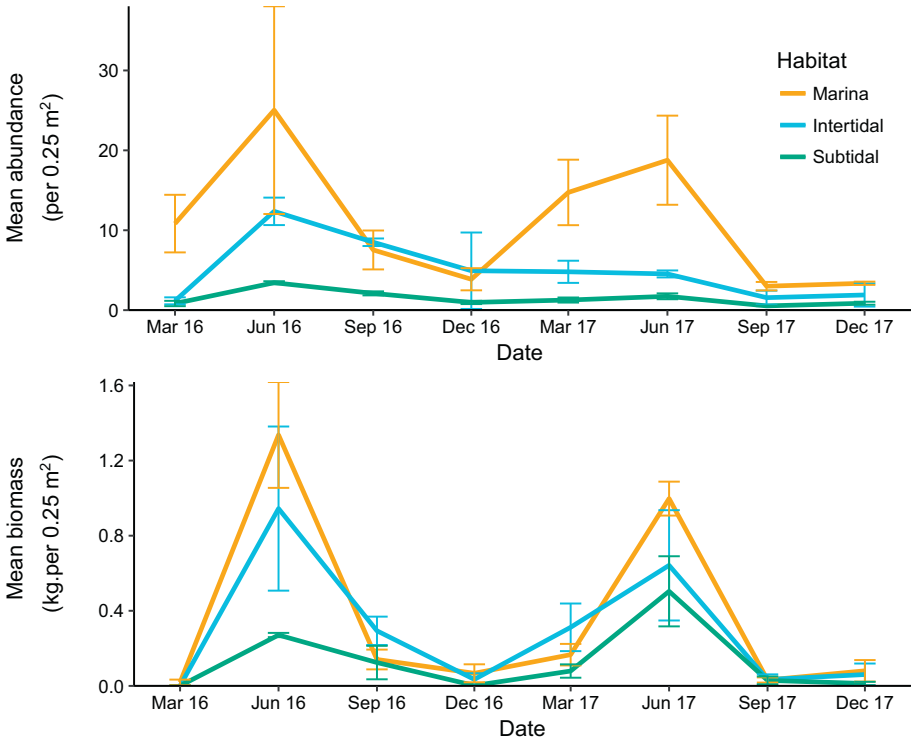

Fig. 5. Mean abundance and biomass of *Undaria pinnatifida* (± standard error) found across the study period in each habitat (marina = orange, intertidal reef = blue, subtidal reef = green). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

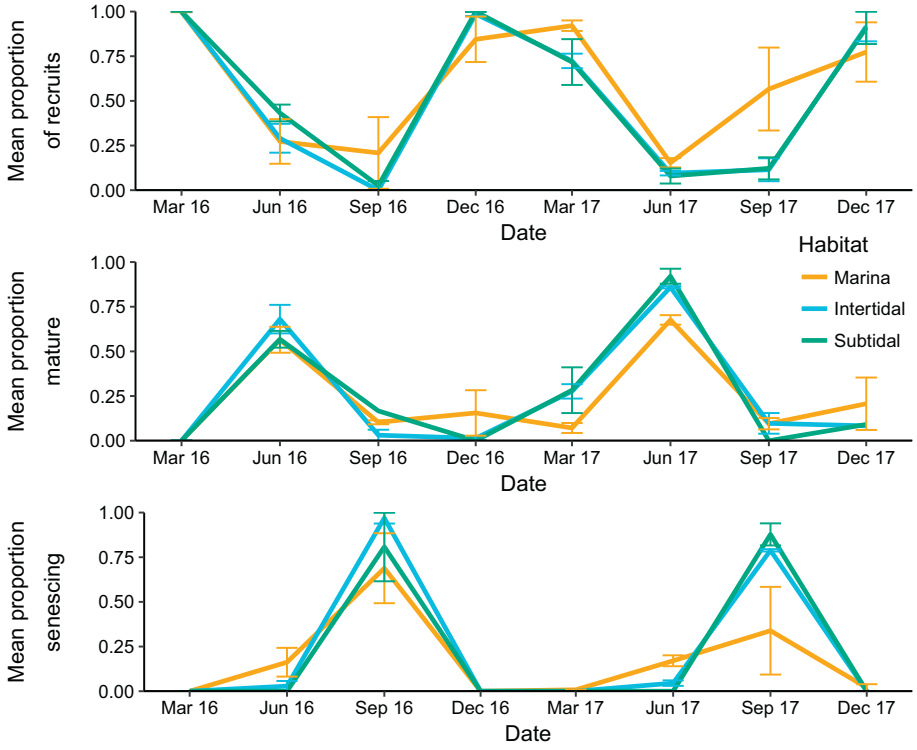

Fig. 6. Mean proportion of recruits, mature and senescing sporophytes of *Undaria pinnatifida* (± standard error) found across the study period in each habitat (marina = orange, intertidal reef = blue, subtidal reef = green). Table 1 describes classification of sporophytes to each developmental category. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.5. Data analysis

Mean abundance and biomass values for *Undaria* were generated for each site and sampling event (from n = 10 quadrats) prior to formal analysis. Reproductive activity was also averaged within site at each sampling event due to uneven sample sizes. Prior to statistical analysis all data were log transformed (log[x + 1]) due to strong right-skewness and heterogeneity of variances. Using three-way ANOVA, values of abundance, biomass and reproductive activity were modelled as a function of "habitat" (categorical; 3 levels: Marina, Intertidal, Subtidal), "month" (categorical; 4 levels: March, June, September, December) and "year" (categorical; 2 levels: 2016, 2017). Optimal models were chosen using backward selection. A full model with all predictor variables and their interactions was constructed first, and model terms were serially

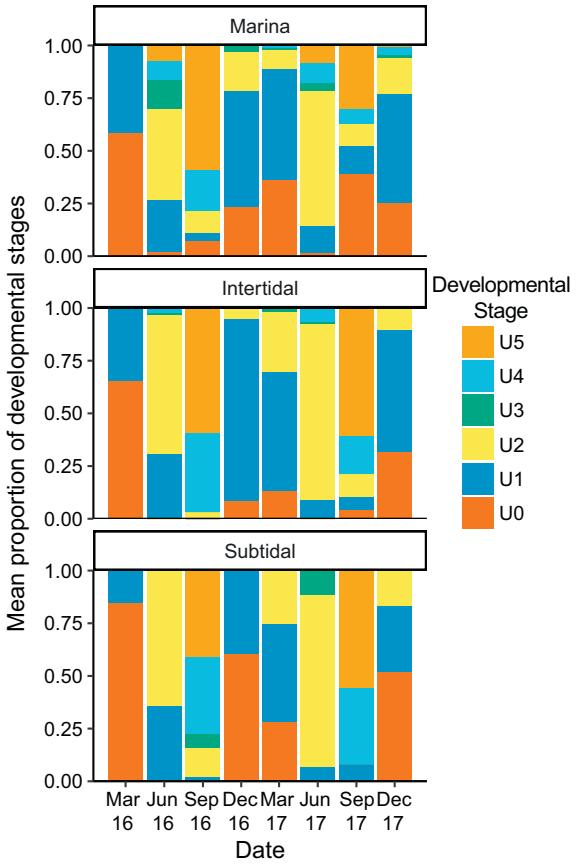

Fig. 7. Proportion of each developmental stage of *Undaria pinnatifida* in each habitat across the study period (Stage 5 = orange, 4 = light blue, 3 = green, 2 = yellow, 1 = dark blue, 0 = red). Table 1 describes classification of sporophytes to each developmental stage. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

excluded based on their complexity and their significance value (i.e. the coefficient with the highest complexity and lowest significance value was dropped and the model rerun). Terms were excluded until the next coefficient that would be dropped had a p value < 0.05. Each model was compared to the subsequent nested model using ANOVA to confirm that a significant term had not been excluded. Validation of the optimal model was carried out using diagnostic plots, and significant pairwise differences between habitats were tested using post hoc F-tests with Holm adjusted p-values.

Population structure was described by calculating the relative proportion of recruits, mature and senescing sporophytes within each site at every sampling event. Statistical differences in population structure were assessed using permutational ANOVA (PERMANOVA) on Bray-Curtis similarity matrices of untransformed proportion data (Anderson et al., 2008; Clarke et al., 2014). Using the same model design as above, a PERMANOVA was initially constructed using all coefficients and their interactions. Optimal model selection was carried out as above, until a coefficient with a p value > 0.05 could not be dropped. Post hoc tests for the effect of individual habitats were carried out using pair-wise PERMANOVA, and similarity percentage breakdowns (SIMPER) were used to determine the principal contributors to the observed dissimilarity within significant pairwise contrasts.

Difference in morphology of *Undaria* between habitats was also assessed using multivariate techniques, with morphological attributes of individual plants treated as a multivariate response. For each developmental stage separately, morphological data were normalised (subtracting the mean and dividing by the standard deviation for each morphological attribute) in order to bring each attribute to comparable dimensionless scales. Resemblance matrices were constructed based on Euclidean distance, and the dissimilarity between habitats was visualised using threshold metric multidimensional scaling (tmMDS) on bootstrap averages with their 95% confidence regions. Statistical differences in morphology between habitats was assessed using PERMANOVA with Habitat (3 levels, fixed factor), and Site (6 levels, random factor nested within habitat) as the independent variables. Post hoc tests for the effect of individual habitat were carried out using pair-wise PERMANOVA.

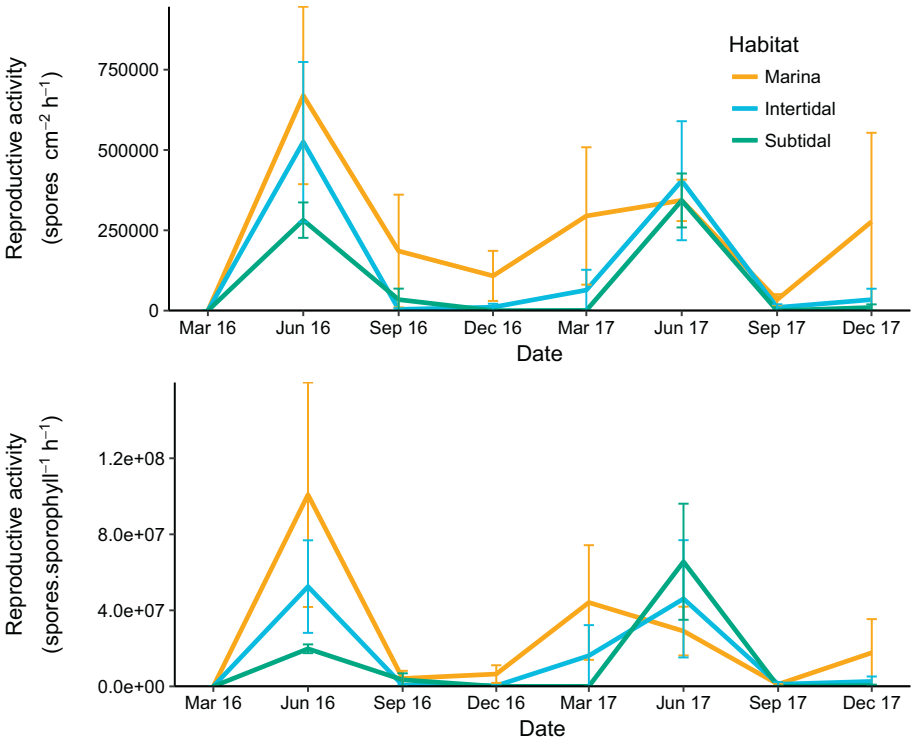

Fig. 8. Mean reproductive activity of *Undaria pinnatifida* (± standard error) found across the study period in each habitat (marina = orange, intertidal reef = blue, subtidal reef = green). Two reproductive metrics are shown: spores per cm^2 of sporophyll tissue per hour, and total spores per sporophyll per hour. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

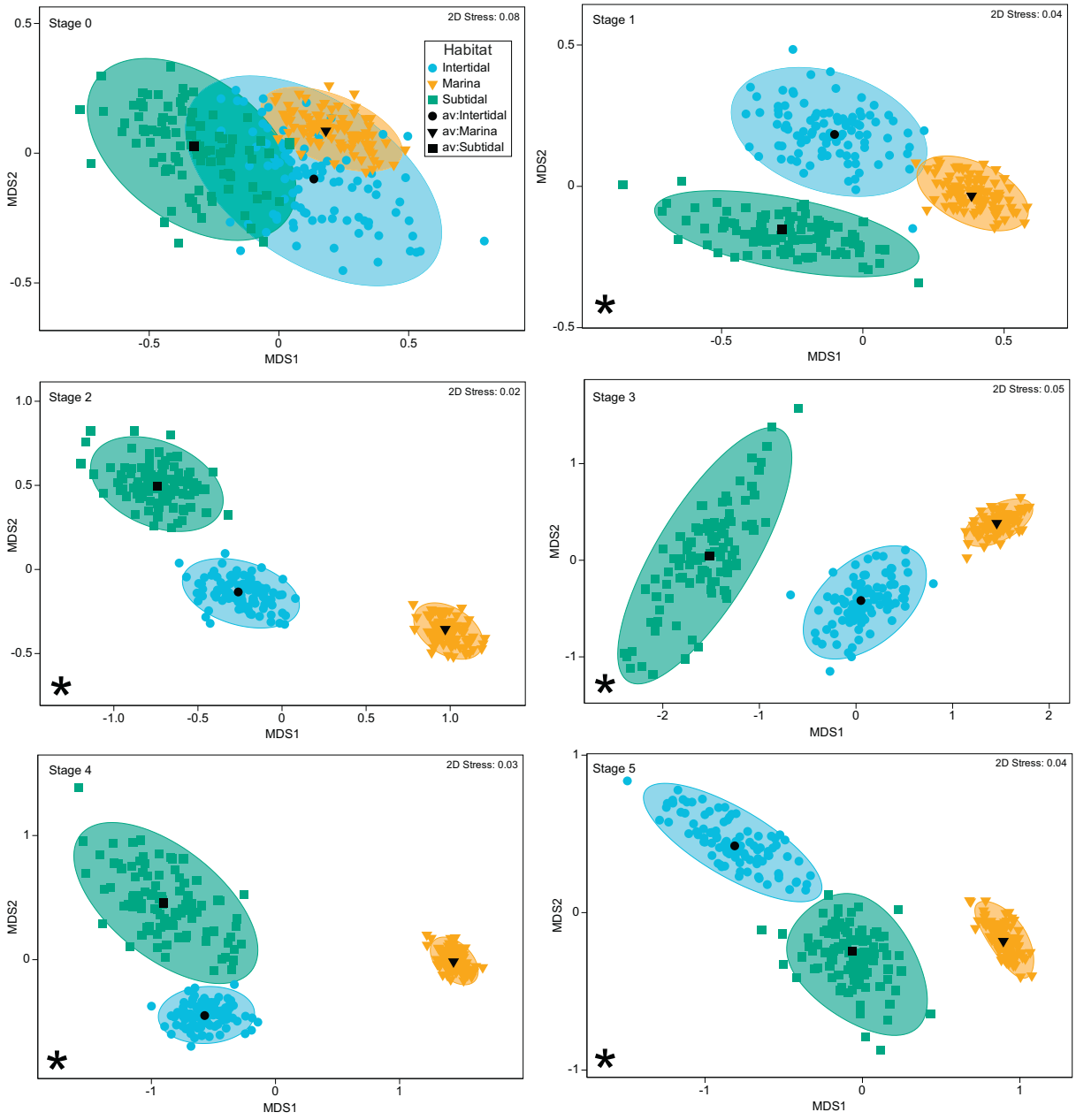

Fig. 9. Threshold metric multi-dimensional scaling (tmMDS) plots of bootstrapped average morphological data within each habitat (orange triangle = marina, blue circle = intertidal reef, green square = subtidal reef). Each developmental stage was assessed separately. Circular areas indicate the 95% confidence region around the bootstrap average. Bootstrapping and tmMDS based on Euclidean distance matrices constructed from normalised data. Asterisks indicate significant difference between habitats based on PERMANOVA (Table S5). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

All ANOVAs were constructed using the *lm* function from base R (R Core Team, 2017), and post hoc pairwise tests were carried out using the *testInteractions* function from the *phia* package (De Rosario-Martinez, 2015). All PERMANOVAs were run with 4999 permutations of residuals under a reduced model with Type 3 (partial) sums of squares. tmMDS plots were visualised using 50 restarts and a minimum stress of 0.01. Bootstrap averages were calculated with 100 bootstraps per group, with automatic selection of dimensions based on $\rho > 0.99$.

Univariate statistics were carried out in R 3.4.3 (R Core Team, 2017), multivariate statistics in PRIMER-e version 7 (Clarke et al., 2014), data manipulation was carried out using *dplyr* (Wickham and Francois, 2015), graphs were created using *ggplot2* (Wickham, 2009) and mapping (Fig. 1) was carried out within ArcMap 10.3.1. All mean values are presented ± Standard Error (SE).

3. Results

Undaria was recorded at all sites during every sampling event, with the exception of a single instance in the intertidal reef habitat at Firestone Bay, in December 2016. Maximum abundance and biomass values were both recorded on marina pontoons, with 50.9 *Undaria* per 0.25 m^2 recorded at marina 1 and 1.9 kg per 0.25 m^2 at marina 2, in June 2016. Across habitats, there was largely an annual cycle with abundance and biomass highest in June (11.0 ± 1.0 inds·0.25 m^{-2} and 0.78 ± 0.06 kg·m^{-2}) and lowest in December (2.7 ± 0.4 inds·0.25 m^{-2} and 0.04 ± 0.01 kg·m^{-2}). There were, however, dissimilarities between habitats, with abundance and biomass generally highest within marinas and lowest on subtidal reefs (Fig. 5). For both abundance and biomass there was significant Habitat * Month

Table 2
Results from the optimal ANOVA models, testing for difference in the abundance and biomass [log(x + 1)] of *Undaria pinnatifida* across the study period. The degrees of freedom (df), mean sum of squares (MS), F-value (F) and *p*-value (*p*) are shown for each coefficient. Significant coefficients shown in bold ($\alpha < 0.05$).

Coefficient	Abundance				Biomass			
	df	MS	F	*p*	df	MS	F	*p*
Habitat	**2**	**10.74**	**44.58**	**< 0.001**	**2**	**0.13**	**7.64**	**0.001**
Month	**3**	**3.86**	**16.02**	**< 0.001**	**3**	**0.99**	**57.87**	**< 0.001**
Year	**1**	**1.12**	**4.66**	**0.035**	1	< 0.01	0.01	0.931
Habitat ∗ Month	**6**	**0.58**	**2.43**	**0.037**	**6**	**0.07**	**3.82**	**0.003**
Month ∗ Year	**3**	**1.70**	**7.04**	**< 0.001**	**3**	**0.07**	**3.95**	**0.013**

and Month ∗ Year interactions indicating that the differences between habitats changed depending on month, and the monthly pattern differed between years (Table 2, Fig. 5). Pairwise tests indicated that the abundance of *Undaria* was significantly higher in marinas when compared to subtidal reef habitats throughout the year, but only significantly higher than intertidal reef habitats in March and June. Intertidal reef habitats supported significantly higher abundances than subtidal habitats, but only in June and September (Table A.1). The significant difference in biomass between habitats was constrained to June, with marinas and intertidal reef greater than subtidal reef (Table A.1). Variation in monthly patterns between years was particularly distinct within reef habitats with higher abundance and biomass in March 2017, but lower in June and September 2017 when compared to the same months in 2016 (Fig. 5).

An overall annual cycle in terms of population structure was identified across habitats; peak recruitment was recorded in December and March (90 ± 4%, 89 ± 4% of sporophytes sampled were recruits in December and March respectively), mature sporophytes dominated in June (71% ± 4% of sporophytes mature in June), and senescence predominantly occurred in September (75 ± 7% of sporophytes senescing in September) (Fig. 6). While the structure of populations on intertidal and subtidal reef habitats was similar across the study, the structure of populations on marina pontoons was distinct (Fig. 6). Recruitment occurred over an extended period within marinas, with a higher proportion of recruits in June and September, outside of the main recruitment period. Populations in marinas were also generally more mixed, with a higher proportion of mature sporophytes in December and senescing sporophytes in June indicating more concurrent generations when compared to reef habitats (Fig. 6). As recorded for abundance and biomass, the Habitat ∗ Month and Month ∗ Year interaction terms were also significant for population structure (Table 3). Pairwise tests between habitats indicated significant differences between marinas and intertidal reef habitats in March, June and September, and between marinas and subtidal reef habitats in June (Table A.2). This dissimilarity was predominantly due to more mixed populations of recruits, mature and senescing plants on marina pontoons when compared to the reef habitats (Table A.3). Comparing the proportion of individual developmental stages at each sampling event also indicated more mixed populations in marinas compared to intertidal and subtidal reef habitats (Fig. 7; mean standard deviation: 0.044 in marinas, 0.067 subtidal, 0.075 intertidal). The significant Month*Year interaction was related to annual variation in population structure in March and June, with a higher proportion of mature sporophytes and a lower proportion of recruits in 2017 compared to 2016 (Fig. 6). This dissimilarity occurred across all habitats but was more pronounced in intertidal and subtidal reef habitats than in marinas (Fig. 6).

Reproductive activity varied markedly between habitats and across sampling events. Where mature sporophytes were found, the lowest activity was recorded on subtidal reef in March 2017 ($6.0 \pm 4.0 \times 10^2$ spores·cm^{-2}·h^{-1} and $2.8 \pm 2.6 \times 10^4$ spores·s porophyll^{-1}·h^{-1}) and the highest reproductive activity was recorded in marinas in June 2016 ($6.7 \pm 2.8 \times 10^5$ spores·cm^{-2}·h^{-1} and $1.0 \pm 0.6 \times 10^8$ spores·sporophyll^{-1}·h^{-1}). Reproductive activity was generally highest on marina pontoons, followed by intertidal reef, and lowest on subtidal reef (Fig. 8). At every sampling event, both reproductive activity metrics were higher in marinas than in reef habitats, with the exception of June 2017 (Fig. 8). For both metrics there was a statistically significant overall effect due to Habitat and a significant Month ∗ Year interaction (Table 4). Due to the high variability in the activity metrics, pairwise tests between individual habitats were only statistically significant between subtidal reef and marinas, however, the overall pattern of marinas > intertidal reef > subtidal reef remained (Table A.4). The significant Month ∗ Year interaction indicates interannual variation in reproductive activity, which was most pronounced in March with higher activity in 2017 than 2016 (Fig. 8).

Morphology of *Undaria* sporophytes also differed between habitats at various developmental stages. Bootstrap averages and tmMDS highlighted lower variation in marina habitats when compared to reef habitats, indicated by the smaller 95% confidence area around the bootstrap mean across all developmental stages (Fig. 9). Greatest dissimilarity in tmMDS was between sporophytes sampled in marinas and reef habitats, particularly in developmental stages 2, 4 and 5; with intertidal and subtidal reef habitats clustering closer on tmMDS (Fig. 9). Statistically significant variation in morphology between habitats was found for all developmental stages except stage 0 sporophytes (Fig. 9, Table A.5) In general, the morphological attributes measured showed that sporophytes were smallest in marinas, and largest on subtidal reef (except for stage 5) (Table A.6). Sporophytes from marinas were statistically distinct from those from subtidal reefs at every developmental

Table 3
Results from the optimal PERMANOVA model, testing for difference in population structure of *Undaria pinnatifida* across the study period. The degrees of freedom (df), mean sum of squares (MS), pseudo F-value (F) and *p*-value (*p*) are shown for each coefficient. Significant coefficients shown in bold ($\alpha < 0.05$).

Coefficient	df	MS	F	*p*
Habitat	2	572.1	1.79	0.159
Month	**3**	**38,720.0**	**121.42**	**< 0.001**
Year	**1**	**1786.1**	**5.60**	**0.008**
Habitat ∗ Month	**6**	**1113.1**	**3.49**	**< 0.001**
Month ∗ Year	**3**	**1448.4**	**4.54**	**0.002**

Table 4
Results from the optimal ANOVA models, testing for difference in two reproductive activity metrics [log(x + 1)] of *Undaria pinnatifida* across the study period. The degrees of freedom (df), mean sum of squares (MS), F-value (F) and *p*-value (*p*) are shown for each coefficient. Significant coefficients shown in bold ($\alpha < 0.05$).

Coefficient	Spores cm^{-2} h^{-1}				Spores sporophyll^{-1} h^{-1}			
	df	MS	F	*p*	df	MS	F	*p*
Habitat	**2**	**70.72**	**4.05**	**0.022**	**2**	**111.75**	**3.41**	**0.039**
Month	**3**	**352.01**	**20.15**	**< 0.001**	**3**	**632.43**	**19.29**	**< 0.001**
Year	1	26.80	1.53	0.220	1	67.50	2.06	0.156
Month ∗ Year	**3**	**72.12**	**4.13**	**0.010**	**3**	**151.41**	**4.62**	**0.006**

stage, except stage 2, and from sporophytes from intertidal reefs at developmental stages 4 and 5 (Table A.6, Table A.7). There was no significant difference in sporophyte morphology between intertidal and subtidal reef habitats at any developmental stage (Table A.6, Table A.7).

4. Discussion

The population dynamics of INNS can greatly influence their success, spread and ecological impact, and can also affect the design and implementation of effective management measures (Bauer, 2012; Ricciardi and Cohen, 2007; Sakai et al., 2001; Simberloff, 2003; Williamson and Fitter, 1996). As such, information on spatiotemporal variability in population structure, reproduction and morphology can be used as evidence to prioritise, or deprioritise, management of a given species or introduction event (Booy et al., 2017; Epstein, 2017; McGeoch et al., 2016; Seebens et al., 2017). Here, we have shown that information garnered from distinct habitats or environments cannot be generalised across the non-native range of a given INNS, even across small spatial scales. This study was conducted at sites < 3 km apart, yet population dynamics differed markedly between habitat-types. Although not considered here, similar variation in population dynamics can also occur over larger spatial scales within the non-native range of *Undaria* (Hay and Villouta, 1993; James et al., 2015; Schiel and Thompson, 2012). This highlights the need for site-specific data when considering the ecology, impact and management of INNS. *Undaria* is one of the most cosmopolitan marine invaders, being found in almost every temperate region of the world (Epstein and Smale, 2017b) and is highly likely to continue its spread into un-invaded regions. A greater volume of data collected from a range of environmental contexts is needed to better predict its invasion dynamics, to inform management decisions and the design of effective containment, removal or eradication methods.

Artificial structures in coastal marine environments are known to experience high propagule pressure of INNS, but low competition from native species, rendering them favourable habitats for the colonisation and proliferation of invaders (Bishop et al., 2015; Dafforn et al., 2012; Glasby et al., 2007). Of the three habitats examined here, the abundance and biomass of *Undaria* was highest in marinas. This pattern is mirrored across its non-native range, with *Undaria* more widespread and abundant on artificial rather than natural substrates (Epstein and Smale, 2017a; Fletcher and Farrell, 1999; James and Shears, 2016b; Kaplanis et al., 2016; South et al., 2017; Veiga et al., 2014).

The current study was able to highlight further differences in population dynamics between artificial and natural habitats. For example, we recorded an extended recruitment period and more concurrent generations in marinas when compared to reef habitats, indicated by higher proportions of recruits and mature individuals outside of the main recruitment/maturation periods. Year-round recruitment events, or multiple recruitment pulses per year, have been recorded for *Undaria* in other parts its non-native range, primarily within artificial habitats (Casas et al., 2008; Cremades et al., 2006; James and Shears, 2016a; James and Shears, 2016b; Primo et al., 2010; Thornber et al., 2004). Similarly, studies conducted in artificial habitats have previously recorded the presence of mature individuals year-round (Hay and Villouta, 1993; James and Shears, 2016a; James and Shears, 2016b; Primo et al., 2010), whereas studies conducted in natural reef habitats have tended to report very low abundances or absences of mature plants during some months of the year (Arnold et al., 2016; Casas et al., 2008; Hay and Villouta, 1993; James and Shears, 2016b; Schaffelke et al., 2005; Schiel and Thompson, 2012). The direct comparison between habitats conducted within the current study allows us to conclude that *Undaria* exhibits extended recruitment periods and more concurrent generations in marina habitats, when compared to natural reefs.

As the presence of a sporophyll is not necessarily a true indication of maturation of the sporophyte, reproductive activity was also measured within the current study. Reproductive activity in reef habitats predominantly occurred in only one of the quarterly sampling events (June), the same period where the highest proportion of mature sporophytes was recorded. Reproductive activity was significantly higher within the marina habitats, and was more sustained throughout the year. Previous studies have shown that at reef sites in Australasia reproductive activity is restricted to around 3–4 months or one season of the year (Schaffelke et al., 2005; Schiel and Thompson, 2012), and that patterns of reproductive activity from some marinas can be more consistent throughout the year (Primo et al., 2010); however these studies were conducted in different regions. The populations monitored in this study show that reproduction is higher and more consistent on marina pontoons than in reef habitats of the same locality. Overall, our formal cross-habitat comparison of population dynamics indicated that *Undaria* populations are significantly dissimilar between marinas and reef habitats, even within a single region. If this dissimilarity was found to be consistent across habitat types and regions, the higher reproduction, recruitment and concurrent generations are likely to be key factors influencing the success of *Undaria* in artificial habitats across its non-native range.

Some dissimilarity in population dynamics was also recorded between intertidal and subtidal reef habitats. Although populations were similar in structure in terms of the proportions of recruits, mature and senescing plants at each sampling event, intertidal reef habitats generally supported higher abundance and biomass than subtidal habitats. There is limited information on depth-related abundance patterns of *Undaria* in its non-native range. It can extend from the low intertidal zone to 12–18 m depth (Epstein and Smale, 2017b; Forrest and Taylor, 2002; Saito, 1975; South et al., 2017; Valentine and Johnson, 2003), but is generally thought to peak in abundance in the intertidal-subtidal fringe and become less abundant with depth (Castric-Fey et al., 1993; Dean and Hurd, 2007; Hay and Villouta, 1993; Russell et al., 2008; South et al., 2017). Our study provides empirical support for this as, on average, standing biomass within intertidal habitats was 4.5 ± 5.2 (SD) times greater than on subtidal reefs. This pattern was likely driven by a range of both biotic and abiotic factors that vary with habitat depth, such as competition from native species (e.g. Raffo et al., 2009), light availability (e.g. Russell et al., 2008) and physical disturbance (e.g. Valentine and Johnson, 2003).

Populations within both intertidal and subtidal reef habitats also exhibited high inter-annual variability in abundance, biomass and structure between the two survey years. At the start of this study (March 2016) we recorded very low abundance and little recruitment within reef habitats. Abundance increased sharply between March and June 2016, indicating that peak recruitment had occurred between these months. In December 2016, however, the next recruitment period had seemingly commenced, indicated by the significantly higher abundance of recruits sampled when compared to March 2016 and little to no increase in abundance between December and March 2017. This earlier seasonal cycle in 2017 was also indicated by the higher proportion of mature sporophytes in March and June 2017 when compared to 2016. Conversely, populations within marinas exhibited a more similar pattern between the survey years. It is likely that reef habitats are subjected to greater environmental variability (i.e. in temperature, light, nutrients, storm events), especially when compared to more sheltered and enclosed marinas, which may lead to high inter-annual variation in population structure. This high inter-annual variation is a major factor that may contribute to difficulties in designing effective and efficient control measures for *Undaria* once it spreads to natural substrates.

Undaria is typically categorised into two growth forms based on the geographical variation in morphology observed in its native range. *Undaria* f. *typica* is characterised by shallow pinnate divisions on the blade, a short stipe and sporophylls confluent with the base of the blade; whereas *Undaria* f. *distans* has a longer stipe, deeper pinnate

divisions and a blade distinct from the sporophylls (Okamura, 1915; Yendo and Rlgakuhakushi, 1911). Although the separation between these growth forms is thought to be largely driven by abiotic environmental factors (Castric-Fey et al., 1999b; Castric-Fey et al., 1993; Stuart et al., 1999), especially water velocity (Nanba et al., 2011), there is also evidence of genetic dissimilarity between certain forms (Niwa et al., 2017). Within the current study, highest dissimilarity in morphology was recorded between sporophytes from marinas and reef habitats. Sporophytes on reef sites generally had longer stipes and wider blades, more typical of f. *distans*. Sporophytes in marinas not only had shorter stipes and narrow blades, but the sporophylls were often more developed, indicated by higher proportions of sporophytes at developmental stage 3 across the study period. Although not formally tested as part of this study, it was noted during the sampling process that sporophytes on marina pontoons often had shallow pinnate divisions on the blade and sporophylls confluent with the base of the blade (Epstein, pers. obs.); overall those sporophytes found in marinas were more typical of f. *typica*. It is highly likely that this variation in morphology is driven by dissimilarity in abiotic environmental factors between marinas and reef sites, particularly in relation to water velocity and exposure; however, genetic distinction between marina and reef populations cannot be discounted. Other factors that may drive the patterns in morphology found in this study may include both inter and intra specific competition, and differences in light intensity, nutrients and disturbance (Carnell and Keough, 2014; Gao et al., 2013; Sfriso and Facca, 2013; Thompson and Schiel, 2012; Watanabe et al., 2014).

There are a number of biotic and abiotic factors which are likely to contribute to the variation in population dynamics and morphology of *Undaria* between habitats and between years. Temperature is often considered as the key driver of *Undaria* population dynamics (Gao et al., 2013; James and Shears, 2016a; Murphy et al., 2016; Saito, 1975; Thornber et al., 2004). Here, average daily temperatures were largely similar between habitats and years, although marinas showed marginally more extremes, with warmer temperatures recorded during spring and summer, and colder temperatures in autumn and winter when compared to reef sites (Fig. A.1). However, temperatures recorded within all habitats throughout the study were well within the thermal niche of *Undaria* throughout the year, and it is therefore unlikely that temperature was a key factor in driving the dissimilarities observed in this study (Epstein and Smale, 2017b; James et al., 2015; James and Shears, 2016a). During spring tides, intertidal reef habitats were exposed to much larger short-term fluctuations in temperatures (i.e. hourly variability) than both marinas and subtidal habitats (Fig. A.2). Intertidal populations were, however, found at higher abundance and biomass than those on subtidal reefs and exhibited similar population dynamic patterns, so were not evidently impacted by greater short-term temperature variability. Light availability was also quantified within each habitat and, although seasonally variable, mean daytime illuminance was lowest on subtidal reef (Figs. A.3, A.4). Mean daytime illuminance in intertidal reef sites was skewed by sporadic high light intensities during exposure at low spring tides but, in general, light levels were higher and more consistent in marinas compared with intertidal reef habitats (Figs. A.3, A.4). As such, light availability may be one of the underlying causes of the observed between-habitat dissimilarity in the population structure of *Undaria*. Light intensity has previously been considered as a potential key driver of the success of *Undaria* within certain invaded communities and a factor limiting its distribution to larger depths (De Leij et al., 2017; Russell et al., 2008; South et al., 2017; Valentine and Johnson, 2003).

Other factors which were not measured as part of this study but could also induce variation in population dynamics and morphology include inter- and intra-specific competition, wave exposure and nutrients. Inter-specific competition from functionally-similar brown macroalgae is likely to be lower on artificial substrates, when compared to reef sites (Airoldi et al., 2015; Connell, 2001; Farrell and Fletcher, 2006; South et al., 2017), which may allow *Undaria* to recruit, mature and reproduce more successfully in marinas. Inter-specific competition is also likely to vary across depth within reefs habitats, and has previously been identified as a potential factor limiting the depths at which *Undaria* can persist at high abundances (Castric-Fey et al., 1993; Cremades et al., 2006; Raffo et al., 2009; Russell et al., 2008). Intra-specific competition will, however, be higher within marinas and may result in the smaller and more stunted f. *typica* forms, which seem to have a higher investment in reproduction rather than growth of the stipe and blade. Marinas will also be inherently more sheltered and nutrient enriched than reef habitats (Bax et al., 2018; Foster et al., 2016; Rivero et al., 2013). Growth of both *Undaria* gametophytes and sporophytes is positively related to nutrient concentration (Dean and Hurd, 2007; Morelissen et al., 2013; Pang and Wu, 1996), and *Undaria* is thought to be negatively impacted by high wave exposure (Epstein and Smale, 2017a; South et al., 2017). *Undaria* individuals also exhibit relatively slow nutrient uptake (Dean and Hurd, 2007) so that increased circulation by high water flow leads to increased growth rate, and overall larger sporophytes when compared to less tidal sites (Nanba et al., 2011). These abiotic factors may, therefore, have led to the distinct population dynamics and morphology of *Undaria* in marinas.

Within its native range *Undaria* has a strictly annual life cycle, with a clear period in late summer/autumn where macroscopic sporophytes are absent due to unfavourably high water temperatures (Koh and Shin, 1990; Saito, 1975). While some degree of annularity was observed for the populations examined here, macroscopic sporophytes were still found at each site, during every sampling event, except for in one instance; while mature individuals were found in at least one site in each habitat throughout the year. In many parts of its non-native range (including the UK) the thermal cues for its strict annual life cycle are lost due to the temperate environmental conditions (James et al., 2015). Indeed, it is this temperature regime that drives the more complex patterns in population dynamics recorded in this study, and allows *Undaria* sporophytes to be present year-round with overlapping generations.

5. Conclusion

Our study confirms that marinas are of significant importance in the establishment potential of *Undaria*. Due to the interconnected nature of the marine environment, the population dynamics of *Undaria* within artificial habitats are likely to be paramount to its successful spread, proliferation and reproductive fitness across its non-native range. They should, therefore, be the principle target of future management actions. This study also showed that there can be significant variation in abundance, biomass and morphology of *Undaria* between habitats, which could greatly alter its ecological impacts (Blackburn et al., 2014; Jeschke et al., 2014; Thomsen et al., 2011). Previous studies on *Undaria* have identified varying levels of ecological impact dependent on the environment under investigation and response variables recorded (Epstein and Smale, 2017b; South et al., 2017). Further research is needed to identify whether the ecological impact of *Undaria* varies considerably between habitats within a single introduced region, and how this may alter management prioritisation.

Designing efficient and effective control methods for an established INNS is dependent on having an adequate knowledge of its ecology and population biology (Sakai et al., 2001). The results shown here highlight that generalisations cannot be made across invaded habitat types, making management highly complex. Site-specific data on the population dynamics and impact of INNS is needed to make truly objective evidence-based management decisions; however, developing an extensive evidence base requires considerable time and resources. Careful consideration is required into whether this would lead to beneficial management outcomes compared to less evidence-based but more rapid response actions (Beric and MacIsaac, 2015; Early et al., 2016; McGeoch et al., 2016). Data will not be available in every instance and management decisions will have to be made on best available evidence.

This study highlights that where site-specific data is not available, uncertainty should be noted within any confidence assessment. Even where substantial data are available, management can be highly labour intensive, ineffective and costly (Early et al., 2016; Hulme, 2006; Larson et al., 2011; Simberloff et al., 2013). The highly plastic life-history characteristics of *Undaria*, both spatially and temporally, coupled with its year-round reproduction and recruitment, makes it a model species to highlight the difficulties in INNS management.

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Conflict of interest

The authors declare that they have no conflict of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2018.10.055.

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