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3 **The influence of native macroalgal canopies on the**  
4 **distribution and abundance of the non-native kelp**  
5 ***Undaria pinnatifida* in natural reef habitats**

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21

22 **Abstract:** The Asian kelp *Undaria pinnatifida* ('Wakame') is one of the most widespread  
23 invasive non-native species in coastal marine habitats and is fast approaching cosmopolitan  
24 status, yet its interactions with native species are poorly understood. Within the Plymouth  
25 Sound (UK) Special Area of Conservation (SAC) *Undaria* has become a conspicuous and  
26 important component of assemblages in shallow rocky reef habitats, where it co-exists with  
27 native canopy-forming brown macroalgae. We examined the hypothesis that rocky reef  
28 habitats supporting dense macroalgal canopies will have more biotic resistance to the  
29 invasion of *Undaria* compared with reef habitats supporting disturbed or sparse native  
30 canopies. Field surveys were completed at 2 spatial scales and sampling resolutions and a  
31 short-term field-based canopy removal experiment was conducted to examine the influence  
32 of native macroalgal assemblages on the abundance, cover, biomass and morphology of  
33 *Undaria*. Field surveys indicated that *Undaria* was negatively related to the cover of  
34 macroalgal 'competitors', particularly *Laminaria* spp. However, multiple, large *Undaria*  
35 sporophytes were observed within dense native canopies, suggesting that disturbance to, or  
36 absence of, canopies is not a prerequisite for *Undaria* colonisation. The short-term canopy-  
37 removal experiment indicated that *Undaria* functions primarily as a pioneer species in this  
38 system. Where native canopies were left intact, *Undaria* sporophytes were far less abundant  
39 and were generally smaller with lower biomass compared with those in disturbed patches.  
40 The spread of *Undaria* into natural habitats is inhibited by the presence of native  
41 competitors, particularly large perennial species such as *Laminaria* spp., although the  
42 persistence of intact dense canopies does not completely prevent assimilation of *Undaria*  
43 into native assemblages.

44

45 **Keywords:** Temperate reefs, macroalgae, invasive species, competition, canopy  
46 disturbance

47

## 48 Introduction

49 The spread of non-native species (NNS) represents a major threat to global biodiversity (Bax  
50 et al. 2003). Due to the inherent connectivity and openness of the marine environment, non-  
51 native species (NNS) are particularly prevalent and widespread in coastal marine  
52 ecosystems (Ruiz et al. 1997; Bax et al. 2003). Determining the ecological and  
53 socioeconomic impacts of marine NNS is critical for prioritising management actions and  
54 conservation measures, yet basic information on the population dynamics of NNS outside of  
55 their native range is often lacking (Byers et al. 2002). A robust understanding of the  
56 mechanisms underpinning the spread of NNS, combined with an appreciation of the  
57 direction and magnitude of ecological interactions with native species across a range of  
58 habitats, are vital for assessing current and future ecological impacts. Marine NNS are often  
59 introduced into, and proliferate within, artificial habitats such as ports, harbours, marinas and  
60 modified embayments (Glasby et al. 2007). Once established, they can spread into nearby  
61 natural habitats where they may interact with native biota and have the potential to drive  
62 ecological change. The rate of spread into natural habitats and the nature of ecological  
63 interactions with native species are likely to depend, to some degree, on the competitive  
64 ability of functionally-similar native species and the biotic resistance of local communities  
65 (Stachowicz et al. 2002; Crooks 2005). This, in turn, will likely vary between invaded regions  
66 due to differences in environmental conditions and the identify of native species, so that  
67 making predictions of ecological impacts across non-native ranges is problematic.

68 Macroalgal NNS are of particular importance as they can cause shifts in the structure and  
69 functioning of entire communities, alter patterns and rates of primary production and have  
70 significant socioeconomic and ecological impacts (Schaffelke and Hewitt 2007; Williams and  
71 Smith 2007). Worldwide there are thought to be >227 different macroalgal species which  
72 have been introduced outside of their native ranges (Schaffelke and Hewitt 2007), however  
73 clear quantitative evidence of their ecological interactions within native communities and  
74 their wider impacts is generally lacking. Native to cold temperate areas of the Northwest  
75 Pacific (i.e. the coastlines of Japan, Korea, Russia and China) the kelp *Undaria pinnatifida*  
76 (Harvey) Suringar, 1873 (Phaeophyceae, Laminariales), or 'Wakame' has a worldwide  
77 introduced range. First identified as a NNS on the Mediterranean coast of France in 1971  
78 (Perez et al. 1981), *Undaria pinnatifida* (hereafter '*Undaria*') is now established on the  
79 coastlines of New Zealand, Australia, Northern France, Spain, Italy, United Kingdom ,  
80 Portugal, Belgium, Holland , Argentina, Mexico and the USA (James et al. 2015 and  
81 references therein).

82 The primary vectors of introduction are thought to be through fouling on the hulls of  
83 commercial vessels (Hay 1990; Fletcher and Farrell 1999), and accidental import with  
84 shellfish (Perez et al. 1981; Floc'h et al. 1991), although it was also intentionally introduced  
85 for cultivation into Brittany, France, in 1981 (Perez et al. 1981). Following the initial  
86 introduction, further regional spread is thought to occur via fouling of leisure crafts and  
87 transport to nearby harbours and marinas (Russell et al. 2008; Minchin and Nunn 2014).  
88 *Undaria* is prevalent in many ports, marinas and aquaculture sites worldwide (e.g. Floc'h et  
89 al. 1991; Fletcher and Manfredi 1995; Veiga et al. 2014; James and Shears 2016). Once  
90 established in artificial habitats or modified environments, *Undaria* can spread into natural  
91 habitats including rocky reefs, seagrass beds and mixed sediments (Floc'h et al. 1996;  
92 Stuart 2003; Farrell and Fletcher 2006; Russell et al. 2008; James and Shears 2016).  
93 *Undaria* is considered by the IUCN Invasive Species Specialist Group as one of the 100  
94 worst invasive species in the world, and the second worst invasive seaweed (Lowe et al.  
95 2000), and is considered to be of significant risk to the natural environment.

96 *Undaria* was first discovered in UK waters in 1994, in the Hamble Estuary in the Solent  
97 (Fletcher and Manfredi 1995). Since *Undaria*'s introduction to the Hamble, it has continued  
98 to spread along the UK coastline with the most northerly population in Europe currently  
99 being the Firth of Forth, Scotland (NBN 2017). It was first recorded within Plymouth Sound in  
100 a marina in 2003 (NBN 2017) and has since successfully colonised natural substrata in  
101 intertidal and subtidal rocky habitats dominated by native kelp species including *Laminaria*  
102 *digitata*, *Laminaria hyperborea*, *Laminaria ochroleuca*, *Saccharina latissima*, and *Saccorhiza*  
103 *polyschides* (Heiser et al. 2014; Arnold et al. 2016). The kelp-dominated communities found  
104 within Plymouth Sound are a targeted conservation feature within the Special Area of  
105 Conservation (SAC) due to their high levels of biodiversity and rates of primary production  
106 (Langston et al. 2003). As *Undaria* has become a major component of macroalgae  
107 assemblages at many sites within the SAC (Heiser et al. 2014), it is important to better  
108 understand its abundance-distribution patterns within native macroalgal stands and the  
109 nature of ecological interactions with native kelps. Examining the role of *Undaria* within kelp  
110 forest habitats is particularly valuable, given that these habitats support high levels of  
111 biodiversity, provide fuel for inshore foodwebs through high levels of primary productivity and  
112 support magnified secondary productivity (Steneck et al. 2002; Smale et al. 2013; Teagle et  
113 al. in press). Non-trophic ecological interactions, both facilitative and competitive, can be  
114 important drivers of community structure and functioning in kelp forests (Flukes et al. 2014;  
115 Bennett et al. 2015). Introduction of NNS into native kelp assemblages can influence  
116 ecological interactions and, in turn, alter the structure of macroalgal canopies and their

117 associated assemblages and overall ecological functioning (e.g. Williams and Smith 2007;  
118 Krumhansl and Scheibling 2012).

119 There is, however, little evidence to suggest that *Undaria* can displace native canopy-  
120 forming macroalgal species in invaded habitats from other regions outside its native range.  
121 Instead, it has been suggested that *Undaria* is characteristic of an opportunistic pioneer  
122 species that can quickly colonise disturbed habitats and attain high abundances in the  
123 absence of native canopy formers (South et al. 2015). Indeed, the low competitive ability of  
124 *Undaria* on rocky shores has been described by several studies (Valentine and Johnson  
125 2003; Edgar et al. 2004; Raffo et al. 2009; Thompson and Schiel 2012; South et al. 2015;  
126 South and Thomsen 2016), with the growth and abundance of *Undaria* in native canopies  
127 generally considered to be suppressed by reduced light levels beneath the canopy  
128 (Valentine and Johnson 2003). However, the low competitive ability of *Undaria* is not as  
129 evident in artificial or highly impacted 'natural' habitats, as in comparison to many native  
130 macroalgae it can tolerate wider fluctuations in environmental conditions, which may yield a  
131 competitive advantage within these habitats (Farrell and Fletcher 2006; Henkel and  
132 Hofmann 2008; James et al. 2015; Bollen et al. 2016). The ability of an invasive species to  
133 assimilate into natural habitats is in part dependant on the resident native biota, which in turn  
134 influences the availability of key resources such as space and light (Levine and D'Antonio  
135 1999; Arenas et al. 2006). The persistence of dense macroalgal canopies on natural  
136 habitats may restrict the ability of *Undaria* to spread from artificial habitats and colonise  
137 native communities (Farrell and Fletcher 2006; Thompson and Schiel 2012), despite high  
138 abundances and associated propagule pressure from nearby 'strongholds' within artificial  
139 habitats. This has yet to be tested, however, within macroalgal canopies on the open coast  
140 of northeast Atlantic, which are comprised of multiple native kelp species with divergent life-  
141 histories, morphological and functional traits.

142 Here, we tested the hypothesis that natural rocky reef habitats supporting dense native  
143 macroalgal canopies will have more biotic resistance to the invasion of *Undaria* than  
144 disturbed or sparse canopies. This hypothesis was examined through three distinct activities:  
145 (i) broad-scale field surveys conducted across the Plymouth Sound SAC, to examine  
146 relationships between the abundance/cover of *Undaria* and the structure of native canopies;  
147 (ii) targeted fine-scale field surveys, where the density, biomass and morphology of *Undaria*  
148 sporophytes were quantified and related to the structure of native canopies; and (iii) a short-  
149 term canopy-removal experiment, whereby patches of native macroalgae were cleared and  
150 colonisation of *Undaria* into disturbed areas was compared with undisturbed canopies. The  
151 first two components were observational surveys that examined correlative relationships

152 between native macroalgae and *Undaria* across different sites and environmental conditions,  
153 whereas the third component was manipulative to test the influence of native macroalgal  
154 canopies and recruitment on early development of *Undaria* sporophytes.

## 155 **Methods**

### 156 **Study region**

157 The Plymouth Sound Special Area of Conservation (SAC) is internationally recognised as an  
158 ecologically important complex of marine and coastal habitats (Knights et al. 2016). The area  
159 supports a wide range of marine habitats and species, many of which are of ecological and  
160 socioeconomic importance. Intertidal and shallow subtidal rocky reef habitat is widespread  
161 throughout the SAC, typically supporting dense stands kelps and fucoids. The SAC is  
162 characterised by strong environmental gradients, in that the outer reefs are more exposed to  
163 wave action but less influenced by environmental variability (i.e. fluxes in salinity, turbidity  
164 nutrients) driven by fluvial inputs from the Tamar and Plym river systems (Fig. 1). Macroalgal  
165 beds within Plymouth Sound and its approaches are dominated by various brown canopy-  
166 forming macroalgae, including the native kelps *Laminaria hyperborea*, *L. ochroleuca*, *L.*  
167 *digitata* and *Saccharina latissima*, the fucoid *Himanthalia elongata*, the Tilopteridale  
168 *Saccorhiza polyschides* and the non-native kelp *Undaria* (Langston et al. 2003; Heiser et al.  
169 2014).

170

### 171 **Field Surveys**

172 To quantify the abundance and distribution of *Undaria* across Plymouth Sound, and to  
173 examine how *Undaria* population structure may be influenced by the composition of native  
174 macroalgal canopies, two field surveys were undertaken. The population dynamics of  
175 *Undaria* are highly seasonal, with the dominant cohort of sporophytes recruiting in spring,  
176 growing through summer and senescing in late summer/autumn (Arnold et al. 2016). To  
177 capture maximum abundance and biomass values, our field surveys were conducted during  
178 the summer months. The first survey was conducted at a 'broad' spatial scale but with lower  
179 sampling resolution (i.e. video transects) whereas the second survey was conducted at only  
180 two sites but with higher sampling resolution (i.e. quadrat harvesting). For both surveys, the  
181 aim was to quantify the abundance and/or cover of large canopy-forming macroalgal  
182 species, which were presumed to be competing (to some extent) with *Undaria* for resources  
183 (e.g. space, light, nutrients). Hereafter, such species are referred to as the native  
184 'competitors' although competition was inferred and not formally tested here. For the broad-  
185 scale video transect survey, eight sites were selected across Plymouth Sound in a

186 haphazard manner (Fig. 1), based on the presence of shore access and suitable rocky  
187 substrate (identified using Google aerial imagery © 2016 and by carrying out site visits).  
188 Surveys were completed by snorkel at low slack-tide between 2<sup>nd</sup> July and 8<sup>th</sup> August 2016.  
189 In order to maintain a similar tidal position on the substrate, large spring and neap tides were  
190 avoided, leading to tidal heights between 0.8 m and 1.7 m above chart datum at the time of  
191 survey (the maximum tidal range recorded in Plymouth Sound during 2016 was 0.2 to  
192 6.0 m CD). At each site, four 25 m transects were laid using a weighted line, each separated  
193 by approximately 25 m. Transects were placed haphazardly, but were stratified to areas of  
194 suitable rocky substrate within the intertidal/subtidal fringe zone. Video of the macroalgal  
195 canopy along the transect was collected using a Panasonic Lumix FT5 waterproof camera  
196 fitted to an underwater tray and handle. A 65 cm scale was fixed to the front of the camera  
197 tray in order to maintain the video at an approximate set distance above the canopy. Both  
198 horizontal and vertical substrates were included in the video, dependent on the topography  
199 at a given site. Following the survey, each video was watched twice. On the first view the  
200 video was played in slow motion and the number of *Undaria* (both entire and partial  
201 sporophytes) was counted. On the second viewing, the percent cover of other canopy-  
202 forming macroalgae (*Laminaria* spp., *S. polyschides*, *S. latissima*) was estimated on a  
203 SACFOR scale (Superabundant [S > 80%], Abundant [A 40-79%], Common [C 20-39%],  
204 Frequent [F 10-19%], Occasional [O 5-9%], Rare [R 1-5%], None [N 0%]). A quantitative  
205 measure of cover for each transect was taken as the median value from the SACFOR scale.  
206 Total percent cover of all 'competitors' was calculated as the sum of individual species  
207 values, and therefore total percent canopy cover could be over 100%. Although video  
208 transects only capture the uppermost layer of the algal assemblage, the approach was  
209 deemed to satisfactorily sample the brown macroalgae because (i) the canopy-forming  
210 species extend to similar heights above the rocky substrate and do not tend to uniformly  
211 cover one another, and (ii) a pilot study indicated that *Undaria* and its native competitors can  
212 be observed and identified within mixed stands.

213 For the fine-scale quadrat survey, two study sites (Firestone Bay and Drakes Island, see Fig.  
214 1) were selected based on the following criteria: (1) a known presence of extensive shallow  
215 subtidal (0-2 m depth below chart datum) rocky reef habitat; (2) a lack of point-source  
216 anthropogenic impact (e.g. sewage outfall, marina entrance); and (3) confirmed  
217 establishment of *Undaria* populations. Both sites were semi-sheltered with respect to wave  
218 exposure, with protection from the predominant south-westerly swells offered by both Drakes  
219 Island and the Plymouth Sound breakwater (Fig. 1). Firestone Bay was generally  
220 characterised by extensive areas of semi-stable boulders and bedrock, interspersed with  
221 patches of soft sediment. The rocky substrata at Firestone Bay, although patchy, extends

222 from the intertidal to depths >20 m (below chart datum), with dense macroalgal assemblages  
223 extending to depths of ~3 m. Drakes Island was characterised by sandy substrate with  
224 extensive rocky outcrops and platforms, extending from the intertidal to ~5 m depth. In July  
225 2015, both Firestone Bay and Drakes Island were surveyed within a one-week period by  
226 SCUBA divers. At both sites, 10 replicate 1 m<sup>2</sup> quadrats were haphazardly placed, at least  
227 2 m apart, within mixed macroalgal canopies at ~0.5-2 m depth (below chart datum). Within  
228 each quadrat the abundance of canopy-forming macroalgae (*U. pinnatifida*, *L. ochroleuca*, *S.*  
229 *polyschides*, *S. latissima*) was quantified and the percent canopy cover of each species was  
230 estimated visually by a single observer. All *Undaria* sporophytes within each quadrat were  
231 harvested by removing beneath the holdfast, placed into separate labelled mesh bags and  
232 then returned to the laboratory for processing. On return to the laboratory, the following  
233 morphological attributes were measured for each sporophyte: lamina length (cm), lamina  
234 width (cm), stipe width (mm), stipe length (cm), sporophyll width (cm), sporophyll fresh  
235 weight (g), total sporophyte fresh weight (g) and total sporophyte dry weight (g).

### 236 **Canopy removal experiment**

237

238 In March 2015, nine 3 m diameter circular plots were marked at Firestone Bay using rock-  
239 bolts secured in the centre of each plot. The plots were established in the low intertidal zone  
240 (~0.7 m above chart datum; set up by hand during a spring low tide), ran parallel to the  
241 shore, and were separated by a distance of >10 m. Plots were stratified for hard substrata  
242 (i.e. bedrock and large boulders) and were established on horizontally-orientated surfaces  
243 (rather than on vertical ledges and crevices). Four of the plots were randomly assigned to an  
244 experimental treatment, whereby all canopy-forming macroalgae were removed (entire thalli  
245 including holdfasts) from the 7 m<sup>2</sup> plot area. The remaining five plots were assigned as  
246 controls, where macroalgal assemblages were left unmanipulated. No *Undaria* sporophytes  
247 were observed in either the control or removal plots when they were established (which was  
248 before the peak recruitment period). After a three-month period, a 1 m<sup>2</sup> quadrat was  
249 randomly placed within each plot (excluding the outer 0.5 m edge). The abundance and  
250 percent cover of all canopy-forming macroalgae (*Undaria*, *L. digitata*, *S. polyschides*, *S.*  
251 *latissima*) was quantified by a single observer, and five mature *Undaria* sporophytes were  
252 randomly selected and harvested for morphological analysis (as outlined above). Total  
253 abundance and percent cover of *Undaria* competitors within each quadrat was calculated as  
254 the sum of individual species values, and therefore total percent canopy cover could be over  
255 100%.

### 256 **Data analysis**



257 For the broad-scale field surveys, the relationship between *Undaria* abundance and  
258 competitor species cover was tested using generalised linear mixed models (GLMM) with a  
259 Poisson distribution to best represent the response data. Site was treated as a random  
260 factor, while the cover of competitor species was the fixed effect. Observations were  
261 modelled as random effects due to overdispersion in the Poisson distribution (Harrison  
262 2014). A model of *Undaria* abundance and total cover of competitor species was constructed  
263 first, and when a significant relationship was identified, individual species effects were  
264 assessed as separate terms.

265 For the fine-scale surveys, the relationship between *Undaria* and competitor species  
266 abundance was also assessed using Poisson GLMMs. For *Undaria* cover and biomass  
267 linear mixed models (LMM) were fitted to better represent the response data. In all cases  
268 site was treated as a random factor, competitor abundance was the fixed factor for the  
269 GLMMs, and competitor cover for LMMs. LMMs were assessed visually for normality and  
270 homogeneity of variance using quantile-quantile plots and predicted versus residual plots.  
271 For all models the relationship between *Undaria* and total abundance or cover of competitor  
272 species was tested first. When a significant relationship was identified, individual species  
273 effects were assessed as separate terms.

274 The effect of the canopy removal treatment on the abundance (log transformed) and percent  
275 cover (arcsin transformed) of kelps was examined with Welch's two sample t-tests. Pairwise  
276 comparisons between disturbed and control treatments were carried out for each kelp  
277 species separately.

278 Variability patterns in the morphology of *Undaria* sporophytes for both the fine-scale field  
279 surveys and the canopy removal experiment were examined with multivariate permutational  
280 analyses of variance (PERMANOVA) and metric multidimensional scaling (mMDS).  
281 Morphological attributes of individual plants were treated as a multivariate response and a  
282 similarity matrices were constructed from Euclidean distances between square-root  
283 transformed data. For visualisation of the data, mMDS was conducted over two dimensions  
284 under Kruskal fit scheme 1 using 100 restarts. For the field survey data, variability between  
285 site, quadrat (nested within site), and either the total percent cover or abundance of  
286 competitors (covariate) was tested by PERMANOVA with 999 permutations under a reduced  
287 model with sequential sums of squares. For the canopy removal experiment, the effects of  
288 treatment (fixed factor) and plot (random factor nested within treatment) on multivariate  
289 morphology was tested with PERMANOVA, using 999 permutations under a reduced model  
290 with partial sums of squares. As significant differences in morphology were observed  
291 between treatments, SIMPER analysis was used to identify the primary morphological

292 response variables contributing to the dissimilarity. All univariate statistics were run in R  
293 3.2.2 using base and *lme4* packages (Bates et al. 2015; R Core Team 2015). The *dplyr*  
294 package (Wickham and Francois 2015) was used for data manipulation and all univariate  
295 graphs were created using *ggplot2* (Wickham 2009) or Sigma Plot v.12. Multivariate  
296 procedures were conducted on the PRIMER v.7 software package with the PERMANOVA  
297 add-on (Clarke et al. 2014).

## 298 Results

### 299 Field surveys

300 From the broad-scale field surveys, the total percent cover of competitors showed a  
301 significant negative relationship with *Undaria* abundance (Table 1, Fig. 2A). When  
302 separating by competitor species this relationship was shown to be due to a mixture of all  
303 species (Table 1). Scatterplots of *Undaria* abundance and each competitor species alone  
304 identified some relationship between *Undaria* abundance and *Laminaria* spp., as *Undaria*  
305 abundance generally decreased with increasing coverage of *Laminaria* spp. (Fig. 2B).  
306 However, no clear relationships between the spatial coverage of the other main competitors,  
307 *Saccorhiza polyschides* and *Saccharina latissima*, and the abundance of *Undaria* were  
308 observed (Fig. 2C and 2D).

309 For the fine-scale surveys at Drakes Island and Firestone Bay, the abundance and percent  
310 cover of kelp species varied between sites (Fig. 3). *Undaria* was higher in abundance and  
311 percent cover at Firestone Bay, and the main competitor at both sites in terms of abundance  
312 and percent cover was *L. ochroleuca* (Fig. 3). The total abundance of competitors showed a  
313 significant negative relationship with *Undaria* abundance (Table 2, Figure 4A). When  
314 separating by competitor species this relationship was shown to be primarily due to *L.*  
315 *ochroleuca* abundance, with no significant effect from *S. latissima* or *S. polyschides* (Table  
316 2). The total percent cover of competitors also exhibited a significant negative relationship  
317 with *Undaria* percent cover (Table 2, Figure 4B). This was due to a combination of *L.*  
318 *ochroleuca* and *S. latissima* percent cover, with no significant effect from the percent cover  
319 of *S. polyschides* (Table 2). Similarly, the total biomass of *Undaria* was negatively related to  
320 the percent cover of native competitors (Table 2, Figure 4C) which, when broken down by  
321 species, was primarily related to the percent cover of *L. ochroleuca*. The morphology of  
322 *Undaria* significantly differed between sites ( $F_{(1,46)} = 6.05$ ,  $p = 0.022$ ), however neither the  
323 total abundance ( $F_{(1,46)} = 0.35$ ,  $p = 0.912$ ) nor percent cover ( $F_{(1,46)} = 1.08$ ,  $p = 0.385$ ) of  
324 competitors had any effect on *Undaria* morphology (Figure 5).

## 325 Canopy removal experiment

326

327 Three months following the canopy removal treatment, *Undaria* was present in both  
328 treatment and control plots (Fig. 6). However, the average number of sporophytes was 5.6  
329 times greater in the removal plots compared with controls and the percent cover was 3.3  
330 times greater in removal plots (Fig. 6); these differences between plots were statistically  
331 significant. With regards to other canopy-forming macroalgae, *L. digitata* was not recorded in  
332 the removal plots but was the dominant species (by cover) in the control plots (Fig. 6); both  
333 abundance and cover of *L. digitata* were significantly greater in control plots. *S. latissima*  
334 was more abundant but covered less area in the removal plots, but these differences were  
335 non-significant (Fig. 6). *S. polyschides* has slightly higher abundance and cover values in the  
336 removal plots but again variability between treatments was non-significant (Fig. 6). An MDS  
337 plot based on the multivariate morphological characteristics of *Undaria* suggested that  
338 sporophytes in removal plots were distinct from those in control plots (Fig. 7); a  
339 PERMANOVA test indicated that differences between treatments were significant ( $F_{(1,8)} =$   
340 2.50,  $p = 0.012$ ). Further examination of morphological variables showed that the  
341 dissimilarity between treatments was primarily due to total fresh weight, sporophyll weight  
342 and lamina length of sporophytes, which were, on average, all greater in removal plots than  
343 those in control plots (Table 3). Additionally, sporophytes from removal plots had greater  
344 average values for total sporophyte length, stipe width, sporophyll width and total dry weight  
345 compared with those in control plots, but these differences were not important contributors to  
346 the observed dissimilarity.

## 347 Discussion

348 The study supports our principal hypothesis that natural habitats supporting dense native  
349 macroalgal canopies have more biotic resistance to invasion by *Undaria* than disturbed or  
350 sparse canopies. Across the field surveys, significant negative relationships between  
351 *Undaria* abundance, cover and biomass and the density or cover of native macroalgal  
352 canopies were observed. Competition for light, nutrients and space may strongly influence  
353 the recruitment, germination, survivorship and growth of *Undaria* (Floc'h et al. 1996;  
354 Valentine and Johnson 2003; Thompson and Schiel 2012; Morelissen et al. 2013).  
355 Decreased light availability beneath macroalgal canopies was likely to have been particularly  
356 important in suppressing the recruitment and growth of *Undaria*, as dense *Laminaria* canopies  
357 can reduce Photosynthetically Active Radiation (PAR) reaching the reef surface by >90%  
358 (Pedersen et al. 2014). Due to intense shading, PAR levels reaching the reef surface below  
359 *Laminaria* canopies may be as low as  $\sim 60 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$  during the daytime

360 (Pedersen et al. 2014) which, although not completely restrictive, is likely to fall below  
361 optimal light levels required for sporophyte development and growth (Saito 1975; Campbell  
362 et al. 1999; Morelissen et al. 2013; Watanabe et al. 2014). Indeed, Gao et al. (2014) showed  
363 that photosynthesis, growth and maturation of *Undaria* sporophytes were enhanced when  
364 grown under reduced canopy density, as a result of increased light penetration. As such, we  
365 suggest that the negative relationships observed between *Undaria* and native competitors  
366 are largely due to competition for light and alterations to the light environment caused by the  
367 presence of large native canopy formers. An alternative possible mechanism could be that  
368 the abiotic conditions which favour *Undaria* are divergent to those that favour *Laminaria*  
369 spp., so that our observed patterns simply reflect differences in ecophysiological tolerances  
370 for light, wave exposure, physical disturbance or some other variable. However, given that (i)  
371 *Laminaria* spp. persist across a wide range of environmental conditions in Plymouth Sound,  
372 from extremely wave exposed to wave sheltered and from highly disturbed (e.g. marinas) to  
373 relatively pristine habitats, (ii) previous work has indicated overlapping environmental  
374 requirements between *Undaria* and *Laminaria* spp. (Yesson et al. 2015), and (iii) competitive  
375 release following canopy removal (see below) increased *Undaria* recruitment and growth, we  
376 suggest that ecological interactions were important drivers of observed patterns.

377 As with previous work in Australia (Valentine and Johnson 2003) we suggest that  
378 competition for space was less important than for light, as there was ample reef surface  
379 available for attachment of *Undaria* propagules and sporophytes, given that the cover of  
380 understory species was generally low (less than ~40%, authors pers. obs.) and the number  
381 of kelp holdfasts attached to the reef was also quite low (i.e. the total abundance of all  
382 competitors was generally <10 inds.m<sup>-2</sup>). Similarly, although *Undaria* is susceptible to low  
383 nutrient availability due to limited storage capacity (Dean and Hurd 2007), nutrient  
384 concentrations within Plymouth Sound are unlikely to be limiting during the spring-to-early-  
385 summer growth season for *Undaria*. To expand, the average surface seawater  
386 concentrations for nitrate and phosphate in March-June exceed 2 µM and 0.2 µM,  
387 respectively (Smyth et al. 2010, Western Channel Observatory data), which surpass  
388 requirements for *Undaria* growth (Wu et al. 2004; Dean and Hurd 2007), and the study area  
389 also receives significant nutrient loading from nearby estuaries (Langston et al. 2003). While  
390 nutrients may become limiting by late summer, with consequent inter-specific competition for  
391 resources perhaps becoming important, the relationships described here were unlikely to  
392 have been driven by competition for nutrients

393 The density and percent cover of *Laminaria* spp. (*L. hyperborea*, *L. digitata* and *L.*  
394 *ochroleuca*) was consistently an important predictor of *Undaria* abundance, cover and

395 biomass. *L. hyperborea* and *L. ochroleuca* are long-lived perennial kelps (both can exceed 6  
396 years of age within Plymouth Sound, Smale unpublished data), which form rigid stipes and  
397 exhibit upright, stipitate growth forms with large lamina that create dense canopies. As such,  
398 the competitive pressure exerted upon understory macroalgae is likely to be intense, and a  
399 high abundance and cover of these species was related to low abundance, cover and  
400 biomass of *Undaria*. Although it is shorter-lived and forms a more flexible stipe, *L. digitata*  
401 also forms dense monospecific canopies and its thick, extensive laminae are likely to restrict  
402 light penetration to the underlying substrate. In contrast, the relationship between *Undaria*  
403 and *Saccharina latissima* was weaker and less consistent. *S. latissima* is a shorter-lived  
404 perennial species (generally 2-3 years old in Plymouth Sound, Smale, unpublished data)  
405 with a short, flexible stipe that exhibits a prostrate growth form. It is plausible that *S.*  
406 *latissima* exerts less competitive pressure on *Undaria* for three reasons: first, it lies flat on  
407 the seabed without forming an elevated canopy and, as such, may allow more light to reach  
408 *Undaria* gametophytes and young sporophytes attached the reef. Second, it can function as  
409 an early successional species under moderately wave exposed conditions, such as at  
410 Drakes Island, where its sporophytes are typically relatively small and short-lived (Leinaas  
411 and Christie 1996). Third, it is more patchily distributed and is often found attached to semi-  
412 stable substrates in more wave-sheltered environments, where it generally does not form  
413 continuous, dense monospecific stands. As such, *S. latissima* may exert less pressure on  
414 resources such as space and light and allow for recruitment and growth of *Undaria*.

415 We did not, however, detect any major influence of the abundance or cover of *S.*  
416 *polyschides* on *Undaria*. This could be due to the fact that like *Undaria*, *S. polyschides* is a  
417 pseudo-annual species, which develops young sporophytes in spring that grow rapidly  
418 throughout summer before senescing during the autumn/winter period (Norton and Burrows  
419 1969). In contrast to established perennial species (i.e. *L. ochroleuca*, *L. hyperborea*, *L.*  
420 *digitata* and *S. latissima*) *S. polyschides* does not produce large canopy-forming sporophytes  
421 during the spring period of recruitment and growth of *Undaria* sporophytes and is unlikely to  
422 exert strong competitive pressure, at least until late summer when both species have  
423 attained maximum size and may compete for resources. Unravelling the strength and  
424 direction of competitive interactions requires formal testing, but it is likely that inter-specific  
425 differences in life histories and morphological/functional traits between native kelp species  
426 will influence the magnitude of competitive superiority over *Undaria* and, as such, variability  
427 in the composition of macroalgal stands will influence their biotic resistance to invasion. For  
428 example, if *S. polyschides* becomes more abundant in the future in response to increased  
429 storminess and temperature, as has been predicted (Hiscock et al. 2004; Smale et al. 2013),  
430 the invasibility of the wider macroalgal canopy may increase relative to a canopy dominated

431 by *Laminaria* spp. Variability in biotic resistance driven by differences in canopy composition  
432 and cover has been observed in macroalgal beds in Australasia (Valentine and Johnson  
433 2004; Thompson and Schiel 2012; South and Thomsen 2016), and may be of increasing  
434 importance in this region in the near future.

435 As the presence of canopy-forming macroalgae can reduce light and space availability for  
436 understory macroalgal species (Wernberg et al. 2005; Pedersen et al. 2014), physical  
437 disturbance to the canopy can reduce competitive pressure for these resources and facilitate  
438 the recruitment and growth of understory species (Goodsell and Connell 2005; Flukes et al.  
439 2014). Canopy removal may result from both physical (i.e. storm damage) (Smale and  
440 Vance 2016) or biological (i.e. grazing) (Rinde et al. 2014; Ling et al. 2015) agents of  
441 disturbance. *Undaria* has been described as an opportunistic species, and evidence of  
442 disturbance facilitating its establishment into native communities has been reported  
443 (Valentine and Johnson 2003; Edgar et al. 2004; Valentine and Johnson 2004; Thompson  
444 and Schiel 2012; South and Thomsen 2016). However, the importance of disturbance on  
445 *Undaria*'s colonisation success may be dependent on the recipient biota, the spatial and  
446 temporal disturbance regime, and the scale of observation (Thompson and Schiel 2012;  
447 Morelissen et al. 2016).

448 Here, canopy removal resulted in a >3 and >5-fold increase in the cover and abundance of  
449 *Undaria* sporophytes, respectively. Given that the majority of mature *Undaria* sporophytes  
450 are present in early-mid summer in the UK (Heiser et al. 2014; Minchin and Nunn 2014;  
451 Arnold et al. 2016), it is very likely that the recruiting sporophytes developed from an existing  
452 gametophyte 'seedbank' attached to the reef surface. Gametophytes can remain viable for  
453 up to 24 months if conditions for sporophyte development are not favourable (Stuart 2003;  
454 Choi et al. 2005) and, as such, disturbance to the canopy likely provided inactive  
455 gametophytes with the adequate light levels needed to stimulate sporophyte development  
456 (Kim and Nam 1997 ; Choi et al. 2005). Morelissen *et al.*, (2013), conducted a study to  
457 evaluate how the development of the microscopic life stages of *Undaria* was affected by  
458 irradiance and nutrient availability. Their results revealed that under low irradiance,  
459 gametophyte growth was stalled and zygotes did not progress to the sporophyte stage.  
460 These results suggest that, with the support of field studies from Valentine and Johnson  
461 (2003), Thompson and Schiel (2012) and the current study, that the development of the  
462 microscopic stages of *Undaria* may be limited by the presence of dense, light-limiting  
463 macroalgal canopies. It should be noted that our manipulative experiment was short-term  
464 and small-scale, and longer-term multi-site experiments are needed to determine the nature  
465 of interactions between *Undaria* and native canopy formers.

466 In our fine-scale field survey we did not observe any clear relationships between the  
467 morphology of *Undaria* sporophytes and the abundance or cover of competitors. We did,  
468 however, observe significant differences in morphology between Drakes Island and  
469 Firestone Bay, suggesting the importance of local environmental conditions in structuring  
470 *Undaria* populations. The influence of water flow dynamics, exposure to waves and tides,  
471 and light availability on *Undaria* growth and morphology has been examined elsewhere  
472 (Castric-Fey et al. 1999; Shibneva et al. 2013) and considerable morphological plasticity in  
473 response to environmental conditions is common in kelp species (Fowler-Walker et al.  
474 2005; Wernberg and Thomsen 2005). The populations at Drakes Island were subjected to  
475 greater water motion related to both tidal flows and wave action, which may explain  
476 difference in morphology between sites. The lack of any observable relationship between  
477 competitors and the morphology of *Undaria* was, to some extent, surprising as previous work  
478 on farmed populations has shown that *Undaria* may allocate more resources to stipe growth  
479 in response to intense competition, in order to elevate its position in the canopy and attain  
480 more light (Gao et al. 2014). In contrast, *Undaria* did exhibit clear morphological responses  
481 to the substantial reduction in competitive pressure following canopy removal. In disturbed  
482 plots, *Undaria* sporophytes had longer lamina and greater biomass (of both entire  
483 sporophytes and sporophylls). Clearly, the ecological performance of recruiting *Undaria*  
484 sporophytes is enhanced when interspecific competition from canopy-forming macroalgae is  
485 minimal, as more energy is available for growth of the thallus and the development of  
486 reproductive structures.

487 Previous studies have found little evidence that *Undaria* can displace native macroalgae  
488 (Forrest and Taylor 2002; Raffa et al. 2009; Thompson and Schiel 2012) although there is  
489 some evidence to suggest that it can alter the structure of associated communities (Casas et  
490 al. 2004; Farrell and Fletcher 2006; Arnold et al. 2016). Indeed, some studies have  
491 suggested that rather than replacing native macroalgae and the species they support,  
492 *Undaria* may instead contribute to the complexity, biodiversity, and productivity of invaded  
493 temperate reef systems (Irigoyen et al. 2011; South et al. 2015; Tait et al. 2015). The nature  
494 and strength of its impacts and influence on native biota appear to be highly context-specific,  
495 and depend largely on the local environmental conditions and composition of recipient native  
496 communities. It is clear that since its introduction in the early 1990s, *Undaria* has steadily  
497 spread along the UK coastline and, can be found as a conspicuous and important  
498 component of macroalgal communities within natural habitats. Better understanding of the  
499 ecological interactions between native and non-native habitat-forming species is needed to  
500 inform management, and future studies should examine the impacts of *Undaria* through  
501 long-term field-based experiments using manipulative or BACI (before after control impact)

502 designs, as has been achieved in Australasia (Forrest and Taylor 2002; Valentine and  
503 Johnson 2005; South et al. 2015; South and Thomsen 2016).

504 Our results suggest that the biotic resistance of macroalgae assemblages to invasion by  
505 *Undaria* is likely to vary spatially, depending on the identity and abundance of competing  
506 native species and environmental context. Overall, the presence of dense *Laminaria*  
507 canopies is likely to limit, but not prevent, assimilation of *Undaria* into native communities,  
508 due to the superior competitive ability of the large, stipitate, perennial kelps. Even so,  
509 *Undaria* sporophytes were still recorded within dense *Laminaria* canopies, suggesting that  
510 disturbance to the canopy is not a prerequisite for successful invasion. Other native  
511 macroalgae are likely to exert weaker competitive pressure, perhaps due to their life history  
512 or morphology. It should be noted that the majority of our findings were based on  
513 observational surveys, which are correlative in nature and cannot determine causation.  
514 Clearly, long-term manipulative experiments are required to fully unravel the strength and  
515 direction of ecological interactions between *Undaria* and native canopy-forming macroalgae.  
516 We suggest that *Undaria* is likely to remain a conspicuous component of macroalgal  
517 assemblages on rocky reefs in Plymouth Sound and elsewhere, given its widespread  
518 distribution and generally high abundances in nearby artificial habitats (Fletcher and Farrell  
519 1999; Farrell and Fletcher 2006; Heiser et al. 2014; Minchin and Nunn 2014). Perhaps the  
520 most effective approach to limiting its spread into native communities is to maintain and  
521 promote favourable environmental conditions for the persistence of dense, highly productive  
522 *Laminaria*-dominated canopies that provide biotic resistance to invasion.

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792 **Table 1:** GLMMs identifying the influence of competitor species on the abundance of  
 793 *Undaria* from the broad-scale survey. Total = total percent cover of competitor species. SL =  
 794 *Saccharina latissima*, Lam = *Laminaria spp.*, SP = *Sacchorhiza polyschides*. Significance of  
 795 terms ( $p < 0.05$ ) is shown by an asterisk (\*).

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	Coefficients	Estimate	Std. Error	z	p	
799	Intercept	5.686	0.257	22.12	< 0.001	*
800	Total	-1.953	0.332	-5.89	< 0.001	*
801	Intercept	5.630	0.273	20.66	< 0.001	*
802	Lam	-1.927	0.409	-4.71	< 0.001	*
	SP	-1.939	0.354	-5.48	< 0.001	*
803	SL	-1.625	0.649	-2.50	0.012	*

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812 **Table 2:** GLMMs and LMMs identifying the influence of competitor species on the  
 813 abundance, percent cover and biomass of *Undaria* from the fine-scale survey. Percent cover  
 814 of competitors was used as a proxy for the biomass analysis. Total = total abundance or  
 815 percent cover of competitor species. SL = *Sacchorina laticornis*, LO = *Laminaria ochroleuca*,  
 816 SP = *Sacchoriza polyschides*. Significance of terms ( $p < 0.05$ ) is shown by an asterisk (\*).

817				
Coefficients	Estimate	Std. Error	z	p
<i>Abundance (GLMM)</i>				
819				
Intercept	1.703	0.444	3.83	< 0.001 *
Total	-0.091	0.041	-2.21	0.027 *
Intercept	1.747	0.573	3.05	0.002 *
SL	-0.229	0.121	-1.89	0.059
LO	-0.097	0.042	-2.33	0.020 *
SP	0.066	0.183	0.36	0.720
824				
Coefficients	Estimate	Std. Error	t	p
<i>Percent cover (LMM)</i>				
826				
Intercept	1.072	0.201	5.33	0.001 *
Total	-0.661	0.184	-3.59	0.002 *
Intercept	1.082	0.246	4.40	0.029 *
SL	-0.917	0.284	-3.23	0.005 *
LO	-0.702	0.191	-3.68	0.002 *
SP	-0.359	0.276	-1.30	0.213
831				
Coefficients	Estimate	Std. Error	t	p
<i>Biomass (LMM)</i>				
833				
Intercept	1.594	0.449	3.55	0.002 *
Total	-1.020	0.470	-2.17	0.044 *
Intercept	1.587	0.485	3.27	0.010 *
SL	-0.938	0.701	-1.34	0.227
LO	-1.248	0.529	-2.36	0.032 *
SP	-0.390	0.770	-0.51	0.620
837				

838 **Table 3:** SIMPER analysis to determine the morphological attributes contributing most to the  
 839 observed dissimilarity in *Undaria* morphology between control and canopy removal plots.  
 840 The 3 morphological attributes contributing most to the observed dissimilarity between  
 841 treatments are shown. Average values (square-root transformed) in control and removal  
 842 plots, average dissimilarity, dissimilarity/standard deviation, and the percentage contribution  
 843 to total dissimilarity are presented.

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Attribute	Control	Removal	Av. Diss.	Diss./SD	Contrib. (%)
Fresh weight	7.45	9.93	5.17	1.47	32.46
Sporophyll weight	1.78	3.18	3.34	1.56	21.01
Lamina length	6.73	7.51	1.81	1.32	11.00

846 **Figure legends**

847 **Figure 1:** Map of study area. Sites used for the broad-scale survey are indicated in grey, the  
848 2 sites sampled for fine-scale survey work (i.e. Drakes Island (B) and Firestone Bay (A)) are  
849 shown in black. Inset map shows position of the study area within the wider context of the  
850 southwest UK.

851 **Figure 2:** Relationship between *Undaria* abundance and total percent cover of competitors  
852 (a), *Laminaria* spp. (b), *Sacchorina lattismia* (c) and *Sacchoriza polyschides* (d) from broad-  
853 scale surveys. Points show raw data from each transect. Plotted lines of fitted values from  
854 GLMM.

855 **Figure 3:** Average abundance (A) and percentage cover (B) of kelp species recorded in  
856 quadrats at Drakes Island and Firestone Bay. Bars show mean values from 10 replicate 1m<sup>2</sup>  
857 quadrats ( $\pm$  SE).

858 **Figure 4:** The total abundance (A) percent cover (B) and total biomass (C) of *Undaria* in  
859 relation to the abundance (A) and percent cover (B&C) of macroalgal competitors from fine-  
860 scale surveys. Points show raw data from each quadrat. Plotted lines of fitted values for  
861 each site from GLMM (A) and LMMs (B&C).

862 **Figure 5:** Metric MDS plot indicating variability in morphology (multivariate response based  
863 on 7 individual uncorrelated descriptors) of *Undaria* sporophytes at each site. Bubble sizes  
864 represent the total percent cover (pTot shown in A) and total abundance (nTot shown in B)  
865 of competitors in the quadrat from which the *Undaria* sporophyte was sampled.

866 **Figure 6:** Average abundance (A) and percentage cover (B) of kelp species recorded in  
867 canopy removal and control plots at Firestone Bay, 3 months after the experiment was  
868 initiated. Bars show mean values from 4 replicate canopy removal plots and 5  
869 unmanipulated control plots ( $\pm$  SE). Significant differences between treatments ( $P < 0.05$ ) are  
870 indicated with an asterisk.

871 **Figure 7:** Metric MDS plot indicating variability in morphology (multivariate response based  
872 on 7 individual uncorrelated descriptors) of *Undaria* sporophytes within each of the 4 canopy  
873 removal plots and the 5 control plots. Ordination is based on a similarity matrix constructed  
874 from Euclidean distance measures between square-root transformed data.

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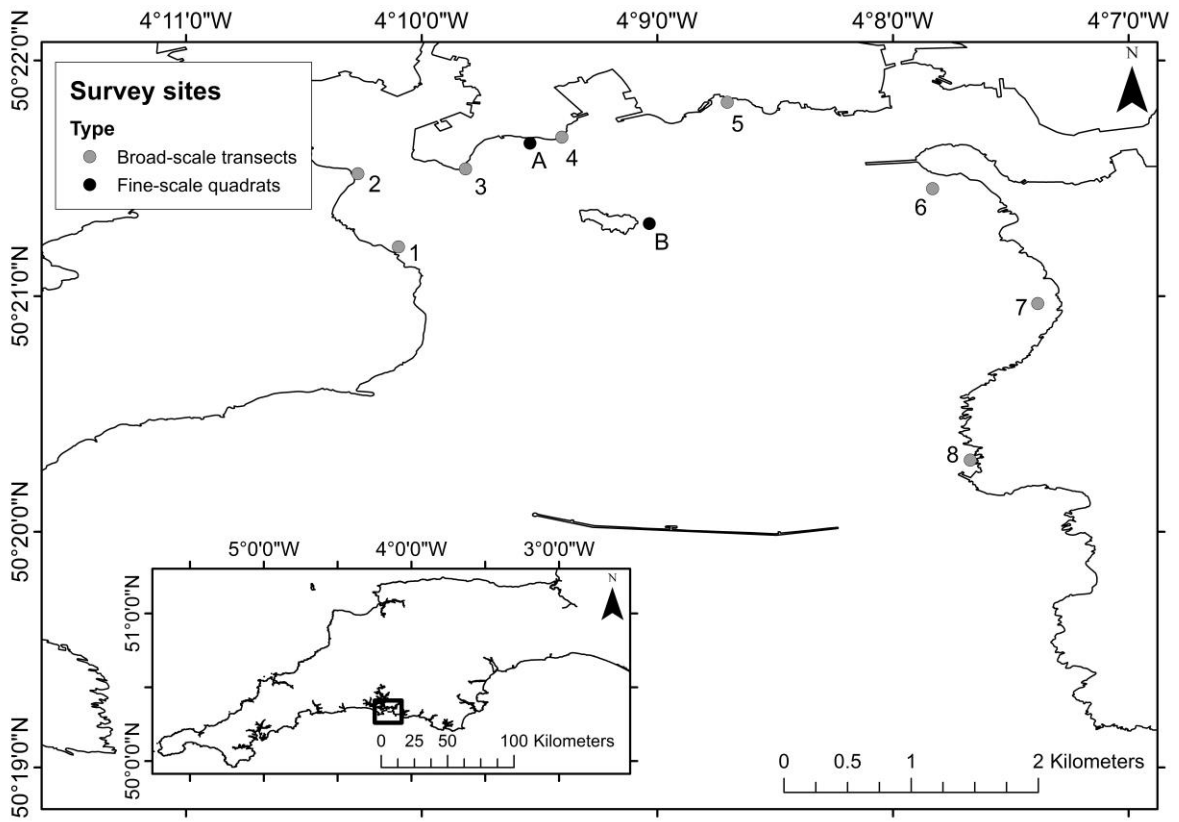


Fig. 1

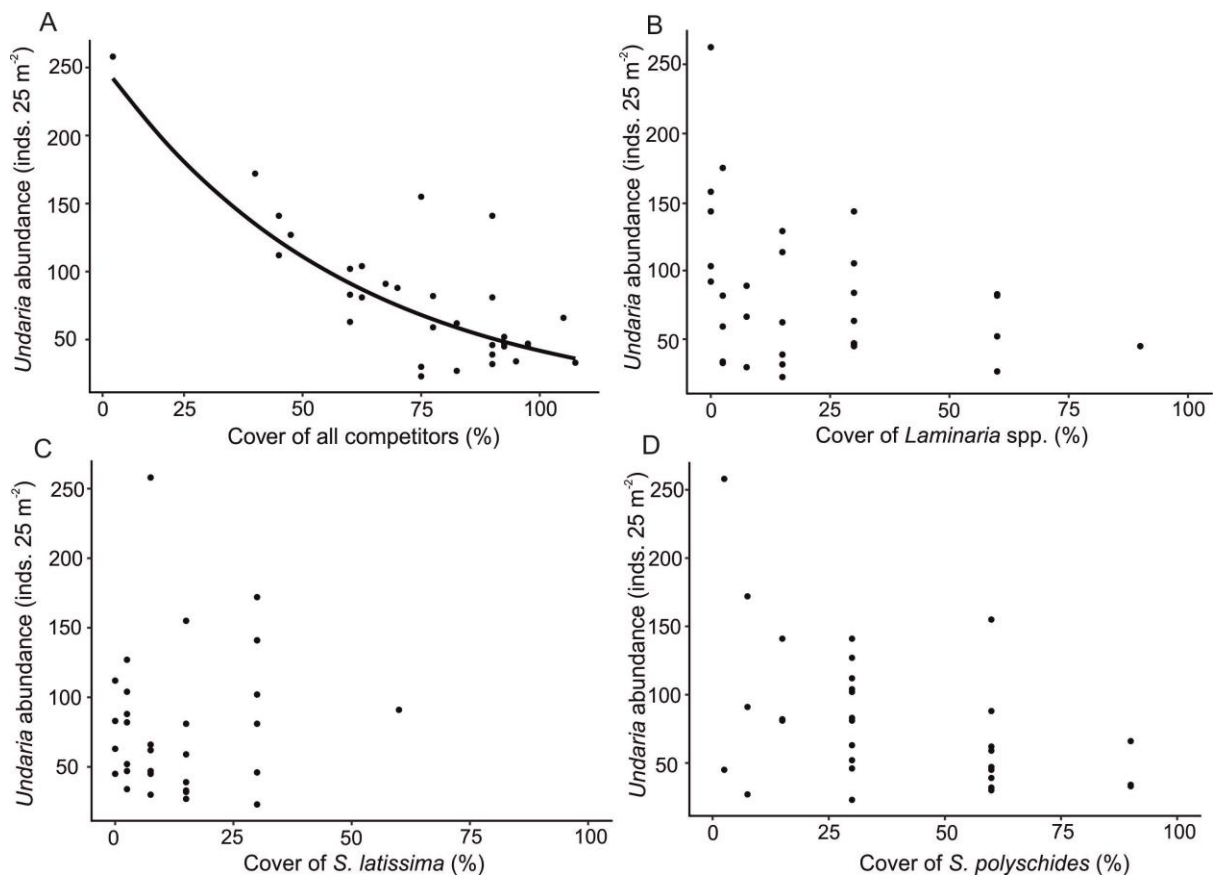


Fig. 2

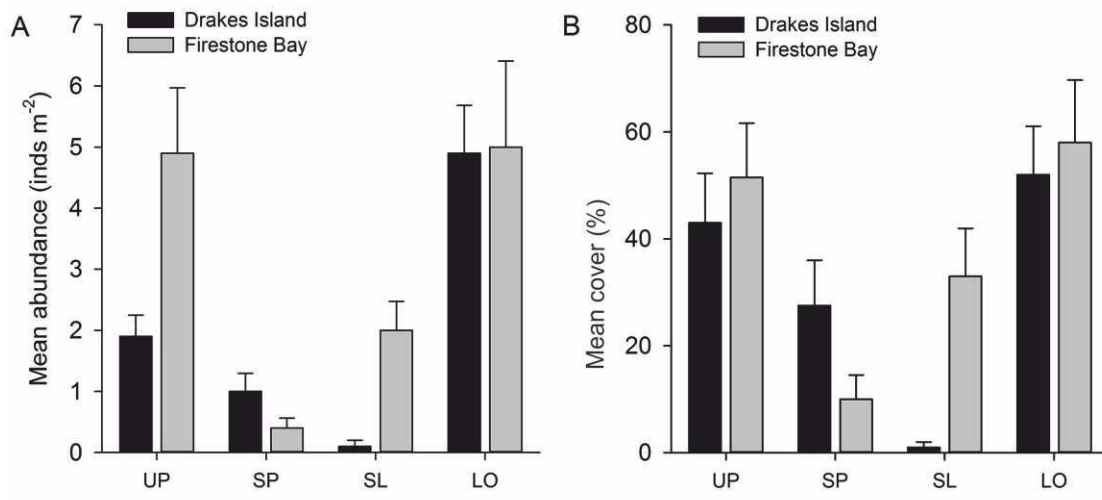


Fig. 3



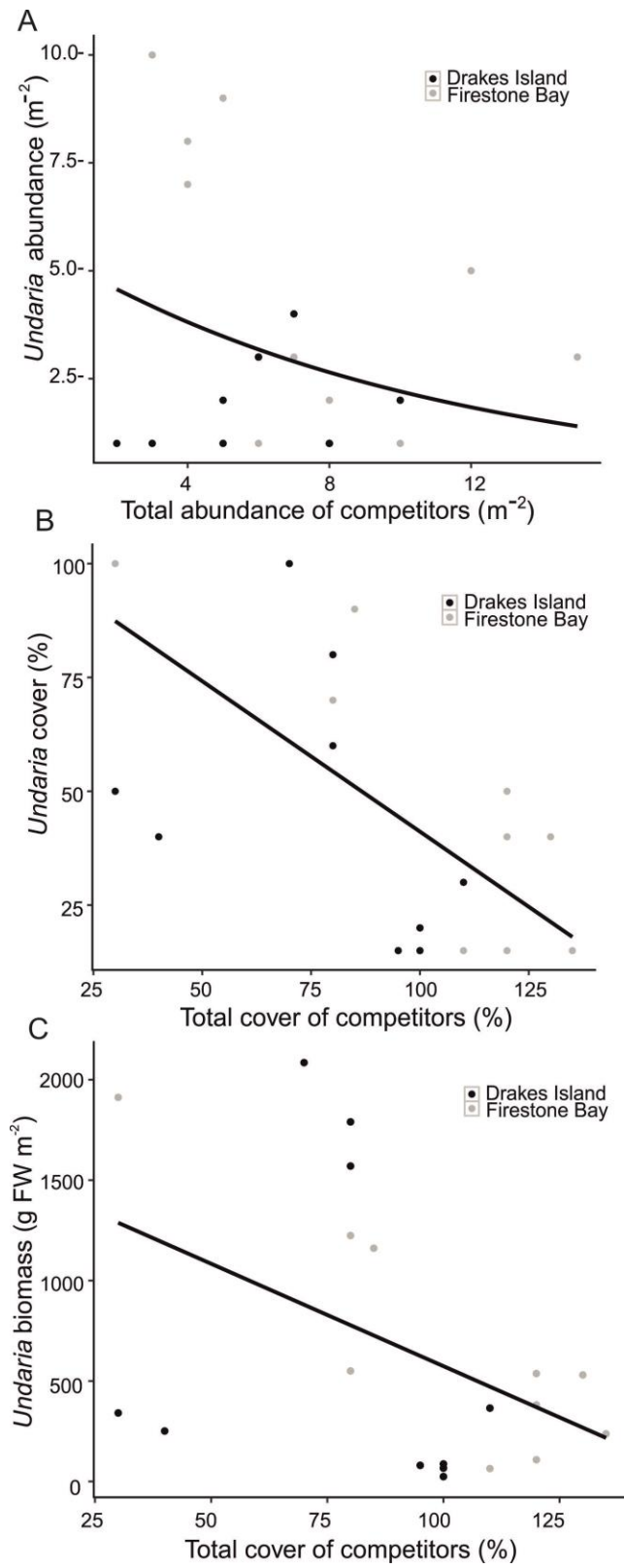


Fig. 4

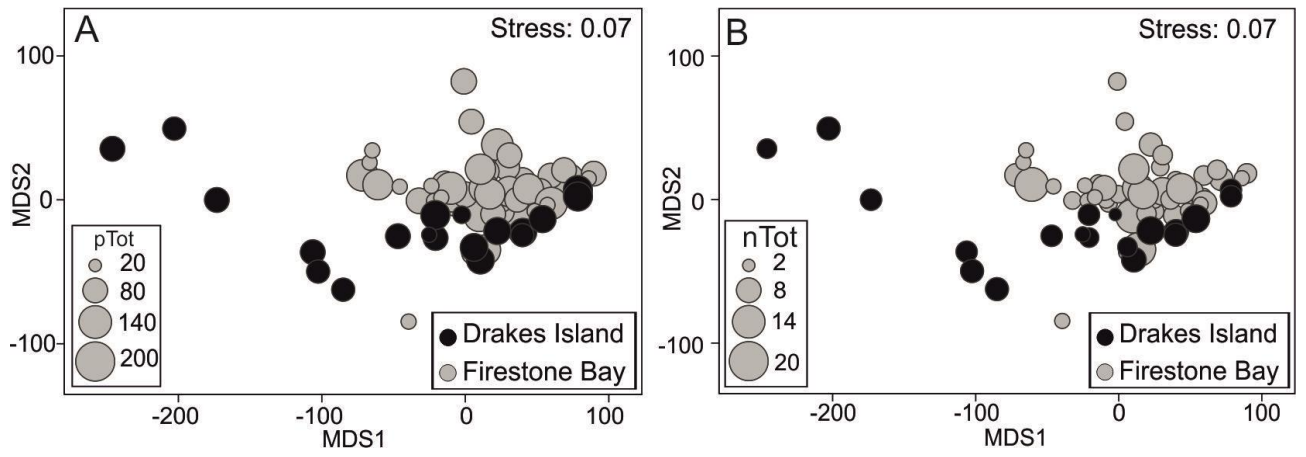


Fig. 5

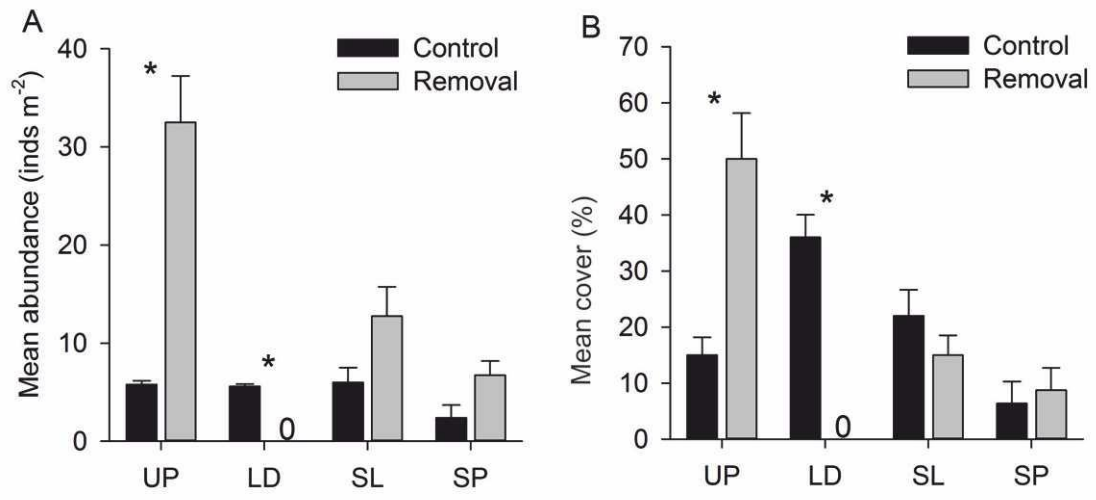


Fig. 6

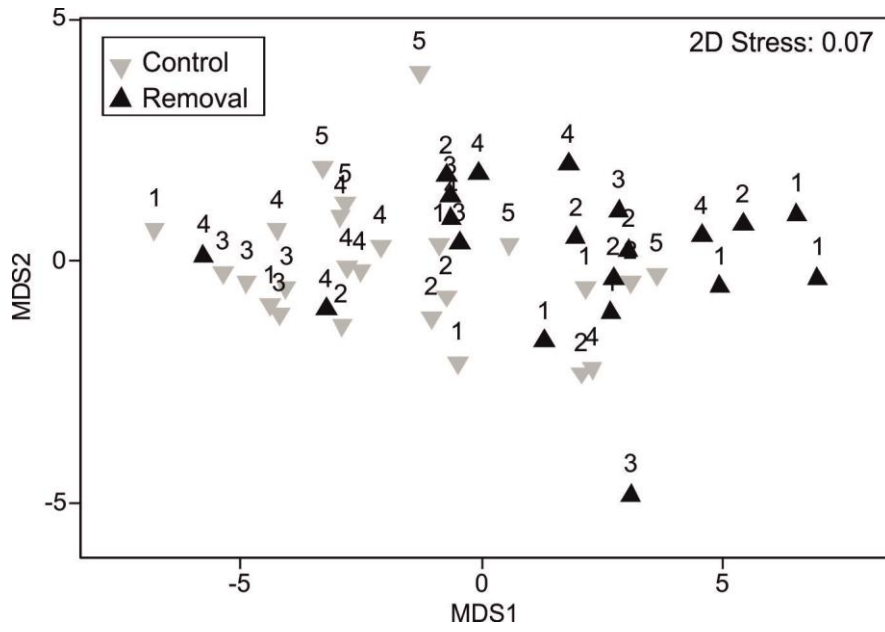


Fig. 7