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Smale, Dan A.; Epstein, Graham; bio, Esther; Mogg, Andrew O. M.; Moore, Pippa J.

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1 Original research submitted to *Biodiversity and Conservation* – accepted Oct 2020

2 Patterns and drivers of understory macroalgal assemblage
3 structure within subtidal kelp forests

4 *Running title: Spatial variation in kelp forest diversity*

5 Dan A. Smale¹, Graham Epstein¹, Esther Hughes¹, Andrew O. M. Mogg^{2,3},
6 Pippa J. Moore⁴

7 ¹Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth PL1 2PB,
8 UK

9 ²Tritonia Scientific Ltd., Oban, Argyll, PA37 1QA, UK

10 ³NERC National Facility for Scientific Diving, Scottish Association for Marine Science, Oban PA37 1QA

11 ⁴Institute of Biological, Environmental and Rural Sciences, Aberystwyth University, Aberystwyth, SY23
12 3DA, UK.

13

14 **Lead author:** Dan Smale: dansma@mba.ac.uk

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23 publication

24 **Abstract**

25 Kelp species are found along ~25% of the world's coastlines, where they provide myriad of
26 ecological goods and services. However, compared with many other terrestrial and marine
27 vegetated ecosystems, kelp forests have been critically understudied in many regions, leading
28 to pressing knowledge gaps that hinder management and conservation efforts. We conducted
29 a large-scale survey of understory macroalgae within subtidal kelp forests dominated by
30 *Laminaria hyperborea* at 12 sites, nested within 4 regions in the United Kingdom (UK).
31 Regions spanned ~9° in latitude and encompassed a gradient in average sea surface
32 temperature of ~2.5°C. We employed a combination of traditional hand-harvesting of quadrat
33 samples and a novel 3D photogrammetry technique to quantify crustose coralline algae. The
34 structure of understory macroalgal assemblages was highly variable but showed clear
35 partitioning at the spatial scales of both regions and sites. At the regional-scale, we observed
36 a general increase in richness, diversity and biomass from north to south, most likely due to
37 biogeographical context, ocean climate and the structure and composition of overlying kelp
38 canopies. Site level variation was most likely driven by concurrent variability in wave exposure
39 and kelp canopy structure. Our study shows that understory macroalgal assemblages
40 represent a rich and abundant component of kelp forests in the northeast Atlantic, with high
41 biodiversity value that warrant conservation measures. As these kelp forest ecosystems are
42 structured by multiple physical and biological processes, current and predicted environmental
43 change will likely alter the diversity and composition of understory macroalgal assemblages.

44 **Keywords:** Coastal ecosystems, marine biodiversity, seaweed assemblages, kelp forest
45 ecology, *Laminaria hyperborea*, northeast Atlantic

46 **Introduction**

47 Understanding patterns of biodiversity and the processes that influence them is a fundamental
48 goal of ecology (Magurran, 2013; Wilson, 1993). Globally, coastal marine ecosystems are
49 critically important in terms of their ecological and socioeconomic value, as they support high
50 levels of biodiversity and productivity, and provide a variety of ecosystem goods and services
51 (Costanza et al., 1997; Gray, 1997). Nearshore environments are, however, highly dynamic
52 and the structure and diversity of coastal marine ecosystems is influenced by a range of
53 processes that operate across multiple spatial and temporal scales (Fraschetti et al., 2005;
54 Hewitt et al., 2007). In addition to naturally occurring processes, human activities have
55 increasingly altered the structure of coastal marine ecosystems (Halpern et al., 2015; Halpern
56 et al., 2008). To effectively manage and conserve marine biodiversity, and to improve the
57 capacity to predict and detect future ecological changes, a deeper understanding of ecological
58 patterns and processes across multiple scales is needed (Edwards et al., 2010; Levin, 2000).

59 Kelp species are distributed along ~25% of the world's coastlines (Steneck et al., 2002;
60 Wernberg et al., 2019), where they play pivotal roles as ecosystem engineers, repositories of
61 biodiversity and expeditious primary producers (Pessarrodona et al., 2018; Smale et al., 2013;
62 Steneck et al., 2002; Teagle et al., 2017). Many kelp species fix and release substantial
63 quantities of organic matter, which is important for inshore carbon cycling, coastal food webs
64 and natural carbon sequestration (Duggins et al., 1989; Krause-Jensen and Duarte, 2016;
65 Krumhansl and Scheibling, 2012). Similarly, kelp forests influence hydrodynamic processes
66 and offer biogenic coastal defence (Dugan et al., 2011; Jackson and Winant, 1983; Løvås and
67 Tørum, 2001) Perhaps most importantly, by offering complex biogenic habitat kelp forests
68 support elevated levels of biodiversity, and provide nursery and foraging areas for
69 socioeconomically important species of invertebrates, fish, birds and mammals (Bertocci et
70 al., 2015; Graham, 2004; Teagle et al., 2017).

71 As habitat-formers, kelps directly support rich and abundant assemblages of algae and
72 invertebrates by providing living space on and within the holdfast (Anderson et al., 2005;
73 Sheppard et al., 1980; Teagle et al., 2018; Tuya et al., 2011) and on the surface of the stipe
74 and lamina (Teagle and Smale, 2018; Whittick, 1983; Włodarska-Kowalczyk et al., 2009).
75 Moreover, accumulations of kelp detritus provide food and shelter for a wide range of
76 organisms (Duggins et al., 2016; Vetter and Dayton, 1998). As well as direct habitat provision,
77 kelps also structure assemblages by altering local environmental conditions (Eckman et al.,
78 1989; Pedersen et al., 2014; Smale et al., 2011b; Wernberg et al., 2005). For example, epilithic
79 assemblages of algae and invertebrates found beneath kelp canopies generally differ in
80 structure from those found on open rocky reefs, due to variation in key factors such as light
81 availability, sedimentation rates, physical disturbance, water motion and grazing pressure
82 (Irving and Connell, 2006; Kennelly, 1987b; Kennelly, 1989; Santelices and Ojeda, 1984;
83 Toohey et al., 2007). Similarly, the space beneath dense kelp canopies may serve as
84 favourable habitat for fish and macroinvertebrates seeking food and shelter (Bodkin, 1988;
85 Christie et al., 2003; Efirid and Konar, 2014; Norderhaug et al., 2005).

86 To date, research conducted on the structure and diversity of epilithic understory algal
87 assemblages within kelp forests has been limited, especially compared with the volume of
88 research on assemblages associated with kelp plants themselves (Teagle et al., 2017). Even
89 so, previous research has shown that epilithic understory assemblages are diverse and
90 important components of kelp forest ecosystems (Clark et al., 2004; Leliaert et al., 2000;
91 Schaal et al., 2016; Thomsen and South, 2019). The few studies that have examined putative
92 drivers of understory assemblage structure – most of which have been conducted over limited
93 spatial scales – have identified local factors such as reef complexity, canopy structure, light
94 availability, physical disturbance and grazing as important determinants of ecological pattern
95 (Clark et al., 2004; Connell, 2003a; Flukes et al., 2014; Kennelly, 1989; Livore and Connell,
96 2012; Toohey and Kendrick, 2008). Large-scale quantitative surveys of understorey algal
97 assemblages have primarily been conducted along Australian and Californian coastlines

98 (Lamy et al., 2018; Wernberg et al., 2003); relatively little is known about kelp forests in the
99 northeast Atlantic, despite their broad geographical distribution and considerable ecological
100 and socioeconomic importance (Araújo et al., 2016; Smale et al., 2013).

101 We examined the structure and diversity of understory macroalgal assemblages within 12
102 subtidal kelp forests (dominated by *Laminaria hyperborea*) in the northeast Atlantic. Three
103 sites were nested within four regions which spanned 9° of latitude and encompassed a
104 gradient in average ocean temperature of ~2.5°C. By conducting surveys across multiple
105 spatial scales, we aimed to examine the relative importance of processes acting at regional
106 scales (e.g. ocean climate, biogeography), local scales (e.g. wave exposure, grazing
107 pressure) and fine scales (e.g. depth, habitat complexity) in structuring understory macroalgal
108 assemblages. This study builds on previous surveys conducted across the same regions (Bué
109 et al., 2020; Smale and Moore, 2017; Teagle et al., 2018) by examining assemblage structure
110 of poorly-studied but highly diverse understory algae at multiple spatial scales and by
111 identifying putative drivers of ecological pattern. Kelp-associated communities have elevated
112 ecological value (Bennett et al., 2016; Steneck et al., 2002), yet a lack of information on
113 patterns and drivers of biodiversity currently hinder management and conservation efforts
114 (Araújo et al., 2016).

115 **Materials and methods**

116 **Study sites**

117 We conducted surveys at 12 subtidal rocky reef sites, with 3 sites nested within each of 4
118 regions (Fig. 1). The regions spanned a latitudinal gradient of ~9° in the northeast Atlantic,
119 with adjacent regions situated between ~180 and 500 km apart (Fig. 1). Within each region a
120 set of candidate study sites were selected based on the following criteria: (i) sites should
121 include sufficient areas of subtidal rocky reef at ~2-6 m depth (below chart datum); (ii) sites
122 should be representative of the wider region (in terms of coastal geomorphology) and not
123 obviously influenced by localised anthropogenic activities (e.g. sewage outfalls, fish farms);

124 and (iii) sites should be 'open coast' and moderately to fully exposed to wave action to ensure
125 the dominance of *L. hyperborea*. From this pool of candidate sites, three were selected for
126 surveys; sites within regions were situated between ~1 and ~13 km apart. All sites were
127 characterised by extensive mono-specific stands of *L. hyperborea*; further information on the
128 environmental and ecological characteristics of the sites is available (Bué et al., 2020;
129 Pessarrodona et al., 2018; Smale et al., 2016; Smale and Moore, 2017; Smale et al., 2020).

130 **Sampling approach**

131 At each site, 8 replicate quadrats (0.125 m²) were haphazardly sampled within the kelp forest
132 by SCUBA divers. Replicate quadrats were deployed at least 3 m apart from one another and
133 centrally within the kelp stand (i.e. rather than at the forest edge). All samples were collected
134 from beneath mono-specific stands of *Laminaria hyperborea*; kelp plants were first removed
135 and then all understory macroalgae was collected by hand and placed in an individually-
136 labelled nylon mesh collection bag. Although some sessile invertebrates (e.g. sponges,
137 anemones, ascidians) were attached to the reef surface, they were generally low in biomass
138 and/or abundance compared with epilithic algae and are not considered further here. All
139 sampling was conducted within a 5-week period in August/September 2016. Once ashore,
140 samples were transferred to plastic freezer bags and frozen for subsequent analysis. During
141 analysis, samples were defrosted, sorted to the finest taxonomic resolution possible (usually
142 species) and weighed (fresh weight biomass). In addition to fine-resolution taxonomic
143 analysis, each taxon was assigned to a coarse functional group, adapted from Steneck and
144 Dethier (1994), to examine wider shifts in structure and putative function (see Table S1 for
145 functional group assignments). While the coarse functional group approach has limitations
146 (e.g. Mauffrey et al., 2020; Phillips et al., 1997), we adopted it here to investigate generality in
147 shifts in assemblage structure along spatial gradients in wave exposure and temperature.

148 **Quantification of crustose coralline algae (CCA) with photogrammetry**

149 In addition to macroalgae that could be collected by hand, we quantified the cover of crustose
150 coralline algae (CCA) on the underlying rocky substratum. The reef beneath each quadrat
151 described above was imaged following a modification of Burns et al (2015), using a GoPro
152 Hero 3+ Black set to 2Hz timelapse at a distance of around 30cm. Illumination was provided
153 by a GoBe 700 video light with a wide-angle head. For photogrammetric processing and
154 analysis, 3D Structure from Motion (SfM) point clouds and mesh models were generated as
155 detailed in Bayley et al. (2019) using Agisoft Metashape on an HPZ8 workstation (128Gb
156 RAM, Dual Xeon Gold CPU, NVIDIA P5200 GPU). Meshes were scaled using the corners of
157 the quadrats and the overall mesh resolution was 5mm. 3D rugosity of the rocky substrate
158 was calculated by dividing the true surface area of the mesh by the planar surface area (i.e.
159 0.125 m²). Coverage of CCA was calculated by classifying all the dense cloud points within a
160 certain RGB colour range (manually assigned and calibrated per survey site) as points of
161 interest and re-extracting the mesh surface using only this point class. Exemplar 2D
162 projections of the 3D models are shown in Fig. S1. Given the high complexity and rugosity of
163 the underlying reef surface, this approach was deemed more appropriate than traditional
164 techniques (e.g. 2D photo-quadrats, *in situ* visual estimates).

165 **Biotic and abiotic predictor variables**

166 We quantified several physical and ecological factors that could potentially influence the
167 structure of understory macroalgal assemblages, in order to examine putative drivers of
168 observed pattern. At each site, we recorded the average depth (below chart datum) of the
169 surveyed quadrats, as well as the density of kelp plants (>95% of which were *Laminaria*
170 *hyperborea*) and sea urchins (exclusively *Echinus esculentus*, hereafter '*Echinus*') within 8
171 replicate larger (1 m²) quadrats. Again, quadrats were haphazardly placed within kelp forest
172 and deployed at least 3 m from one another. We also randomly collected 12 canopy-forming
173 mature *Laminaria hyperborea* plants to obtain average plant biomass per site, which was
174 converted to an estimate of standing biomass based on average recorded densities.
175 Additionally, average rugosity of the underlying substratum at each site (as determined by the

176 photogrammetry technique described above) was calculated from the replicate quadrat
177 samples and included as an abiotic variable of interest. As rugosity was calculated by dividing
178 the surface area of the substratum by the planar surface area, a higher value indicated a more
179 complex and heterogenous substratum topography.

180 Remotely-sensed data were also obtained for each site to provide broad-scale metrics of
181 temperature, chlorophyll *a* (chl *a*) and wave exposure. Annual mean temperature (2005 to
182 2014) based on 9 km resolution data from the Pathfinder AVHRR satellite was obtained for
183 each site. Estimates of chl *a* concentrations, which describe 'ocean colour', were generated
184 from optical properties of seawater derived from satellite images. Ocean colour has been
185 shown to be a useful proxy for pelagic productivity and light attenuation, which can influence
186 the distribution of macroalgae in this system (Burrows, 2012). Data were collected by the
187 MODIS Aqua satellite at an estimated 9 km resolution and averaged for the period 2002 to
188 2012 (see Burrows, 2012 for a similar approach). Wave exposure values were obtained from
189 a wave fetch model (Burrows et al., 2008), based on distances to the nearest land in all
190 directions around each ~200 m coastal cell for the UK coastline.

191 **Data analysis**

192 All data were analysed in PRIMER-e version 7 (Clarke et al., 2014) with the PERMANOVA+
193 add on (Anderson et al., 2008). Univariate measures (species richness, biomass, Shannon-
194 Wiener diversity and CCA cover in each quadrat) were analysed using univariate
195 permutational analysis of variance (PERMANOVA). Each response variable was modelled as
196 a function of "region" (fixed factor; 4 levels) and "site" (random factor nested within region; 12
197 levels) using untransformed data and Euclidean distance matrices. Where significant effects
198 between regions were identified ($\alpha = 0.05$), pairwise differences between regions were tested
199 using pairwise PERMANOVA. Due to the limited possible permutations in pairwise testing,
200 approximate significance values were constructed using Monte Carlo *p*-values ($\alpha = 0.05$)
201 (Anderson and Robinson, 2003). Prior to analysis, differences in variance heterogeneity

202 between levels of the factors were checked using the PERMDISP routine. Relationships
203 between univariate responses and predictor variables were then examined using distance-
204 based linear models (DistLM). Predictor variables included biotic and abiotic data shown in
205 Table 1. Prior to analysis, draftsman's plots were generated and Pearson's correlation
206 coefficients were used to check for collinearity between variables; if two variables were
207 correlated at $p > 0.85$ one was excluded from the analysis (only latitude and mean temperature
208 were strongly colinear, so latitude was excluded from the model. The DistLM routine was used
209 to calculate the proportion of variation explained by each predictor variable alone (using
210 marginal testing), as well as the most parsimonious model using the "Best" selection from all
211 possible models based on an AICc selection criterion.

212 Patterns of variability in multivariate assemblage structure between regions, and the
213 association with predictor variables, were assessed using the same method to that for
214 univariate responses. Multivariate biomass data was however, fourth root transformed to
215 downweight the influence of highly dominant taxa and a Bray-Curtis similarity matrix was
216 constructed. Dissimilarity between assemblages were visualised at both the individual quadrat
217 level and site centroid level using threshold metric multi-dimensional scaling (tmMDS).
218 Similarity percentage breakdowns (SIMPER) were also used to determine the five main
219 species principally contributing to the observed dissimilarity within significant pairwise
220 contrasts. To examine differences in within-group variability between regions, the PERMDISP
221 routine was used to calculate and test for differences in mean multivariate dispersion, an
222 analogue for beta diversity (Anderson et al., 2006), at both the quadrat and site centroid level.
223 Finally, to examine spatial trends in the relative abundance of coarse functional groups, we
224 compared the proportion of total biomass represented by each group at each site and region.

225 All PERMANOVAs, DistLMs and PERMDISPs were run with 9,999 permutations.
226 PERMANOVAs used a permutation method of residuals under a reduced model with Type 3
227 (partial) sums of squares. PERMDISPs were calculated by distances to centroids and p-values
228 from permutation. tmMDS plots were visualised using 50 restarts and a minimum stress of

229 0.01. All univariate plots were created in R 3.5.1 (R Core Team, 2018) using the *dplyr*
230 (Wickham and Francois, 2015) and *ggplot2* (Wickham, 2009) packages, multivariate plots
231 were created in PRIMER-e version 7 (Clarke et al., 2014), and mapping was carried out within
232 ArcMap 10.3.1. Where relevant, all data are shown as mean values \pm standard error.

233 **Results**

234 **Understory macroalgal assemblages**

235 Across the entire study, 53 different understory algae taxa were identified (Table S1). The total
236 number of taxa recorded in each region increased from north to south, with A (24) < B (25) <
237 C (29) < D (38) (Table S1). With regards to the distribution of taxa, 19% of taxa recorded were
238 found in all four regions, 32% were recorded in only one region, 24% were recorded in only
239 (one or both) cold regions and 30% were recorded in only (one or both) warm regions (Table
240 S1)

241 At the scale of quadrat sample, richness ranged from 2 to 19 taxa, biomass ~2 to ~268 g, and
242 diversity from 0.1 to 1.9. The cover of CCA ranged from 12 to 82%. Although there was high
243 variation between quadrats and sites, mean richness and diversity tended to increase from
244 north to south (Fig. 2). Biomass and CCA cover were far more variable between samples and
245 sites and did not exhibit a clear latitudinal trend (Fig. 2). Statistically, we recorded significant
246 differences between regions for both richness and diversity, but not for biomass or CCA cover
247 (Fig 2, Table 2). The dissimilarity in mean richness between regions was driven by significantly
248 higher richness in region D when compared to all other regions; whereas dissimilarity in
249 diversity was due to regions B and C having significantly higher diversity when compared to
250 region A (Fig 2, Table S2).

251 A significant difference in macroalgal assemblage structure was also recorded between
252 regions in multivariate analyses (Table 2). Although there was large variation both within and
253 between sites, tmMDS identified clear partitioning between regions at both the quadrat and
254 site centroid levels (Fig 3). Pairwise tests on multivariate community data identified significant

255 differences in between all regions except for regions B and C (Table S2). There were 8 species
256 principally contributing to the observed dissimilarities between regions (Table S3). The two
257 most common species to drive the dissimilarity were *Heterosiphonia plumosa* and *Delesseria*
258 *sanguinea* which followed the pattern of biomass in region C>D>B>A; while *Odonthalia*
259 *dentata* had the reverse relationship (Fig 4, Table S3). *Plocamium spp.* and *Phycodrys rubens*
260 followed the relationship region B>C>D>A; while *Dilsea carnosa* and *Corallina officinalis* had
261 the reverse relationship (Fig 4, Table S3). Finally, *Cryptopleura ramosa* was highest in region
262 C>B>D>A (Fig 4, Table S3). There was no significant difference in beta-diversity (multivariate
263 dispersion) between regions at either the quadrat ($F_{(3,92)} = 2.046$, $p = 0.149$) or site centroid
264 level ($F_{(3,8)} = 1.061$, $p = 0.594$); however region A had highest beta-diversity between
265 quadrats, and region D the highest between sites (Table S4).

266 The relative abundances of coarse functional groups varied markedly between sites and
267 regions (Fig 5), with no clear trends along gradients of wave exposure (i.e. sites within regions)
268 or latitude (i.e. from northern to southern regions). Overall, foliose algae (FG3) and corticated
269 terete algae dominated the assemblages, although leathery algae and articulated calcareous
270 algae were notably more common in regions A and D (Fig 5). At the regional scale, regions A
271 and D and regions B and C were broadly similar to one another, with regards to the
272 proportional biomass of coarse functional groups.

273 **Biotic and abiotic drivers**

274 The amount of variability explained by the eight predictor variables measured during this study
275 varied greatly between assemblage metrics, ranging from ~15% for diversity to ~49% for
276 richness (Table 3). Variation in richness was best explained by mean temperature, which
277 accounted for ~40% of total observed variability, combined with kelp biomass, kelp density
278 and chl a (Table 3). Variation in biomass was best explained by a combination of mean
279 temperature, kelp biomass, wave exposure and depth (accounting for ~32% of total
280 variability), while variation in diversity was best explained by temperature and rugosity,

281 although this most parsimonious model only explained ~15% of total observed variability
282 (Table 3). The best model for CCA cover (accounting for ~35% total variability) included kelp
283 biomass, wave exposure, *Echinus* density and depth (Table 3). Finally, the best model for
284 multivariate assemblage structure included all variables (accounting for ~46% total variability);
285 with mean temperature and kelp biomass having the most explanatory power (Table 3).

286 **Discussion**

287 Overall, the structure of understory macroalgal assemblages was highly variable over
288 multiple spatial scales, with different assemblage-level metrics exhibiting different patterns.
289 That said, the taxonomic richness, multivariate structure and (to a lesser extent) diversity of
290 macroalgal assemblages did vary between regions, with a general increase in richness and
291 diversity from north to south, and clear partitioning in multivariate assemblage structure
292 between most regions. Variability in the structure of populations and communities at regional
293 spatial scales may be driven by multiple factors that operate across similar scales, including
294 biogeochemical and oceanographic processes (Reddin et al., 2015), herbivore pressure
295 (Sangil et al., 2011), recruitment dynamics (Connolly et al., 2001) and biogeographic divisions
296 (Steigleder et al., 2019). Regional scale studies on macroalgal assemblages have reported
297 both negative relationships between richness and latitude (Santelices and Marquet, 1998)
298 and, more commonly, positive relationships, with increased richness at higher latitudes (Konar
299 et al., 2010; Liuzzi et al., 2011; Santelices and Marquet, 1998; Smale et al., 2011a). At the
300 scale of the Atlantic Ocean, however, macroalgal diversity peaks in temperate regions and
301 declines towards the tropics and poles (Kerswell, 2006; Tittley, 2002).

302 Here, we recorded greatest richness and diversity at the lowest latitudes and highest ocean
303 temperatures. A pattern of increasing diversity for some groups of marine flora and fauna from
304 north-to-south in the British Isles is well described (Forbes, 1858; Hiscock et al., 2004; Lewis,
305 1964), being principally driven by large-scale biogeographic processes. In brief, the region
306 around southwest England supports relatively higher diversity due to the co-existence of both

307 warm-adapted (Lusitanian) and cold-adapted (Boreal) species and because of post-glaciation
308 recolonisation and expansion from climatic refugia (Hiscock et al., 2004; Provan and Bennett,
309 2008; Tittley, 2002). As such, the observed increase in richness and (to a lesser extent)
310 diversity with increasing temperature is likely to reflect a broader-scale diversity gradient in
311 the northeast Atlantic, rather than an effect of temperature *per se*. Previous work conducted
312 in these regions showed that invertebrate assemblages associated with both holdfasts (Teagle
313 et al., 2018) and understory algae (Bué et al., 2020) also increase in richness and/or diversity
314 with increasing temperature, again providing support for a wider latitudinal diversity gradient.

315 The observed regional-scale variability in richness, diversity and multivariate assemblage
316 structure may, however, also be related to variation in habitat structure across similar spatial
317 scales. Specifically, it is known that the composition of the kelp forest habitat itself changes
318 with latitude in this region, with a warm-adapted kelp (*Laminaria ochroleuca*) being present in
319 the southern locations and a cold-adapted kelp (*Alaria esculenta*) more common in northern
320 regions (Smale and Moore, 2017). Moreover, the population structure (i.e. plant size, biomass,
321 canopy density) of the dominant kelp species at these sites, *Laminaria hyperborea*, also shifts
322 along the latitudinal temperature gradient examined here (Pessarrodona et al., 2018; Smale
323 et al., 2016). As such, changes in the structure of the kelp canopy may alter abiotic conditions
324 in the subcanopy environment (i.e. light, water motion, space) and in turn influence
325 understory algal assemblages; further focused manipulative work is needed to better
326 understand how *L. hyperborea* canopies influence the local environment. The importance of
327 the structure and composition of macroalgal canopies in shaping understory assemblages
328 has been documented in other systems (Clark et al., 2004; Irving and Connell, 2006; Smale
329 et al., 2011a; Wernberg et al., 2011) and is likely to be important here.

330 The biomass of the overlying kelp canopy varied considerably between sites, ranging from 3.2
331 g FW m⁻² at site C3 to 18.9 kg FW m⁻² at site A1, with a clear disparity between the colder
332 northern sites and the warmer southern sites, where kelp biomass was notably lower. This
333 regional-scale latitudinal pattern is driven by variability in the growth and performance of *L.*

334 *hyperborea*, as individual plants attain a greater size and biomass in colder waters
335 (Pessarrodona et al., 2018; Smale et al., 2016). In north and west Scotland, kelp canopies are
336 particularly high, dense and compact and, although we did not measure subcanopy light
337 penetration here, the amount of light reaching the underlying reef surface was notably lower
338 than in southwest Wales and southwest England, where kelp plants are shorter and have
339 smaller, thinner laminae (Pessarrodona et al., 2018; Smale et al., 2016). Given that kelp
340 biomass was identified as a key driver of variation in understory richness, biomass and
341 multivariate structure, and that biomass and richness were greatest in the regions with lowest
342 kelp canopy biomass, interspecific competition for light and space between kelps and
343 understory algae may be a key structuring process, as has been shown elsewhere (Flukes
344 et al., 2014; Pedersen et al., 2014).

345 At the population level, some taxa exhibited pronounced regional scale variability, which in
346 turn contributed to the observed dissimilarity in multivariate assemblage structure between
347 regions. For example, the red algae *Delesseria sanguinea* and *Heterosiphonia plumosa* were
348 common at most sites but tended to increase in occurrence and biomass at the warmer
349 southern regions. These species are widely distributed across the Atlantic Ocean and are not
350 considered to be found at their range edge in the UK (Guiry and Guiry, 2020; OBIS, 2020),
351 and therefore variability between regions was unlikely to be due to biogeographic patterns but
352 perhaps related to resource availability and population dynamics. Conversely, *Odonthalia*
353 *dentata* was common and abundant in the cooler regions, particularly north Scotland, and was
354 absent in the southern regions. *O. dentata* is a cold-water species, most commonly found in
355 cold waters of the northeast Atlantic and found towards its southernmost range edge in the
356 UK (Guiry and Guiry, 2020; OBIS, 2020). Similarly, some of the species that were only
357 recorded in the southern regions (e.g. *Calliblepharis ciliata*, *Dictyota spiralis*, *Halopteris filicina*,
358 *Dictyopteris polypodioides*) have a distinctly warm-water Lusitanian distribution and are found
359 towards their northernmost range edge in the UK (Guiry and Guiry, 2020; OBIS, 2020). It is
360 likely, therefore, that pronounced regional-scale variation in the abundance of these species

361 was due to sampling across species' range edges. Clearly, the biogeographic distributions
362 and environmental requirements of individual species manifested as pronounced regional-
363 scale variability and contributed to the overall differences in assemblage structure at these
364 scales. The western shores of the British Isles and Ireland are influenced by large scale current
365 systems (e.g. Gulf Stream, North Atlantic Drift) and populations and communities along
366 western coastlines are thought to be fairly well connected with no clear obstructions to
367 dispersal, such as upwelling zones or land barriers (Reuschel et al., 2010; Vincent, 1990). As
368 such, the regional-scale variability detected across our study area was unlikely to be driven
369 by oceanographic processes or biogeographic breakpoints, in contrast to large scale drivers
370 of pattern in some other regions (Fenberg et al., 2015).

371 For some metrics, including total biomass and multivariate assemblage structure, we also
372 recorded high variability between sites within regions, located just a few kms apart. For
373 example, within northern Scotland biomass increased five-fold from site A3 to A1, and within
374 southwest Wales biomass more than doubled between site C1/C2 and site C3. Multivariate
375 assemblages were also structured to some degree by site; for example, site B3 in west
376 Scotland and C3 in southwest Wales were largely dissimilar to other sites within their
377 respective regions. Although the underlying drivers of between-site variability remain unclear,
378 understory assemblages are likely to be structured by processes operating at similar spatial
379 scales, such as variation in wave exposure, light availability, substrate heterogeneity and
380 grazing pressure. It is well known that wave exposure is a key structuring force on both kelp
381 canopies (Graham et al., 1997; Pedersen et al., 2012; Smale et al., 2016) and understory
382 assemblages (Goldberg and Kendrick, 2004; Harrold et al., 1988), as wave-driven
383 hydrodynamic forces can alter benthic communities both directly through physical dislodgment
384 (Filbee-Dexter and Scheibling, 2012; Smale and Vance, 2015) and indirectly by mediating
385 ecological interactions including competition and grazing pressure (Rinde et al., 2014;
386 Vanderklift et al., 2009). Although our sites were all moderately-to-fully wave exposed, fetch

387 did vary between sites and these differences in wave exposure were likely to have contributed
388 to the observed between-site variability in ecological pattern.

389 In other similar studies, site-level variation in sea urchin grazing (Bekkby et al., 2015) and
390 physical reef structure (Toohey, 2007) have been linked with variation in understory algal
391 assemblages. Here, however, sea urchin densities were consistently low and did not explain
392 a high proportion of the observed variability in assemblage structure. Indeed, sea urchin
393 grazing on both kelps and associated macroalgae is not an important driver of pattern within
394 the study area, in contrast to many other kelp forest ecosystems in the world (Ling et al., 2015).
395 Although we did not quantify the abundance and potential influence of other herbivorous
396 invertebrates and fish, studies to date suggest that grazing in general is not a strong driver of
397 pattern in this system (Hargrave et al., 2017; Hereward et al., 2018). Similarly, although reef
398 rugosity varied to some extent between sites, it did not explain much of the observed variability
399 in ecological pattern. While increased reef rugosity in other kelp forest ecosystems has been
400 shown to increase habitat heterogeneity and niche availability, thereby promoting local
401 diversity (Toohey et al., 2007), this was not the case in the current study. It should be noted
402 that we did not examine temporal variability in the structure of understory macroalgal
403 assemblages, and that the spatial patterns and putative drivers described here are drawn from
404 a single sampling event in late summer. While studies on short-term temporal variability in
405 understory assemblages have found clear seasonality in structure (Shaffer, 2000; Wernberg
406 and Goldberg, 2008), the biomass and richness of macroalgal assemblages tends to peak in
407 summer in the northeast Atlantic (e.g. Neto, 2001; Rubal et al., 2011) and it is likely that
408 spatial patterns described here would be reflected in other seasons. However, further work on
409 temporal variability in the diversity of kelp-associated assemblages is clearly warranted.

410 An assessment of shifts in assemblage structure based on the proportional abundance of
411 coarse functional groups did not any clear general patterns or trends across wave exposure
412 of latitude. While the functional group approach for macroalgal assemblages can yield
413 generality across systems not evident at the species level (Steneck and Dethier, 1994), fine-

414 scale ecological information can also be lost when using coarse groupings (Phillips et al.,
415 1997). Here, regions B and C were similar based on functional group abundances, whereas
416 regions A and D were comparable in that they were characterised by a greater proportional
417 biomass of leathery and articulated calcareous algae. On average, regions A and D are slightly
418 more exposed to long-distance wave fetch and coastal waters may be slightly less turbid, with
419 lower sediment loading compared to regions B and C (Table 1, Smale *et al.* 2016). Such
420 conditions may be more favourable for species assigned to the leathery and articulated
421 calcareous algal functional groups (Nishihara and Terada, 2010), and may explain, at least in
422 part, the higher similarity of regions B and C, which was also evident in the species-level
423 multivariate analysis.

424 Crustose coralline algae (CCA) plays an important role in the ecology of reef systems globally
425 (Fabricius and De'ath, 2001; Steneck, 1986) and in kelp-dominated systems CCA influences
426 substrate stability, recruitment processes and post-disturbance succession (Ayling, 1981;
427 Steneck, 1986). Previous work has shown that sea urchins and other herbivores can facilitate
428 CCA (Bulleri et al., 2002; Vance, 1979), which is largely grazer-resistant and that, once
429 established, CCA can inhibit the recruitment of competitors, particularly fleshy erect
430 macroalgae (Breitburg, 1984; Bulleri et al., 2002). We employed a 3D photogrammetry
431 technique to quantify the space occupancy of CCA, and showed that percent cover varied
432 considerably between sites, with no clear trend between regions or with latitude. The cover of
433 CCA was significant, typically more than 50% of the reef's surface, indicating the likely
434 importance of CCA as a key component of these kelp dominated habitats. Monopolization of
435 rocky substrata by CCA beneath dense kelp canopies is commonplace (Connell, 2003b; Irving
436 and Connell, 2006), as reduced light levels can favour some species of CCA, which are
437 adapted to low-light (Roberts et al., 2002) and are less susceptible to overgrowth by turf-
438 forming algae in shaded conditions (Kennelly, 1987a). Here, high variability in CCA cover
439 between sites was likely related to differences in light availability, in turn due to variation in
440 depth and kelp canopy biomass. Moreover, wave exposure and *Echinus* density were

441 identified as potentially useful predictors and, in general, cover of CCA was lowest at sites
442 with the lowest wave fetch values, which also tended to have higher densities of *Echinus*. This
443 is perhaps related to greater rates of sedimentation and detritus accumulation at the less
444 wave-exposed sites, which can negatively affect development of CCA (Connell, 2005;
445 Kendrick, 1991); further manipulative work should examine the influence of sedimentation
446 rates on understory algal assemblages within this system.

447 **Conclusion**

448 Understorey macroalgal assemblages represent a rich and abundant component of kelp
449 forests in the northeast Atlantic. Although the structure of understorey assemblages was highly
450 variable at multiple spatial scales, we observed clear partitioning at the scale of both site and
451 region, with key drivers of pattern (e.g. ocean climate, kelp canopy structure, wave exposure)
452 operating across similar spatial scales. While further manipulative work is needed to ascertain
453 the relative importance of different biotic and abiotic drivers of pattern, it is clear that overlying
454 kelp canopies alter environmental conditions and influence the structure and diversity of
455 understorey macroalgal assemblages. Given that the structure and composition of these
456 canopies is shifting in response to ocean warming and other change factors (Pessarrodona et
457 al., 2019; Pessarrodona et al., 2018; Smale et al., 2013), consequent changes in kelp-
458 associated assemblages can be expected. Overall, understorey macroalgal assemblages in
459 our southernmost regions exhibited highest levels of richness, biomass, diversity and
460 distinctiveness, indicating that these kelp forests are of considerable conservation value. From
461 a management perspective, maintaining favourable environmental conditions for populations
462 of canopy-forming kelp to thrive is imperative for conserving the structure and diversity of
463 understorey macroalgal assemblages. Specifically, this could involve the establishment of
464 marine protected areas targeted for extensive kelp canopies, maintaining favourable water
465 quality in coastal environments through effective catchment management, and minimising
466 impacts of local stressors such as invasive species, fishing practises and kelp harvesting.

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469

470 **References**

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- 793 Assessing species richness of macrofauna associated with macroalgae in Arctic kelp forests
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- 795 **Data accessibility:** All data will be made available in Dryad following publication
- 796

Tables

Table 1 Biotic and abiotic predictor variables recorded at 12 study sites (1-3) within 4 regions (A-D) in the UK. ‘Depth’ is the average depth below chart datum. ‘Mean SST’ is the annual mean temperature calculated from satellite-derived sea surface temperature (SST) data (2005-2014). ‘Log wave fetch’ is the log of the sum of wave fetch values of sectors surrounding each site. ‘Log chl a’ is the average annual concentration of chlorophyll a (\log_{10} mg m⁻³ from MODIS Aqua satellite data, 2002-2012). The density of *Echinus* and kelp plants (almost exclusively *Laminaria hyperborea*) was estimated using 8 replicate (1 m²) quadrats at each site. Kelp standing biomass was estimated by obtaining the fresh weight biomass of 12 mature canopy-forming *L. hyperborea* plants at each site, and multiplying mean plant biomass by mean plant density. Rugosity was estimated using photogrammetry of the underlying substratum to generate 3D mesh models; rugosity is the ratio of actual surface area to planar surface area, higher values indicate increased heterogeneity.

Site	Latitude (°N)	Depth (m BCD)	Mean SST (°C)	Log wave fetch (km)	Log chl a (mg m ⁻³)	<i>Echinus</i> density (inds m ⁻²)	Kelp density (inds m ⁻²)	Kelp biomass (kg FW m ⁻²)	Rugosity
A1	58.96	4	9.7	3.6	0.21	0.06	10.5	18.9	1.97
A2	58.94	3	9.7	3.5	0.26	0.06	9.3	17.7	1.78
A3	58.92	3	9.8	3.4	0.26	0.37	8.6	15.8	1.13
B1	56.37	5	10.8	3.3	0.59	0.13	9.3	18.6	1.82
B2	56.39	4	10.7	3.1	0.65	0.06	7.9	10.1	2.05

B3	56.44	3	10.8	3.0	0.69	0.25	7.2	7.9	2.86
C1	51.76	5	11.7	3.6	0.43	0.19	9.7	5.4	1.48
C2	51.77	3	11.8	3.5	0.43	0.25	8.6	3.3	1.49
C3	51.77	3	11.8	3.4	0.43	0.00	9.1	3.2	1.44
D1	50.29	3	12.4	4.1	0.28	0.06	9.1	7.9	1.53
D2	50.30	4	12.4	3.9	0.28	0.00	8.6	5.8	3.07
D3	50.31	3	12.5	3.5	0.38	0.13	8.2	4.4	1.82

1 **Table 2** PERMANOVAs testing for differences in understory macroalgae species richness,
 2 biomass, Shannon-Wiener diversity, percent cover of crustose coralline algae (CCA) and
 3 multivariate community structure between survey regions and sites (nested within regions).
 4 Each coefficient is shown with the associated degrees of freedom (df), mean-squares (MS),
 5 F-value (F) and p-value (p). Significant coefficients shown in bold ($p < 0.05$).

Coefficient	df	MS	F	p
<i>Richness</i>				
Region	3	140.4	14.33	0.001
Site(Region)	8	9.8	2.07	0.047
Residuals	84	4.73		
<i>Biomass</i>				
Region	3	9702.0	1.56	0.263
Site(Region)	8	6232.6	4.91	<0.001
Residuals	84	1268.2		
<i>Diversity</i>				
Region	3	0.8	3.18	0.027
Site(Region)	8	0.3	1.58	0.146
Residuals	84	0.2		
<i>%CCA</i>				
Region	3	644.4	0.50	0.664
Site(Region)	8	1278.3	16.02	<0.001
Residuals	84	79.8		
<i>Multivariate community</i>				

Region	3	27652.0	4.67	<0.001
Site(Region)	8	5917.6	4.83	<0.001
Residuals	84	1224.1		

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7

8 **Table 3** DISTLM of understory macroalgae species richness, biomass, Shannon-Wiener
 9 diversity, percent cover of crustose coralline algae (CCA) and multivariate community
 10 structure based on a set of seven predictor variables. Values indicate proportion of variance
 11 (R^2) explained by each individual predictor from marginal testing. Those terms in bold indicate
 12 the most parsimonious models using the “Best” selection from all possible models based on
 13 an AICc selection criterion.

Variable	R^2 marginal tests				
	Richness	Biomass	Diversity	%CCA	Multivariate community
Mean SST	0.399	0.137	0.125	0.052	0.202
Kelp biomass	0.215	0.124	0.070	0.031	0.174
Kelp density	0.039	0.004	0.015	0.038	0.059
Wave exposure	0.126	0.014	0.033	0.015	0.120
Log Chl a	0.021	0.001	0.003	0.001	0.121
Echinus density	0.037	0.112	0.004	0.072	0.046
Depth	0.006	0.015	0.013	0.158	0.052
Rugosity	0.047	0.002	0.040	0.004	0.035
<i>R² of best solution</i>	0.495	0.321	0.153	0.350	0.463

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15

16 **Figure Legends**

17 **Fig 1** Location of regions (A-D) and study sites (1-3) along the coast of the UK. Three randomly
18 selected study sites were nested within each region, numbered from most to least wave
19 exposed. Panels on right show locations of study regions within the UK and a representative
20 example of understory macroalgal assemblage beneath a *Laminaria hyperborea* stand in
21 region A.

22 **Fig 2** Mean understory macroalgae species richness (A), biomass (B) Shannon-Wiener
23 diversity (C) and percent cover of crustose coralline algae (D) for each survey site (\pm quadrat
24 SE) and region (\pm site SE). Lowercase letters in region plots identify significant pairwise
25 groupings from PERMANOVA analyses (Table 2, Table S2).

26 **Fig 3** Threshold metric multi-dimensional scaling (tmMDS) plots of understory macroalgae
27 assemblage data from individual quadrats (A) and site centroid averages (B). Colour of points
28 identifies region (orange = A, blue = B, green = C, yellow = D). tmMDS based on Bray-Curtis
29 distance matrices constructed from 4th root transformed data.

30 **Fig 4** Shade plot of 30 most important understory taxa (those that contribute at least 5%
31 biomass to a single quadrat sample). Grey shading scale within individual cells is linearly
32 proportional to fourth-root transformed biomass. Quadrats (x-axis) grouped by survey region
33 and seriated by coherent species groupings; symbols identify survey site and colour identifies
34 region. Species (y-axis) clustered based on standardised data and an Index of Association
35 resemblance matrix. See Table S1 for mean biomass of individual taxa in each region.

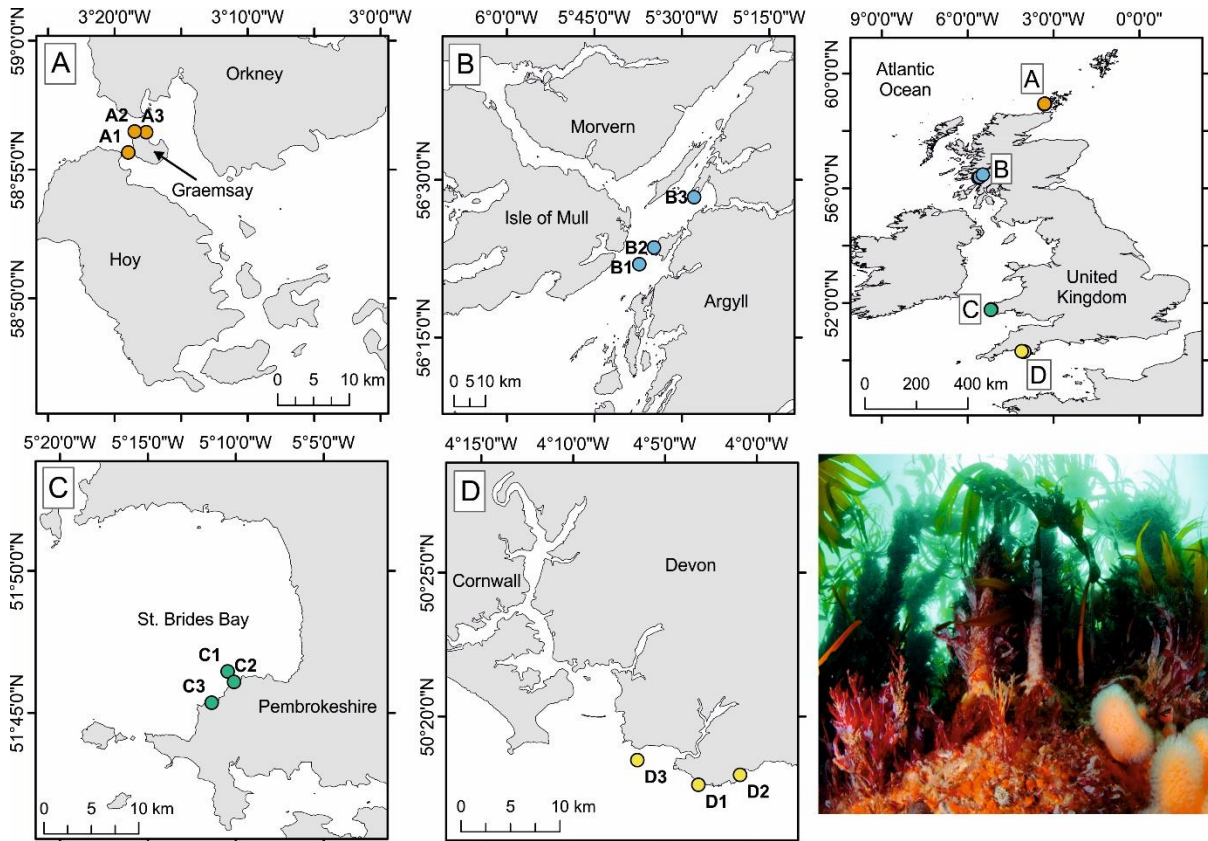
36 **Fig 5** Mean proportion of each functional group contributing to total biomass at each survey
37 site and region. Colour indicates functional group [FG: 2 = filamentous, 3 = foliose, 4 =
38 corticated terete, 5 = leathery, 6 = articulated calcareous; adapted from Phillips et al. (1997)]

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42 **Figures**



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44

45 **Fig 1**

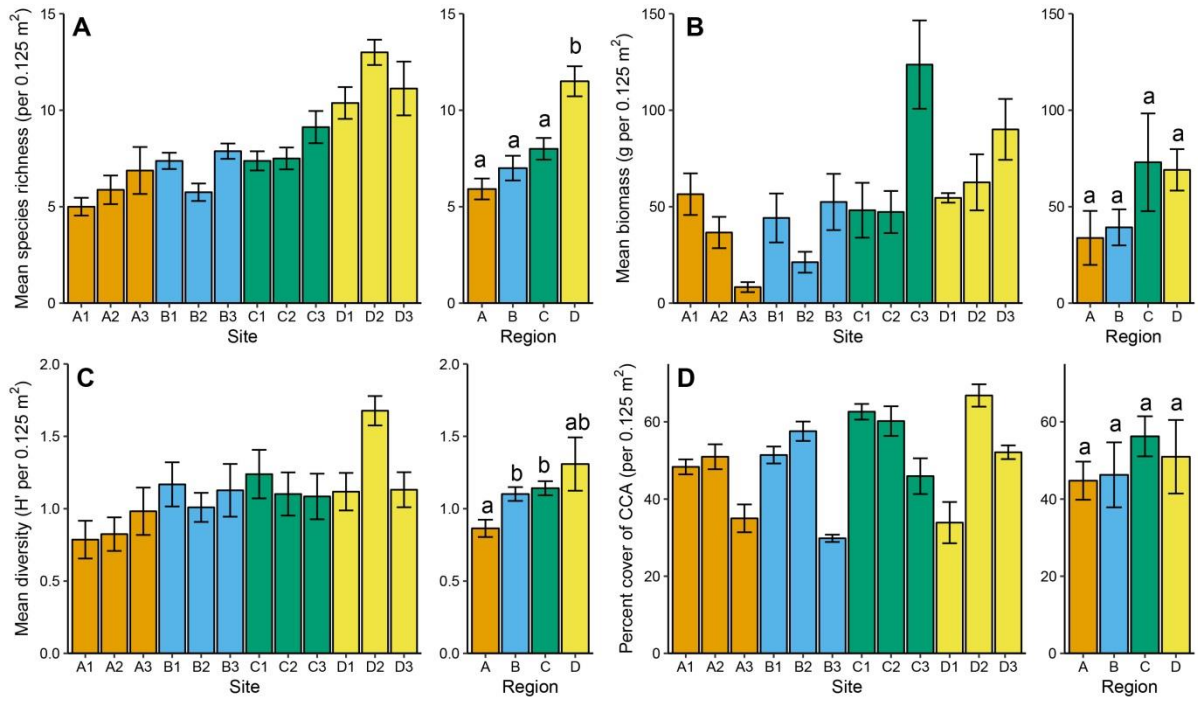


Fig 2

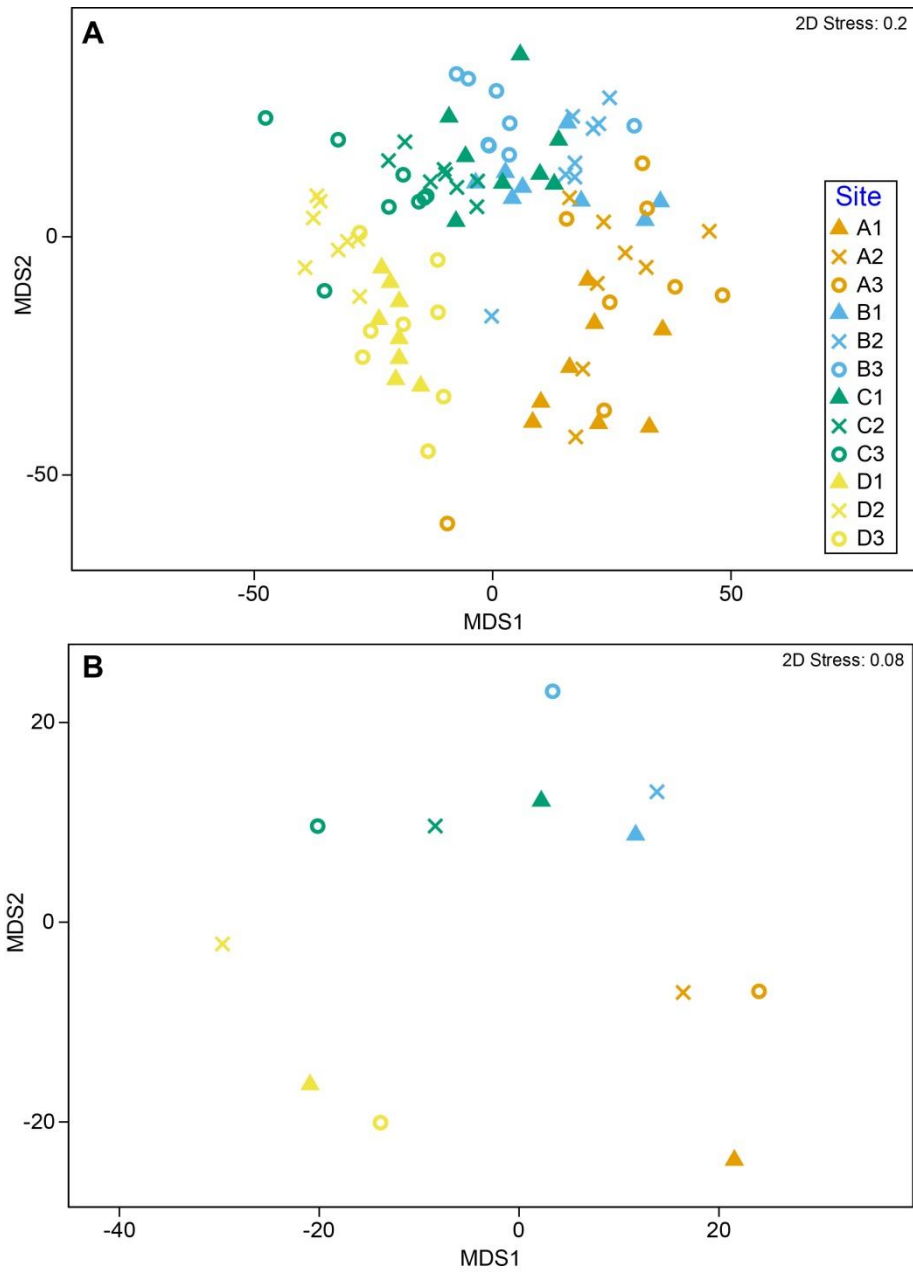


Fig 3

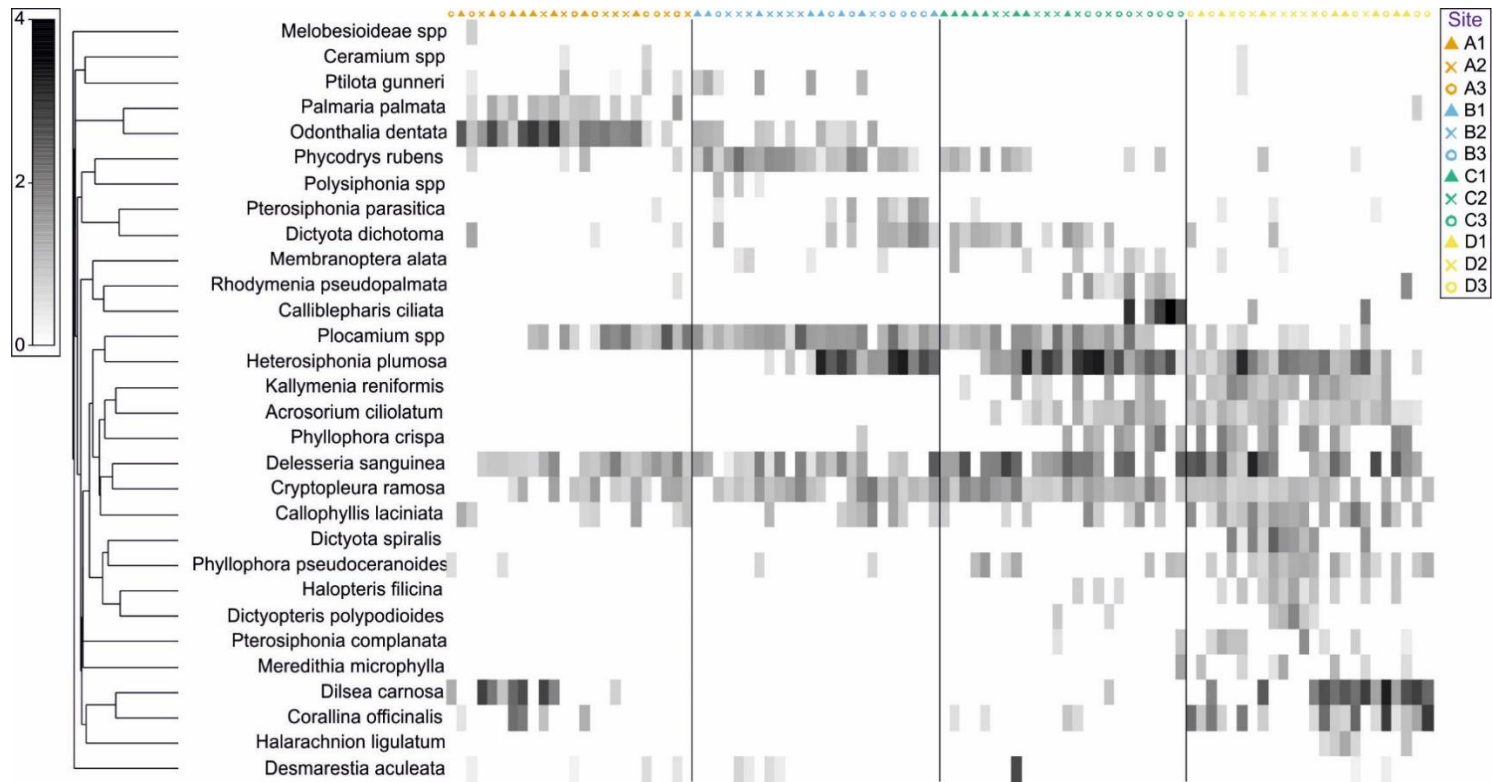


Fig 4

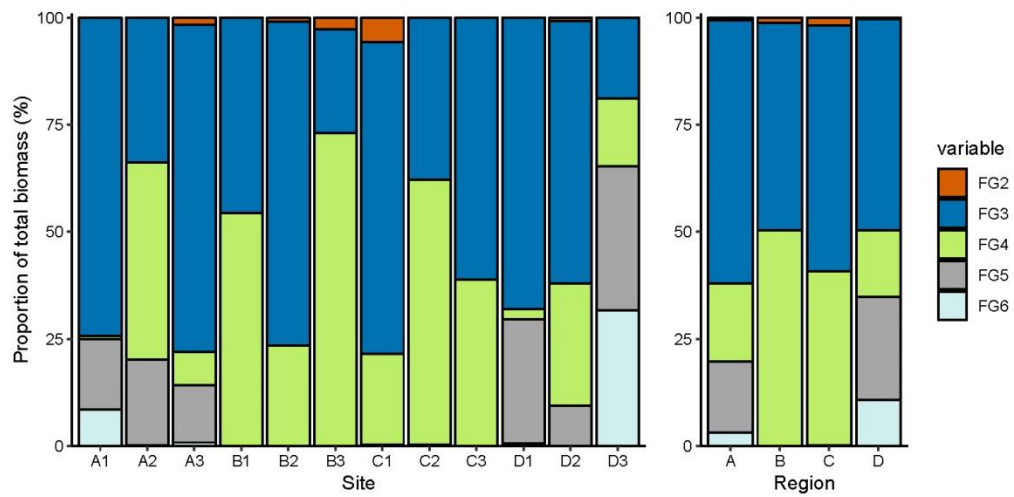


Fig 5