

1 Original Research to *Journal of Experimental Marine Biology and Ecology*

2

3

4

5

6 **Seasonal variability in the population structure of a habitat-forming**  
7 **kelp and a conspicuous gastropod grazer: do blue-rayed limpets**  
8 **(*Patella pellucida*) exert top-down pressure on *Laminaria digitata***  
9 **populations?**

10

11

12 Hannah F.R. Hereward<sup>a,b,c</sup>, Andrew Foggo<sup>a</sup>, Sarah L. Hinckley<sup>a</sup>, Joanna  
13 Greenwood<sup>c,d</sup> and Dan A. Smale<sup>b\*</sup>

14

15 <sup>a</sup> Marine Biology and Ecology Research Centre, Plymouth University, Drake Circus,  
16 Plymouth PL4 8AA, UK

17 <sup>b</sup> Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill,  
18 Plymouth PL1 2PB, UK

19 <sup>c</sup> A Rocha UK, 18-19 Avenue Road, Southall, London, UB1 3BL, UK

20 <sup>d</sup> Lee Abbey Devon, Lynton, North Devon, EX35 6JJ, UK

21

22

23

24 \*corresponding author: [dansma@mba.ac.uk](mailto:dansma@mba.ac.uk) +44(0)1752 426489

25

26

27

28

29

30

31

32

33

34

35

## 36 Abstract

37

38 Kelp forests dominate wave-exposed rocky reefs along mid-to-high latitude coastlines. The  
39 distribution and structure of kelp forests is determined by a range of physical and biological  
40 processes operating across varying spatial and temporal scales. Many kelp forest systems  
41 are strongly influenced by herbivory, and overgrazing by urchins, in particular, is a  
42 recognised driver of kelp forest distribution and structure. The ecological significance of  
43 herbivory by kelp-associated limpets, however, has received far less attention. We quantified  
44 seasonal population dynamics of *Laminaria digitata* and the blue-rayed limpet *Patella*  
45 *pellucida* on two rocky shores in North Devon, UK. For the kelp, we quantified density,  
46 percent cover, morphology, standing biomass, elongation and erosion rates, and C:N and  
47 phenol content. For the limpet, we measured abundance, biomass, and morphology, and for  
48 the limpet-kelp interaction we recorded observable grazing damage on the blade. Both  
49 populations exhibited typical seasonality with kelp growth rates peaking in spring, maximum  
50 standing biomass observed in summer and increased erosion rates in autumn. Blue-rayed  
51 limpets, which were recorded within kelp holdfasts as well as on stipes and blades, recruited  
52 in spring and peaked in abundance in late summer, with length and biomass generally  
53 increasing through the year. The area of kelp blade damaged by limpet grazing was low (a  
54 maximum of ~ 4 %) and relatively consistent throughout the year, and the number and size  
55 of grazing scars exhibited limited seasonality. Survey data from other *L. digitata* populations  
56 in the UK suggested that the limpet abundances recorded in North Devon were comparable  
57 with other sites in the region. Although the impact of *P. pellucida* grazing on kelp blade  
58 tissue appears to be minimal, further research into cavity grazing by limpets on the stipe and  
59 in the holdfast is needed to formerly assess the impact these cavities have on dislodgement  
60 and fracture rates, especially when increased occupancy and grazing coincides with periods  
61 of intense wave action. We conclude that while herbivory is an important processes acting  
62 upon many kelp populations globally, the grazing pressure exerted by *P. pellucida* on *L.*  
63 *digitata* is unlikely to strongly influence population structure on UK rocky shores.

64

## 65 Key Words

66 Temperate reefs; Northeast Atlantic; Macroalgal beds; Laminariales; Grazers; Herbivory

67

## 68 Highlights

- 69
- 70 • Typical seasonality in *Laminaria digitata* and *Patella pellucida* population dynamics.
  - 71 • Despite high limpet abundances, little evidence of significant grazing effects.
  - Limpet grazing unlikely to impact *L. digitata* population structure in southwest UK.

72 1. Introduction

73 Kelp forests are widely distributed across wave-exposed coasts at mid-to-high latitude  
74 regions in both hemispheres (Dayton, 1985; Kain, 1979; Teagle et al., 2017). Kelps function  
75 as ecosystem engineers by altering environmental conditions and providing food and habitat  
76 for associated organisms (Dayton, 1985; Kain, 1979; Smale et al., 2013; Steneck et al.,  
77 2002; Teagle et al., 2017). The distribution, extent, structure and productivity of kelp forests  
78 is influenced by a range of physical and biological processes (Dayton et al., 1984; Smale et  
79 al., 2016; Wernberg et al., 2011), the importance of which vary considerably across spatial  
80 and temporal scales. For example, strong top-down control on kelp populations, through  
81 intense herbivory, has been recorded in eastern Canada (Bernstein et al., 1981; Mann,  
82 1977; Scheibling et al., 1999), Iceland (Hjorleifsson et al., 1995), northern Norway (Leinaas  
83 and Christie, 1996), parts of South Africa (Bustamante et al., 1995), eastern Australia  
84 (Andrew and Underwood, 1993; Fletcher, 1987), and New Zealand (Shears and Babcock,  
85 2002). In contrast, some kelp populations appear to be far less influenced by herbivory,  
86 including those in Western Australia (Fowler-Walker and Connell, 2002; Vanderklift and  
87 Kendrick, 2004), other parts of South Africa (Day and Branch, 2002; Velimirov et al., 1977),  
88 Argentina (Barrales and Lobban, 1975), Chile (Vasquez et al., 2006) and potentially those in  
89 the British Isles (Hargrave et al., 2017; Smale et al., 2013). The majority of studies pertaining  
90 to grazing pressure have focussed on sea urchins, which can overgraze kelp forests and  
91 drive phase shifts to urchin barrens (Filbee-Dexter and Scheibling, 2014; Law and Morton,  
92 1993; Ling et al., 2014; Paine and Levin, 1981).

93  
94 Non-urchin grazers may also exert top-down control over kelp populations but have received  
95 far less research attention. A number of studies have identified grazing by molluscs,  
96 crustaceans and fish as a key process within kelp forests (e.g. Krumhansl and Scheibling,  
97 2011), although major knowledge gaps pertaining to the role of non-urchin grazers within  
98 many systems still persist. For example, in the northeast Atlantic, only a handful of studies  
99 have examined the role of limpet grazing on natural kelp populations (e.g. Graham and  
100 Fretter, 1947; Kain and Svendsen, 1969; McGrath, 1992). More generally, studies on kelp-  
101 grazer interactions have been concentrated within a few geographic regions, including  
102 eastern Canada (e.g. Scheibling et al., 1999), eastern Australia (e.g. Andrew, 1993),  
103 California (e.g. Harrold and Reed, 1985) and Norway (e.g. Hagen, 1983). To add to our  
104 understanding of limpet-kelp interactions, we adopted the North Atlantic canopy forming kelp  
105 *Laminaria digitata* and the blue-rayed limpet *Patella pellucida* as a model system to examine  
106 the influence of a non-urchin grazer on kelp forest structure.

107

108 *Laminaria digitata* is a perennial species, reaching maturity between one and two years and  
109 surviving for up to six years (Smale et al., 2013). Kain and Jones (1975) found adult *L.*  
110 *digitata* to be fertile between August and December with spores appearing to settle  
111 throughout most of the year, but less so during mid-winter. In addition, it can grow  
112 throughout the year (Schaffelke and Lüning, 1994), but exhibits seasonality in growth rates,  
113 with peak elongation and growth occurring in late spring (May-June in the northern  
114 hemisphere) (Kain, 1979; Parke, 1948; Perez, 1969). Further to these growth-rate  
115 fluctuations, the biochemical content of kelp tissue also changes seasonally (Hargrave et al.,  
116 2017), which is likely in part to be influenced by the availability of nutrients in the water  
117 (Arnold and Targett, 2003; Black, 1950; Dayton, 1985; Gevaert et al., 2008; Hay and  
118 Fenical, 1988; Jormalainen and Honkanen, 2008; Targett and Arnold, 1998). This seasonal  
119 fluctuation also possibly reduces the palatability of the tissue for the associated grazers  
120 (Graham and Fretter, 1947; McGrath, 1992; Norderhaug et al., 2006).

121

122 Kelp tissue loss also occurs seasonally, as dislodgement of the whole or part of the plant or  
123 the substrate beneath the holdfast, or as erosion of the blade (de Bettignies et al., 2013;  
124 Mann, 1972). Chronic erosion of blade (or 'lamina') tissue may occur year-round, although  
125 many species exhibit periodic peaks in erosion rates, leading to a seasonal pulse of detritus  
126 production (Krumhansl and Scheibling, 2012). Dislodgement can occur throughout the year  
127 (de Bettignies et al., 2013; Krumhansl and Scheibling, 2012) but may increase during  
128 extreme storm events (Filbee-Dexter and Scheibling, 2012; Smale and Vance, 2015).

129 Alongside this seasonal tissue loss, kelp-derived material is also consumed by a wide range  
130 of organisms, either as living material or as kelp detritus (Krumhansl and Scheibling, 2012;  
131 Vanderklift and Wernberg, 2008). If live kelp tissue is overgrazed, for example by fish or  
132 invertebrate herbivores, it can drive widespread kelp biomass loss (Dayton, 1985;  
133 Krumhansl and Scheibling, 2012; Orr et al., 2005; Smale et al., 2013; Steneck et al., 2002).  
134 This grazing-related biomass loss can occur directly through the consumption of kelp plants  
135 (e.g. Steneck et al., 2002), and/or indirectly, through weakening of kelp tissue and  
136 consequent increases in kelp plant fracturing and/or dislodgement (Black, 1976; Choat and  
137 Black, 1979; Muñoz and Santelices, 1989).

138

139 Of the various kelp-associated gastropods, at least five limpets have been identified as  
140 almost exclusively feeding on one or a few kelp species and, once settled as larvae, all but  
141 one spend most of their life on kelp (*Discurria insessa*, *Cymbula compressa*, *Scutellastra*  
142 *argenvillei*, *Scurria scurra* and *Patella pellucida*) (Black, 1976; Branch, 1975; Kain and  
143 Svendsen, 1969; McGrath, 1992; Toth and Pavia, 2002a). Of these species the only one to  
144 be found in the northeast Atlantic is the blue-rayed limpet *Patella pellucida* (Graham and  
145 Fretter, 1947; Leblanc et al., 2011; Steneck and Watling, 1982; Toth and Pavia, 2002a),  
146 which is distributed from Portugal polewards to Norway and Iceland (Fretter and Graham,  
147 1976; Vahl, 1971). It can reproduce throughout the year but recruitment tends to peak during  
148 the spring; most individuals exhibit an annual life cycle as few survive more than a year,  
149 although those inhabiting kelp holdfasts may overwinter (Fretter and Graham, 1976; Vahl,  
150 1971). Recently-settled *P. pellucida* individuals found on kelp blades and stipes are typically  
151 0.1 - 0.3 cm in length, and may attain a maximum length of ~ 1 cm (McGrath, 1992) whilst  
152 individuals over-wintering within kelp holdfasts can reach 2 cm in length (Fretter and  
153 Graham, 1976). Limited research has been conducted on *Laminaria* spp. and *P. pellucida*  
154 interactions and, consequently, the importance of limpet grazing remains largely unexplored  
155 (Hargrave et al., 2017; Kain and Svendsen, 1969; Toth and Pavia, 2002a).

156

157 We examined the population dynamics of *L. digitata* and *P. pellucida* at two intertidal reef  
158 sites in the southwest of the UK. Specifically, we examined the seasonal patterns of (i) kelp  
159 density, biomass, length, elongation, erosion, dislodgement and biochemical composition;  
160 (ii) limpet abundance and morphology and; (iii) evidence of grazing damage on kelp blades.  
161 Our overall aims were to benchmark seasonal population dynamics for these critically under-  
162 studied kelp and limpet species and to determine whether grazing pressure by *P. pellucida*  
163 may exert top down control over *L. digitata* populations.

164

## 165 2. Methods

### 166 2.1. Study Sites

167 The study was conducted at two sites, Lynmouth Bay and Wringcliff Bay in North Devon, UK  
168 (Fig. 1). Both are open-coast rocky reef sites comprising of a mix of boulders and bedrock,  
169 and experience typical mid-latitude seasonality in key environmental variables (Fig. 1). Both  
170 sites sit within Exmoor National Park, mid-way along the Bristol Channel and within the  
171 Bideford to Foreland Point Marine Conservation Zone. Preliminary observations indicated  
172 that these sites support fairly extensive stands of *Laminaria digitata* and associated fauna,  
173 including *Patella pellucida* (Fig. 1).

174

175 2.2. Field Surveys

176 All surveys were conducted in the low intertidal zone (~ 0.8 m above chart datum), within  
177 stands of *L. digitata* exposed during spring low tides. At each site, three fixed points parallel  
178 to the low tide line and ~ 10 m apart were established using GPS and marked by drilling a  
179 bolt with a fluorescent tag into the bedrock. The density of mature canopy-forming *L. digitata*  
180 plants (i.e. fully formed thalli with stipe length > 10 cm) was quantified by haphazardly  
181 placing four 0.25 m<sup>2</sup> quadrats within 3 m of each of the fixed points. Quadrat surveys were  
182 completed monthly from March 2016 to March 2017 (excluding July and August 2016 at both  
183 sites, November 2016 and January 2017 at Lynmouth and June 2016 and March 2017 at  
184 Wringcliff due to a limited tidal window). To determine kelp elongation rates, 20 mature  
185 canopy-forming *L. digitata* plants were randomly selected from areas between the fixed  
186 points at Lynmouth Bay and tagged (with fluorescent tubes on cable ties) during the spring  
187 low tides of March 2016. Plants were revisited monthly (March 2016 to March 2017) and  
188 blade length and elongation were measured in the field. Monthly blade elongation was  
189 determined following the hole punch method, whereby the blade was punctured at distances  
190 of 5 and 10 cm from the stipe/meristem junction and re-measured on return (Parke 1948).  
191 The erosion rate of the blades was calculated using the blade length and elongation rate  
192 data in the equation:

193

$$194 \text{ Erosion (cm day}^{-1}\text{) =}$$
$$195 \frac{\text{((blade length month1 + elongation during month1) - blade length month2)}}{\text{Number of days between month1 and month2}}$$

196

197

198 Kelp standing crop biomass values were obtained by randomly harvesting 10 mature *L.*  
199 *digitata* plants per site per month outside the immediate vicinity but adjacent to the fixed  
200 points at the same tidal height on the shore at both sites. These were returned to the  
201 laboratory to determine stipe and blade length ( $\pm 0.5$  cm) (later combined for the total length  
202 of each plant) and stipe/holdfast and blade biomass ( $\pm 1$  g). Harvested biomass data and  
203 density estimates were then used to calculate estimated standing crop biomass. To  
204 determine dislodgement rates of *L. digitata* over the winter, a further three fixed points were  
205 established per site (~ 0.8 m a.c.d.), each > 5 m apart from one another. Within a 3 m radius  
206 of each point, 10 mature *L. digitata* plants were tagged with fluorescent tubing and cable ties  
207 during the October 2016 (Wringcliff Bay) and November 2016 (Lynmouth Bay) spring low  
208 tides. These were revisited in March 2017, when the number of tagged plants remaining was  
209 quantified.

210

211 The harvested kelp plants were also used to examine the population structure of associated  
212 *P. pellucida*. Any limpets attached to the kelp plants were removed and retained in 70%  
213 Industrial Methylated Spirits (IMS). The length and fresh-weight biomass of *P. pellucida* were  
214 then quantified. To determine the total area of each kelp blade, the area of grazed tissue,  
215 the number and size of grazing scars and a measure of relative grazing damage, a digital  
216 image of each side of each kelp blade was taken by placing the blades between two pieces  
217 of acrylic sheet. These images were later analysed with ImageJ software (National Institutes  
218 of Health, USA); the total area of the blade and the total area of grazed tissue were used to  
219 calculate the total percentage of each blade damaged by limpet grazing. In addition, to  
220 assess the grazing pressure on new growth tissue per month an index of relative grazing  
221 damage was calculated for a randomly selected sub-set (n=5) of Lynmouth Bay blades,  
222 using the formula:

223

224

225

226

227

$$\text{Relative grazing damage} = \frac{\text{average area new growth for that month (cm}^2\text{)}}{\text{total area new tissue grazed (cm}^2\text{)}}$$

228 The average area of new growth for that month was identified in ImageJ using the monthly  
229 elongation rate averages from the tagged kelp plants. Within this area of new tissue, the  
230 total area of grazed tissue was also calculated.

231

232 Finally, in order to place our *P. pellucida* density values in a broader regional context, we  
233 collated existing unpublished data on limpet abundances associated with intertidal *L. digitata*  
234 populations in the UK. Data were collected in the same manner as described above, and  
235 comparisons between our main study sites and these additional survey sites were made for  
236 corresponding months.

237

### 238 2.3. Biochemical Analysis

239 To assess seasonality in the biochemical composition of *L. digitata*, samples of basal and  
240 distal sections of blade (> 20 cm<sup>2</sup>) were collected from the harvested kelp plants (10 plants  
241 were harvested per site per month). The samples were cut (basal = immediately above the  
242 stipe-blade/meristem junction; distal = from ~ 5 cm below the tips of the blade), externally  
243 cleaned using deionised water, blotted dry, placed in pre-labelled bags and put on ice,  
244 before being transferred to a freezer for storage. Samples were then freeze-dried (Lablyo  
245 Freezedrier, Frozen in Time Ltd) for at least 48 hours before being ground to a 250 µm  
246 powder. To represent the seasonal biochemical content of *L. digitata* at both sites, four  
247 months were selected to reflect each season (March for winter, June for spring, September

248 for summer and December for autumn; Gevaert et al., 2008); within each month five or six  
249 samples were randomly selected to represent basal and distal tissues. Both basal and distal  
250 samples were analysed in an Elemental Microanalysis CHN Analyser (EA1110, CE  
251 Instruments Ltd, Wigan) for carbon, hydrogen and nitrogen content following Gevaert et al.  
252 (2008) but using cyclohexanone-2,4-dinitrophenylhydrazone as the standard and L-cystine  
253 as the Certified Reference Material. The Certified Reference Material was replicated in  
254 triplicate and each basal/distal sample was sub-sampled in duplicate to account for machine  
255 error. The powdered samples were also analysed for phenols following methods based upon  
256 Van Alstyne (1988) and Hargrave et al. (2017). Each basal/distal sample was sub-sampled  
257 twice and each sub-sample was assayed in triplicate to eliminate machine error; resulting  
258 data were averaged for use in statistical analysis. For each sub-sample, a measured mass  
259 (100 mg  $\pm$  10 mg) of powder was added to 1 ml of 50 % aqueous methanol in a 1.5 ml  
260 Eppendorf tube. Each tube was vortexed for 30 seconds and then extracted in a fridge (4  
261 °C) for 24 hours. Samples were then vortexed again and centrifuged for two minutes at  
262 13000 rpm. 0.5 ml of the supernatant was decanted into another 1.5 ml Eppendorf tube and  
263 diluted with 0.5 ml of deionised water. 0.48 ml of this solution was transferred into another  
264 1.5 ml Eppendorf tube and combined with 60  $\mu$ l of Folin Ciocalteu reagent. After five  
265 minutes incubation at room temperature, 30  $\mu$ l of 1.5 Molar sodium carbonate was added.  
266 Samples were then sealed and vortexed and left to stabilise in the fridge (4 °C) for a further  
267 24 hours to ensure the plateau of absorbance was reached. Subsequently, samples were  
268 centrifuged again and triplicate samples of the supernatant were loaded into multiwell plates  
269 and the absorbance was read at 765 nm on a SpectraMax 190 microplate reader.  
270 Absorbances were then converted to soluble phenolic equivalents per unit mass by  
271 reference to a phloroglucinol (Sigma-Aldrich, Gillingham) standard curve.

272

#### 273 2.4. Statistical analysis

274 Variability in the various population-level metrics between sampling months and sites for  
275 *Laminaria digitata* and *Patella pellucida* were visualised plotting mean values ( $\pm$  SE) across  
276 time. Comparisons of dislodgement rates at both sites were analysed using a Mann-Whitney  
277 *U* test in R (R Core Team, 2016) due to the small data set. Variability between seasons and  
278 sites in the biochemical composition of *L. digitata* (i.e. C:N values and phenol content) was  
279 examined using univariate permutational analysis of variance (PERMANOVA; Anderson et  
280 al., 2008) in PRIMER v.7 software (Primer-E Ltd, Plymouth). Basal and distal sections were  
281 analysed separately using a two-factor model with Season and Site as fixed factors. Tests  
282 were conducted using a similarity matrix based on Euclidean distances between  
283 untransformed data, and 4999 permutations were conducted under a reduced model. Where  
284 main factors or interactions were significant (at  $p < 0.05$ ), further pairwise tests were



285 conducted. Variability in grazing metrics (i.e. total percentage blade area grazed, total  
286 number of grazing scars and average size of grazing scars) was examined in a similar  
287 manner. Finally, variability between months in relative grazing pressure at Lynmouth was  
288 examined with a one-factor model. Univariate PERMANOVA was used as opposed to other  
289 statistical approaches as it is more robust to heterogeneity in variance and does not assume  
290 normal distributions. Even so, differences in within-group dispersion between treatments can  
291 influence main tests. As such, the PERMDISP routine was used to examine differences in  
292 within-group dispersion between levels of the treatments and, where significant, a more  
293 conservative  $p$ -value of 0.01 was adopted to accept significance from the univariate  
294 PERMANOVA tests.

295

### 296 3. Results

297 The structure of *L. digitata* populations, which was similar across both sites, exhibited  
298 distinct seasonality (Fig. 2). The density of mature plants ranged from 4 inds.  $m^{-2}$  (at  
299 Wringcliff in December) to 20 inds.  $m^{-2}$  (at Wringcliff in March 2016), while standing biomass  
300 ranged from 422 g  $m^{-2}$  (at Wringcliff in December) to 2116 g  $m^{-2}$  (at Lynmouth in  
301 September). However, in general, densities were moderately consistent at  $\sim 10$  inds.  $m^{-2}$   
302 (Fig. 2A). This was reflected in the percent cover of *L. digitata*, which ranged from 14 % (at  
303 Lynmouth in October) to 55 % (at Lynmouth in June) but was averaged  $\sim 30 - 40$  % through  
304 most of the year (Fig. 2B). The mean biomass of individual plants did exhibit a degree of  
305 seasonality, with values generally increasing through spring and summer before decreasing  
306 sharply in winter (Fig. 2C). The mean length of plants meanwhile varied little through the  
307 year, although greatest values were recorded in spring (Fig. 2D).

308

309 Total standing biomass was comparable at both sites and fairly stable through the year, with  
310 the exception of a marked decline in biomass at Wringcliff in winter (Fig. 2E). Data from  
311 Lynmouth indicated marked seasonality in patterns of blade growth and erosion, with  
312 maximal elongation values recorded in spring/early summer and negligible elongation  
313 observed through summer and autumn (Fig. 2F). Erosion exhibited a contrasting pattern,  
314 with peak erosion rates observed in autumn and winter (Fig. 2F). The winter dislodgement  
315 rates did not differ significantly between sites ( $U = 0$ ,  $n = 6$ ,  $p = 0.174$ ); nevertheless,  
316 Lynmouth had a lower rate of dislodgement ( $\sim 10 - 20$  %) whereas the maximum  
317 dislodgment was found at Wringcliff, where almost 40 % of tagged individuals were lost (Fig.  
318 2G).

319

320 C:N values in basal and distal tissue did not vary significantly between sites but exhibited  
321 marked variability between seasons (Table 1; Fig. 3A&B). Specifically, C:N values were

322 significantly higher in summer/autumn compared with winter/spring (Fig. 3A&B, Table 1;  
323 post-hoc tests  $p < 0.05$ ). In addition, a significant Site x Season interaction was detected for  
324 distal tissue, with post-hoc tests showing that differences between sites were only significant  
325 in autumn ( $p < 0.05$ ). For phenol concentrations in basal tissue a significant Site x Season  
326 interaction was detected, as variability between sites was only significant in autumn (Fig. 3C,  
327 Table 1). The phenol content of distal tissue was consistent across sites and between  
328 seasons, with no significant variability detected (Fig. 3D, Table 1).

329

330 Across the study *P. pellucida* individuals were frequently recorded on *L. digitata* plants,  
331 specifically, one or more *P. pellucida* were observed on 50 % of blade samples, 13 % of  
332 stipes and within 30 % of holdfasts. The abundance of *P. pellucida* associated with kelp  
333 plants exhibited strong seasonality, with maximum densities observed during summer and  
334 autumn (Fig. 4A-C). The maximum observed abundance was on kelp blades with 47 limpets  
335 recorded at Wringcliff Bay in September (Fig. 4A). However on average, ~ 10 limpets per  
336 plant blade were observed at both sites during summer (Fig. 4A), whereas average limpet  
337 abundances on stipes and within holdfasts were consistently less than one per plant and  
338 more temporally consistent across the year (Fig. 4 B&C). In general *P. pellucida* became  
339 larger and increased in biomass from an initial period of recruitment in May through to the  
340 end of the year (Fig. 4D-I). An exception was a single large individual sampled on a kelp  
341 blade at Wringcliff in April 2016 (Fig. 4D&G), which had presumably over-wintered. The  
342 habitat preference of *P. pellucida* also exhibited seasonality (Fig. 5), where *P. pellucida* were  
343 almost exclusively recorded on the central and distal portions of blade surfaces through the  
344 summer months (i.e. June-August), after which the relative abundance of *P. pellucida* found  
345 on the basal meristematic area of the blade increased (Fig. 5). However, through winter (i.e.  
346 November to February), *P. pellucida* were predominantly recorded on stipes and within  
347 holdfasts (Fig. 5).

348

349 The total area of *L. digitata* blades grazed by *P. pellucida* varied significantly between both  
350 months and sites (Fig. 6A, Table 2). Post-hoc tests indicated that, overall, grazing was  
351 higher at Wringcliff and that grazing damage was greater in April 2016 compared with other  
352 months. Indeed, grazing damage reached ~ 4 % at Wringcliff in April 2016, whereas typical  
353 grazing damage was ~ 1 - 2 % of kelp blade surfaces across all other months (Fig. 6A). For  
354 the Lynmouth population (where elongation rates were recorded), we observed no  
355 significant variability in the area of newly-formed tissue grazed by *P. pellucida* between  
356 months ( $F_{11,59} = 0.94$ ,  $p = 0.387$ ), although a marked peak of ~ 6 % of newly formed tissue  
357 was recorded in September (Fig. 6B). The number of grazing scars on *L. digitata* blades was  
358 not significantly different between sites but varied significantly between months (Fig. 6C,

359 Table 2), with lowest values recorded in May and highest in September (Fig. 6C). Finally, the  
360 average size of grazing scars was highly variable between plants but did not vary  
361 significantly between sites or months (Fig. 6D, Table 2). The densities of *P. pellucida* we  
362 recorded at our study sites were, on the whole, comparable to survey data collected from  
363 other sites in the southwest of the UK, with the exception of a single study site near  
364 Plymouth (Fig. 7).

365

#### 366 4. Discussion

367 The structure of *L. digitata* populations was similar across both sites and several  
368 characteristics varied seasonally in agreement with previous studies (Kain, 1979; Kain and  
369 Jones, 1975; Parke, 1948; Perez, 1969). Specifically, we recorded spring-time peaks in  
370 density and percentage cover (Chapman, 1984), total length (slightly later than previously  
371 recorded, likely due to continued stipe growth after peak blade growth ended) (Delebecq et  
372 al., 2016; Kain, 1979; Schaffelke and Lüning, 1994), elongation rates (Kain, 1979; Parke,  
373 1948; Perez, 1969), nitrogen levels (in winter/spring compared with summer/autumn)  
374 (Chapman and Craigie, 1978; Gagné et al., 1982; Gevaert et al., 2008; Young et al., 2007)  
375 and phenols in the distal blade tissue (Adams et al., 2011; Connan et al., 2004; Leblanc et  
376 al., 2011). These spring peaks are likely influenced by increasing light levels (Dayton, 1985;  
377 Leblanc et al., 2011) and high concentrations of nutrients in the water column (Dayton, 1985;  
378 Gagné et al., 1982; Targett and Arnold, 1998). Meanwhile, low elongation rates recorded  
379 during the summer were inversely related to the seawater temperature (Delebecq et al.,  
380 2016; Kain, 1979; Raybaud et al., 2013; Wilson et al., 2015; Yesson et al., 2015). Plant  
381 biomass and standing crop tended to peak in summer/autumn, as expected given the timing  
382 of peak growth and winter storm-induced blade erosion and dislodgement (Black, 1950;  
383 Kain, 1979; Schaffelke and Lüning, 1994). Carbon content (as shown by C:N) also increased  
384 in summer/autumn, likely due to increased photosynthate storage (Celis-Plá et al., 2015;  
385 Gevaert et al., 2008; Young et al., 2007). In contrast to these other seasonal patterns, we  
386 observed peaks in erosion rates in the winter, coinciding with a period of increased  
387 storminess and wave action, which likely resulted in increased fragmentation and tissue loss  
388 (Krumhansl and Scheibling, 2012; Lüning, 1979; Mann, 1972). Increased wave action during  
389 winter also led to the loss of entire kelp plants, as seen in the dislodgement rates discussed  
390 below.

391

392 The population structure of *P. pellucida* also exhibited marked seasonality, largely similar to  
393 that observed in other parts of its range (Graham and Fretter, 1947; Kain and Svendsen,  
394 1969; McGrath, 1992). For example, peak recruitment occurred in May/June and maximum  
395 abundance in September, in keeping with previous studies on *P. pellucida* populations in the

396 northeast Atlantic (Graham and Fretter, 1947; Kain and Svendsen, 1969; McGrath, 1992).  
397 Limpet abundances on kelp blades decreased markedly after September, most likely due to  
398 dislodgement (Vahl, 1971), predation (Norderhaug et al., 2005), or migration towards the  
399 stipe and holdfast (Graham and Fretter, 1947; Kain and Svendsen, 1969; McGrath, 1992).  
400 Measurements of *P. pellucida* biomass and shell length were used to infer the age of  
401 individuals sampled in spring (McGrath, 1997, 1992) and confirmed that *P. pellucida* can and  
402 do overwinter (Fretter and Graham, 1976; Kain and Svendsen, 1969; McGrath, 1992); the  
403 low abundances of adults recorded during the spring months, however, suggest that most  
404 individuals persist for < 1 year (Fretter and Graham, 1976; Vahl, 1971).

405  
406 While *Patella pellucida* were conspicuous, common and at times abundant, there was limited  
407 evidence of ecologically-significant grazing damage on the blade. This is in contrast to other  
408 kelp-associated limpets, such as *Discurria insessa* (Black, 1976; Choat and Black, 1979)  
409 and *Scurria scurra* (Muñoz and Santelices, 1989), which can cause significant damage to  
410 kelp blades and stipes and consequent increases in erosion and defoliation. Or in  
411 comparison to the littorinid gastropod *Lacuna vincta*, a common kelp-associated grazer in  
412 the Northern Hemisphere, which has also been shown to induce tissue weakening and  
413 fragmentation through grazing activity (Chenelot and Konar, 2007; Egan and Yarish, 1999;  
414 Johnson and Mann, 1986; Krumhansl and Scheibling, 2011; Toth and Pavia, 2002a). In  
415 contrast to these, *P. pellucida* scrapes the surface tissue of kelp blades and causes only  
416 superficial damage that may be less likely to increase breakage and erosion, particularly  
417 when compared to species that create excavations and perforations, such as *L. vincta*  
418 (Krumhansl and Scheibling, 2011; Toth and Pavia, 2002b). As such, although the total area  
419 of tissue damage associated with *Patella pellucida* grazing was similar to that of *L. vincta* in  
420 previous studies (Johnson and Mann, 1986; Krumhansl and Scheibling, 2011; Toth and  
421 Pavia, 2002a), the impact is likely to be less. *Patella pellucida* individuals are markedly  
422 smaller than most other kelp-associated limpets (e.g. *Discurria insessa* and *Scurria scurra*,  
423 see Muñoz and Santelices, 1989) and, consequently, may consume less kelp material and  
424 cause less direct grazing damage. Similarly, the maximum densities of *P. pellucida* recorded  
425 here were 47 per plant or approximately 200 m<sup>-2</sup>, whereas previous studies focussing on *L.*  
426 *vincta* have reported densities of up to 300 individuals per plant and > 4500 m<sup>-2</sup> (Johnson  
427 and Mann, 1986). The higher densities recorded for other kelp-associated gastropods could  
428 indicate stronger grazing pressure exerted by these species.

429  
430 The limited blade grazing damage we observed varied markedly through the year. Grazing  
431 pressure was low from late spring to late summer, coinciding with the period of peak kelp  
432 growth and the generally small sizes of limpet recruits. Both absolute and relative grazing

433 damage increased slightly into autumn and winter, corresponding with a reduction in kelp  
434 growth rates and an increase in limpet size. Even so, the total area of grazed tissue was <  
435 1.5 % through most of the year, with the exception being April 2016 when grazing damage  
436 peaked at ~ 4.5 %. These values are considerably lower than the percentage area of grazing  
437 damage caused by *L. vincta* on *L. digitata* populations in Helgoland, Germany (Molis et al.,  
438 2010), and lower than the observed grazing pressure of *P. pellucida* on subtidal populations  
439 of *Saccorhiza polyschides* in Ireland (Ebling et al., 1948). This is consistent with the  
440 conclusion that top-down control by *P. pellucida* on *L. digitata* blades within the current study  
441 region is limited. Interestingly, we did observe notable mobility in limpet grazers across  
442 sections of the plant and, probably, between plants. Limpets tended to congregate on the  
443 central and distal parts of the blade in summer, before migrating down to the base of the  
444 blade and then to the stipe and holdfast. This has previously been shown to occur on *L.*  
445 *hyperborea* (Kain and Svendsen, 1969) but not for *L. digitata*. The explanation is most likely  
446 related to limpets seeking shelter from increased water motion and blade erosion during  
447 autumn and winter, as holdfasts and stipes are more physically stable and offer more  
448 protection from hydrodynamic forces (Vahl, 1972), rather than any changes in factors such  
449 as plant palatability. Moreover, observations from a pilot experiment conducted at the same  
450 sites in which limpets were actively removed from kelp plants each month (authors'  
451 unpublished data), suggested that mature limpets recolonised plants fairly rapidly and  
452 moved between kelp individuals. This level of intra- and inter- plant mobility, postulated  
453 previously (McGrath, 1997) and corroborated by our observations, suggests that *P. pellucida*  
454 exhibits far less host-fidelity than other kelp-associated limpets (e.g. *Discurria insessa*,  
455 Choat and Black 1979, and *Scurria scurra*, Munoz and Santelices 1989).

456

457 While the impact of *P. pellucida* grazing on the blade appears to be minimal, the increase in  
458 stipe and holdfast *P. pellucida* abundance and percentage occupancy during the winter  
459 months would likely lead to an increase in grazing scars in these parts of the algae (Graham  
460 and Fretter, 1947; McGrath, 1992; Toth and Pavia, 2002a). Although water movement is an  
461 important factor in determining kelp dislodgement, it is often aided by prior weakening of the  
462 blade, stipe and/or holdfast by grazing scars (Duggins et al., 2001; Krumhansl and  
463 Scheibling, 2012). Given the relatively high rates of winter kelp loss we observed and the  
464 sustained winter occupancy of *P. pellucida* within holdfasts and on stipes, it is possible that  
465 dislodgement of whole plants and stipe breakage may be exacerbated by tissue weakening  
466 from grazing damage (Graham and Fretter, 1947; Kain and Svendsen, 1969; McGrath,  
467 1992). Cavity grazing by *P. pellucida* has previously been speculated as a cause of *L.*  
468 *hyperborea* dislodgement (Kain and Svendsen, 1969) and has similarly been found for other  
469 kelp grazers, including urchins (Tegner et al., 1995). Alternatively, grazing activity may

470 decrease in winter during periods of lower water temperatures and relative dormancy  
471 (Thompson et al., 2000). As such, it is currently unknown whether cavity grazing by limpets  
472 infesting kelp holdfasts increases the likelihood of dislodgement during periods of intense  
473 wave action, and further research into the importance of this process is needed.

474

475 Our study suggests that grazing by *P. pellucida* does not exert strong top-down control on *L.*  
476 *digitata* populations in the UK. The abundance patterns of *P. pellucida* observed at our main  
477 study sites were broadly comparable to limpet abundances recorded elsewhere in the  
478 southwest of the UK. It should be noted that our study was purely mensurative, and without  
479 controlled manipulations of grazer density (i.e. limpet removals/exclusions) it is not possible  
480 to conclude that grazing is not ecologically significant in shaping kelp dynamics in this  
481 system. However, the relatively low density, small size and superficial grazing action of *P.*  
482 *pellucida* on the blade, combined with high growth rates of *L. digitata* at certain times of the  
483 year, strongly suggest that top-down pressure from limpets is not a key driver.

484

485 Other kelp-associated grazers, meanwhile, could induce top-down control of kelp  
486 populations in the UK through direct consumption. Grazing by *L. vincta*, as discussed above,  
487 has been shown to increase fragmentation and erosion of kelp tissue, leading to canopy loss  
488 (Johnson and Mann, 1986; Krumhansl and Scheibling, 2011; Toth and Pavia, 2002a).  
489 However, this species has a distinctly northern distribution and is more prevalent in kelp-  
490 dominated habitats around Scotland (Smale, pers. obs.), being uncommon in southern  
491 regions of the UK. Its potential grazing impacts in the UK are poorly known, and while  
492 research conducted elsewhere indicates that it could be locally important (Johnson and  
493 Mann 1986; Toth and Pavia 2002b; Krumhansl and Scheibling 2011), anecdotal evidence  
494 suggests that densities are generally low and unlikely to cause significant defoliation (Smale,  
495 pers. obs.).

496

497 Sea urchins are keystone species within many kelp forest ecosystems (e.g. Steneck et al.,  
498 2002), and three urchin species are common within shallow subtidal habitats around the UK  
499 and Ireland (Jones and Kain, 1967; Kitching and Thain, 1983). Of these, *Strongylocentrotus*  
500 *droebachiensis* is at its southern range edge in northern Scotland, where it is patchily  
501 distributed and is unlikely to form extensive barrens, as it has done further north along the  
502 Norwegian coastline (Hagen, 1983; Sivertsen, 2006). *Paracentrotus lividus* is also found in  
503 coastal waters surrounding the UK and Ireland but, populations are patchy and, with isolated  
504 exceptions, densities would not be high enough to induce barren formation (Kitching and  
505 Thain, 1983; O'Sullivan and Emmerson, 2011). Finally, while *Echinus esculentus* is widely  
506 distributed and at times common, it tends to feed on drift algae and exhibit omnivorous

507 feeding habits, rather than consuming mature kelp plants and forming extensive barrens  
508 (Leclerc et al., 2015; Sjøtun et al., 2006). As such, kelp populations in coastal waters in the  
509 UK appear to be less structured by top-down processes compared with those in many other  
510 regions (e.g. eastern Canada (Mann, 1977), Iceland (Hjorleifsson et al., 1995), northern  
511 Norway (Leinaas and Christie, 1996), parts of South Africa (Bustamante et al., 1995),  
512 eastern Australia (Andrew and Underwood, 1993), and New Zealand (Shears and Babcock,  
513 2002). Rather, other factors such as intense wave action (Burrows, 2012; Smale and Vance,  
514 2015), localised nutrient and pollutant inputs (Moy and Christie, 2012; Sheppard et al.,  
515 1980), light availability (Burrows, 2012; Smale et al., 2016) and sea temperature (Smale et  
516 al., 2015; Smale and Moore, 2017) are likely to be more important in structuring these kelp  
517 populations and their associated communities.

518

519

520

#### 521 Acknowledgements

522 We acknowledge A Rocha UK, A Rocha International and Lee Abbey Devon for support for  
523 the project. Thanks to the fieldwork assistants: Emma Renshaw, Rachel Oates, Robert  
524 Sluka, Jeremy Lindsell, Anthony and Pauline Hereward, Samantha Evans, Bea Davis, Rob  
525 Wilson-North, Philip Kiberd, Benjamin Cowburn, Kornelia Toth, Ella McKnight, Ben Porter,  
526 Abigail Leach and Dan Lay. We thank Dr Pippa Moore, Dr Nathan King and Albert  
527 Pessarrodona for sharing their unpublished *Patella pellucida* abundance data and Jane  
528 Richards for support during write up. DAS is supported by an Independent Research  
529 Fellowship awarded by the Natural Environment Research Council of the UK  
530 (NE/K008439/1).

531

532

#### 533 References

- 534 Adams, J.M.M., Ross, A.B., Anastasakis, K., Hodgson, E.M., Gallagher, J.A., Jones, J.M.,  
535 Donnison, I.S., 2011. Seasonal variation in the chemical composition of the bioenergy  
536 feedstock *Laminaria digitata* for thermochemical conversion. *Bioresour. Technol.* 102,  
537 226–234. doi:10.1016/j.biortech.2010.06.152
- 538 Anderson, M., Gorley, R.N., Robert, K.C., 2008. *Permanova+ for Primer: Guide to Software*  
539 *and Statistical Methods*. Primer-E Limited.
- 540 Andrew, N.L., 1993. Spatial Heterogeneity, Sea Urchin Grazing, and Habitat Structure on  
541 Reefs in Temperate Australia. *Ecology* 74, 292–302.
- 542 Andrew, N.L., Underwood, A.J., 1993. Density-Dependent Foraging in the Sea Urchin  
543 *Centrostephanus Rodgersii* on Shallow Subtidal Reefs in New South Wales, Australia.

544 Mar. Ecol. Prog. Ser. 99, 89–98. doi:Doi 10.3354/Meps099089

545 Arnold, T.M., Targett, N.M., 2003. To grow and defend: lack of tradeoffs for brown algal  
546 phlorotannins. *Oikos* 100, 406–408. doi:10.1034/j.1600-0706.2003.11680.x

547 Barrales, H.L., Lobban, C.S., 1975. The Comparative Ecology of *Macrocystis Pyrifera*, with  
548 Emphasis on the Forests of Chubut, Argentina. *Br. Ecol. Soc.* 63, 657–677.

549 Bernstein, B.B., Williams, B.E., Mann, K.H., 1981. The role of behavioral responses to  
550 predators in modifying urchins' (*Strongylocentrotus droebachiensis*) destructive grazing  
551 and seasonal foraging patterns. *Mar. Biol.* 63, 39–49. doi:10.1007/BF00394661

552 Black, R., 1976. The effects of grazing by the limpet, *Acmaea insessa*, on the kelp, *Egregia*  
553 *laevigata*, in the intertidal zone. *Ecology* 57, 265–277. doi:doi:10.2307/1934815

554 Black, W., 1950. The Seasonal Variation in Weight and Chemical Composition of the  
555 Common British Laminariaceae. *J. Mar. Biol. Assoc. United Kingdom* 29, 45–72.

556 Branch, G.M., 1975. Mechanisms Reducing Intraspecific Competition in *Patella* Spp.:  
557 Migration, Differentiation and Territorial Behaviour. *J. Anim. Ecol.* 44, 575–600.

558 Burrows, M.T., 2012. Influences of wave fetch, tidal flow and ocean colour on subtidal rocky  
559 communities. *Mar. Ecol. Prog. Ser.* 445, 193–207. doi:10.3354/meps09422

560 Bustamante, R.H., Branch, G.M., Eekhout, S., 1995. Maintenance of an exceptional  
561 intertidal grazer biomass in South Africa: Subsidy by subtidal kelps. *Ecology* 76, 2314–  
562 2329. doi:10.2307/1941704

563 Celis-Plá, P.S.M., Bouzon, Z.L., Hall-Spencer, J.M., Schmidt, E.C., Korbee, N., Figueroa,  
564 F.L., 2015. Seasonal biochemical and photophysiological responses in the intertidal  
565 macroalga *Cystoseira tamariscifolia* (Ochrophyta). *Mar. Environ. Res.* 1–9.  
566 doi:10.1016/j.marenvres.2015.11.014

567 Chapman, A.R.O., 1984. Reproduction, recruitment and mortality in two species of  
568 *Laminaria* in southwest Nova Scotia. *J. Exp. Mar. Bio. Ecol.* 78, 99–109.  
569 doi:10.1016/0022-0981(84)90072-8

570 Chapman, A.R.O., Craigie, J.S., 1978. Seasonal growth in *Laminaria longicuris*: Relations  
571 with reserve carbohydrate storage and production. *Mar. Biol.* 46, 209–213.  
572 doi:10.1007/BF00390682

573 Chenelot, H., Konar, B., 2007. *Lacuna vincta* (Mollusca, Neotaenioglossa) herbivory on  
574 juvenile and adult *Nereocystis luetkeana* (Heterokontophyta, Laminariales).  
575 *Hydrobiologia* 583, 107–118. doi:10.1007/s10750-006-0484-6

576 Choat, J.H., Black, R., 1979. Life histories of limpets and the limpet-laminarian relationship.  
577 *J. Exp. Mar. Bio. Ecol.* 41, 25–50.

578 Connan, S., Goulard, F., Stiger, V., Deslandes, E., Gall, E.A., 2004. Interspecific and  
579 temporal variation in phlorotannin levels in an assemblage of brown algae. *Bot. Mar.*  
580 47, 410–416. doi:10.1515/BOT.2004.057



581 Day, E., Branch, G.M., 2002. Effects of Sea Urchins (*Parenchinus angulosus*) on recruits  
582 and Juveniles of Abalone (*Haliotis midae*). *Ecol. Monogr.* 72, 133–149.  
583 doi:10.1890/0012-9615(2002)072[0133:EOSUPA]2.0.CO;2

584 Dayton, P.K., 1985. Ecology of Kelp Communities. *Annu. Rev. Ecol. Syst.* 16, 215–245.

585 Dayton, P.K., Currie, V., Gerrodette, T., Keller, B.D., Rosenthal, R., Tresca, D. V., 1984.  
586 Patch Dynamics and Stability of Some California Kelp Communities. *Ecol. Soc. Am.* 54,  
587 253–289.

588 de Bettignies, T., Wernberg, T., Lavery, P.S., Vanderklift, M. a., Moring, M.B., 2013.  
589 Contrasting mechanisms of dislodgement and erosion contribute to production of kelp  
590 detritus. *Limnol. Oceanogr.* 58, 1680–1688. doi:10.4319/lo.2013.58.5.1680

591 Delebecq, G., Davoult, D., Janquin, M., Oppliger, L.V., Menu, D., Dauvin, J., Gevaert, F.,  
592 2016. Photosynthetic response to light and temperature in *Laminaria digitata*  
593 gametophytes from two French populations. *Eur. J. Phycol.* 51, 71–82.  
594 doi:10.1080/09670262.2015.1104556

595 Duggins, D., Eckman, J.E., Siddon, C.E., Klinger, T., 2001. Interactive roles of mesograzers  
596 and current flow in survival of kelps. *Mar. Ecol. Prog. Ser.* 223, 143–155.  
597 doi:10.3354/meps223143

598 Ebling, F.J., Kitching, J.A., Purchon, R.D., Bassindale, R., 1948. The Ecology of the Lough  
599 Ine Rapids with Special Reference to Water Currents. *J. Anim. Ecol.* 17, 223–244.

600 Egan, B., Yarish, C., 1999. Productivity and life history of *Laminaria longicuris* at its  
601 southern limit in the Western Atlantic Ocean. *Mar. Ecol. Prog. Ser.* 67, 263–273.  
602 doi:10.2307/24816783

603 Filbee-Dexter, K., Scheibling, R.E., 2014. Sea urchin barrens as alternative stable states of  
604 collapsed kelp ecosystems. *Mar. Ecol. Prog. Ser.* 495, 1–25. doi:10.3354/meps10573

605 Filbee-Dexter, K., Scheibling, R.E., 2012. Hurricane-mediated defoliation of kelp beds and  
606 pulsed delivery of kelp detritus to offshore sedimentary habitats. *Mar. Ecol. Prog. Ser.*  
607 455, 51–64. doi:10.3354/meps09667

608 Fletcher, W.J., 1987. Interactions Among Subtidal Australian Sea Urchins, Gastropods, and  
609 Algae: Effects of Experimental Removals. *Ecol. Monogr.* 57, 89–109.

610 Fowler-Walker, M.J., Connell, S.D., 2002. Opposing states of subtidal habitat across  
611 temperate Australia: Consistency and predictability in kelp canopy-benthic associations.  
612 *Mar. Ecol. Prog. Ser.* 240, 49–56. doi:10.3354/meps240049

613 Fretter, V., Graham, A., 1976. The Prosobranch Molluscs of Britain and Denmark. Part 1 –  
614 Pleurotomariacea, Fissurellacea and Patellacea. *J. Molluscan Stud.* 42, 1–37.

615 Gagné, J.A., Mann, K.H., Chapman, A.R.O., 1982. Seasonal patterns of growth and storage  
616 in *Laminaria longicuris* in relation to different patterns of availability of nitrogen in the  
617 water. *Mar. Biol.* 69, 91–101. doi:10.1007/BF00396965

618 Gevaert, F., Janquin, M.A., Davoult, D., 2008. Biometrics in *Laminaria digitata*: A useful tool  
619 to assess biomass, carbon and nitrogen contents. *J. Sea Res.* 60, 215–219.  
620 doi:10.1016/j.seares.2008.06.006

621 Graham, A., Fretter, V., 1947. The life history of *Patina pellucida* (L.). *J. Mar. Biol. Assoc.*  
622 United Kingdom 26, 590–601.

623 Hagen, N.T., 1983. Destructive grazing of kelp beds by sea urchins in Vestfjorden, Northern  
624 Norway. *Sarsia* 68, 177–190. doi:10.1080/00364827.1983.10420570

625 Hargrave, M.S., Foggo, A., Pessarrodona, A., Smale, D.A., 2017. The effects of warming on  
626 the ecophysiology of two co-existing kelp species with contrasting distributions.  
627 *Oecologia* 183, 531–543. doi:10.1007/s00442-016-3776-1

628 Harrold, C., Reed, D.C., 1985. Food Availability, Sea Urchin Grazing, and Kelp Forest  
629 Community Structure. *Ecol. Soc. Am.* 66, 1160–1169.

630 Hay, M.E., Fenical, W., 1988. Marine Plant-Herbivore Interactions: The Ecology of Chemical  
631 Defense. *Annu. Rev. Ecol. Syst.* 19, 111–145.

632 Hjørleifsson, E., Kassa, O., Gunnarsson, K., 1995. Grazing of kelp by green sea urchins in  
633 Eyyjafjordu, North Iceland, in: *Ecology of Fjords and Coastal Waters*. pp. 593–597.

634 Johnson, C.R., Mann, K.H., 1986. The importance of plant defence abilities to the structure  
635 of subtidal seaweed communities: The kelp *Laminaria longicruris* de la Pylaie survives  
636 grazing by the snail *Lacuna vincta* (Montagu) at high population densities. *J. Exp. Mar.*  
637 *Bio. Ecol.* 97, 231–267. doi:10.1016/0022-0981(86)90244-3

638 Jones, N.S., Kain, J.M., 1967. Sub-tidal algal colonisation following removal of *Echinus*.  
639 *Helgol. Mar. Res.* 15, 460–466.

640 Jormalainen, V., Honkanen, T., 2008. Macroalgal Chemical Defenses and Their Roles in  
641 Structuring Temperate Marine Communities, in: *Amsler, C. (Ed.), Algal Chemical*  
642 *Ecology*. Springer Berlin Heidelberg, Berlin, Germany, pp. 57–89.

643 Kain, J.M., 1979. A view of the genus *Laminaria*. *Oceanogr. Mar. Biol. Annu. Rev.* 17, 101–  
644 161.

645 Kain, J.M., Jones, N.S., 1975. Algal Recolonization of Some Cleared Subtidal Areas. *J. Ecol.*  
646 63, 739–765.

647 Kain, J.M., Svendsen, P., 1969. A note on the behaviour of *Patina pellucida* in Britain and  
648 Norway. *Sarsia* 38, 25–30.

649 Kitching, J.A., Thain, V.M., 1983. The ecological impact of the sea urchin *Paracentrotus*  
650 *lividus* (Lamarck) in Lough Ine, Ireland. *Can. J. Fish. Aquat. Sci.* 300, 513–552.  
651 doi:10.1139/f99-163

652 Krumhansl, K., Scheibling, R., 2012. Production and fate of kelp detritus. *Mar. Ecol. Prog.*  
653 *Ser.* 467, 281–302. doi:10.3354/meps09940

654 Krumhansl, K.A., Scheibling, R.E., 2011. Spatial and temporal variation in grazing damage

655 by the gastropod *Lacuna vincta* in Nova scotian kelp beds. *Aquat. Biol.* 13, 163–173.  
656 doi:10.3354/ab00366

657 Law, R., Morton, R.D., 1993. Alternative Permanent States of Ecological Communities.  
658 *Ecology* 74, 1347–1361.

659 Leblanc, C., Schaal, G., Cosse, A., Destombe, C., Valero, M., Riera, P., Potin, P., 2011.  
660 Trophic and biotic interactions in *Laminaria Digitata* beds: Which factors could influence  
661 the persistence of marine kelp forests in northern brittany? *Cah. Biol. Mar.* 52, 415–427.

662 Leclerc, J.C., Riera, P., Laurans, M., Leroux, C., Lévêque, L., Davoult, D., 2015. Community,  
663 trophic structure and functioning in two contrasting *Laminaria hyperborea* forests.  
664 *Estuar. Coast. Shelf Sci.* 152, 11–22. doi:10.1016/j.ecss.2014.11.005

665 Leinaas, H.P., Christie, H., 1996. Effects of Removing Sea Urchins (*Strongylocentrotus*  
666 *droebachiensis*): Stability of the Barren State and Succession of Kelp Forest Recovery  
667 in the East Atlantic. *Oecologia* 105, 524–536. doi:10.1007/S00442-004-V

668 Ling, S.D., Scheibling, R.E., Rassweiler, A., Johnson, C.R., Shears, N., Connell, S.D.,  
669 Salomon, A.K., Norderhaug, K.M., Perez-Matus, A., Hernandez, J.C., Clemente, S.,  
670 Blamey, L.K., Hereu, B., Ballesteros, E., Sala, E., Garrabou, J., Cebrian, E., Zabala, M.,  
671 Fujita, D., Johnson, L.E., 2014. Global regime shift dynamics of catastrophic sea urchin  
672 overgrazing. *Phil. Trans. R. Soc. B* 370, 20130269. doi:10.1098/rstb.2013.0269

673 Lüning, K., 1979. Growth strategies of three *Laminaria* species (Phaeophyceae) inhabiting  
674 different depth zones in the sublittoral region of Helgoland (North Sea). *Mar. Ecol. Prog.*  
675 *Ser.* 1, 195–207. doi:10.3354/meps001195

676 Mann, K.H., 1977. Destruction of kelp-beds by sea-urchins: A cyclical phenomenon or  
677 irreversible degradation? *Helgolander Wissenschaftliche Meeresuntersuchungen* 30,  
678 455–467. doi:10.1007/BF02207854

679 Mann, K.H., 1972. Ecological energetics of the sea-weed zone in a marine bay on the  
680 Atlantic coast of Canada. II. Productivity of the seaweeds. *Mar. Biol.* 14, 199–209.  
681 doi:10.1007/BF00348685

682 McGrath, D., 1997. Colonisation of Artificially Cleared *Laminaria digitata* (Huds.) Lamour. By  
683 the Blue-Rayed Limpet *Helcion pellucidum* (L.) (Mollusca, Gastropoda), in: *Biology and*  
684 *Environment: Proceedings of the Royal Irish Academy.* Royal Irish Academy, pp. 245–  
685 248.

686 McGrath, D., 1992. Recruitment and Growth of the Blue-Rayed Limpet, *Helcion-Pellucidum*  
687 (L), in South East Ireland. *J. Molluscan Stud.* 58, 425–431. doi:10.1093/mollus/58.4.425

688 Molis, M., Enge, A., Karsten, U., 2010. Grazing impact of, and indirect interactions between  
689 mesograzers associated with kelp (*Laminaria digitata*). *J. Phycol.* 46, 76–84.  
690 doi:10.1111/j.1529-8817.2009.00787.x

691 Moy, F.E., Christie, H., 2012. Large-scale shift from sugar kelp (*Saccharina latissima*) to

692 ephemeral algae along the south and west coast of Norway. Mar. Biol. Res. 8, 309–  
693 321. doi:10.1080/17451000.2011.637561

694 Muñoz, M., Santelices, B., 1989. Determination of the distribution and abundance of the  
695 limpet *Scurria scurra* on the stipes of the kelp *Lessonia nigrescens* in Central Chile.  
696 Mar. Ecol. Prog. Ser. 54, 277–285. doi:10.3354/meps054277

697 Norderhaug, K.M., Christie, H.C., Fossô, J.H.O., Fredriksen, S.P., Fosså, J.H., Fredriksen,  
698 S.P., 2005. Fish-macrofauna interactions in a kelp (*Laminaria hyperborea*) forest. J.  
699 Mar. Biol. Assoc. UK 85, 1279–1286. doi:10.1017/S0025315405012439

700 Norderhaug, K.M., Nygaard, K., Fredriksen, S., 2006. Importance of phlorotannin content  
701 and C : N ratio of *Laminaria hyperborea* in determining its palatability as food for  
702 consumers. Mar. Biol. Res. 2, 367–371. doi:10.1080/17451000600962789

703 O’Sullivan, D., Emmerson, M., 2011. Marine reserve designation, trophic cascades and  
704 altered community dynamics. Mar. Ecol. Prog. Ser. 440, 115–125.  
705 doi:10.3354/meps09294

706 Orr, M., Zimmer, M., Jelinski, D.E., Mews, M., 2005. Wrack Deposition on Different Beach  
707 Types: Spatial and Temporal Variation in the Pattern of Subsidy. Ecology 86, 1496–  
708 1507. doi:10.1890/04-1486

709 Paine, R.T., Levin, S.A., 1981. Intertidal Landscapes: Disturbance and the Dynamics of  
710 Pattern. Ecol. Monogr. 51, 145–178. doi:10.2307/2937261

711 Parke, M., 1948. Studies on British Laminariaceae. I. Growth in *Laminaria saccharina* (L.)  
712 Lamour. J. Mar. Biol. Assoc. United Kingdom 27, 651–709.

713 Perez, R., 1969. Étude biometrique d’une population de *laminaria digitata* lamouroux de  
714 l’etage infralittoral profond. Rev. des Trav. l’Institut des Pêches Marit. 33, 117–135.

715 R Core Team, 2016. R: A language and environment for statistical computing.

716 Raybaud, V., Beaugrand, G., Goberville, E., Delebecq, G., Destombe, C., Valero, M.,  
717 Davoult, D., Morin, P., Gevaert, F., 2013. Decline in Kelp in West Europe and Climate.  
718 PLoS One 8, e66044. doi:10.1371/journal.pone.0066044

719 Schaffelke, B., Lüning, K., 1994. A circannual rhythm controls seasonal growth in the kelps  
720 *Laminaria hyperborea* and *L. digitata* from Helgoland (North Sea). Eur. J. Phycol. 29,  
721 49–56. doi:10.1080/09670269400650471

722 Scheibling, R.E., Hennigar, A.W., Balch, T., 1999. Destructive grazing, epiphytism, and  
723 disease: the dynamics of sea urchin - kelp interactions in Nova Scotia. Can. J. Fish.  
724 Aquat. Sci. 56, 2300–2314. doi:10.1139/f99-163

725 Shears, N.T., Babcock, R.C., 2002. Marine reserves demonstrate top-down control of  
726 community structure on temperate reefs. Oecologia 132, 131–142. doi:10.1007/s00442-  
727 002-0920-x

728 Sheppard, C.R.C., Bellamy, D.J., Sheppard, A.L.S., 1980. Study of the fauna inhabiting the

729 holdfasts of *Laminaria hyperborea* (gunn.) fosl. along some environmental and  
730 geographical gradients. *Mar. Environ. Res.* 4, 25–51. doi:10.1016/0141-  
731 1136(80)90057-4

732 Sivertsen, K., 2006. Overgrazing of kelp beds along the coast of Norway. *J. Appl. Phycol.*  
733 18, 599–610. doi:10.1007/s10811-006-9064-4

734 Sjøtun, K., Christie, H., Fosså, J.H., 2006. The combined effect of canopy shading and sea  
735 urchin grazing on recruitment in kelp forest (*Laminaria hyperborea*). *Mar. Biol. Res.* 2,  
736 24–32. doi:10.1080/17451000500537418

737 Smale, D.A., Burrows, M., Evans, A., King, N., Sayer, M., Yunnice, A., Moore, P., 2016.  
738 Linking environmental variables with regional-scale variability in ecological structure  
739 and standing stock of carbon within kelp forests in the United Kingdom. *Mar. Ecol.*  
740 *Prog. Ser.* 542, 79–95. doi:10.3354/meps11544

741 Smale, D.A., Burrows, M.T., Moore, P., O'Connor, N., Hawkins, S.J., 2013. Threats and  
742 knowledge gaps for ecosystem services provided by kelp forests: A northeast Atlantic  
743 perspective. *Ecol. Evol.* 3, 4016–4038. doi:10.1002/ece3.774

744 Smale, D.A., Moore, P.J., 2017. Variability in kelp forest structure along a latitudinal gradient  
745 in ocean temperature. *J. Exp. Mar. Bio. Ecol.* 486, 255–264.  
746 doi:10.1016/j.jembe.2016.10.023

747 Smale, D.A., Vance, T., 2015. Climate-driven shifts in species' distributions may exacerbate  
748 the impacts of storm disturbances on North-east Atlantic kelp forests. *Mar. Freshw.*  
749 *Res.* 67, 65–74. doi:10.1071/MF14155

750 Smale, D.A., Wernberg, T., Yunnice, A.L.E., Vance, T., 2015. The rise of *Laminaria*  
751 *ochroleuca* in the Western English Channel (UK) and comparisons with its competitor  
752 and assemblage dominant *Laminaria hyperborea*. *Mar. Ecol.* 36, 1033–1044.  
753 doi:10.1111/maec.12199

754 Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J. a.,  
755 Tegner, M.J., 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future.  
756 *Environ. Conserv.* 29, 436–459. doi:10.1017/S0376892902000322

757 Steneck, R.S., Watling, L., 1982. Feeding capabilities and limitation of herbivorous molluscs:  
758 A functional group approach. *Mar. Biol.* 68, 299–319. doi:10.1007/BF00409596

759 Targett, N.M., Arnold, T.M., 1998. Predicting the effects of brown algal phlorotannins on  
760 marine herbivores in tropical and temperate oceans. *J. Phycol.* doi:10.1046/j.1529-  
761 8817.1998.340195.x

762 Teagle, H., Hawkins, S.J., Moore, P.J., Smale, D.A., 2017. The role of kelp species as  
763 biogenic habitat formers in coastal marine ecosystems. *J. Exp. Mar. Biol. Ecol. Spec.*  
764 *Issue.* doi:10.1016/j.jembe.2017.01.017

765 Tegner, M.J., Dayton, P.K., Edwards, P.B., Riser, K.L., 1995. Sea urchin cavitation of giant

766 kelp (*Macrocystis pyrifera* C. Agardh) holdfasts and its effects on kelp mortality across a  
767 large California forest. *J. Exp. Mar. Bio. Ecol.* 191, 83–99. doi:10.1016/0022-  
768 0981(95)00053-T

769 Thompson, R.C., Roberts, M.F., Norton, T.A., Hawkins, S.J., 2000. Feast or famine for  
770 intertidal grazing molluscs: A mis-match between seasonal variations in grazing  
771 intensity and the abundance of microbial resources. *Hydrobiologia* 440, 357–367.  
772 doi:10.1023/A:1004116505004

773 Toth, G.B., Pavia, H., 2002a. Intraplant habitat and feeding preference of two gastropod  
774 herbivores inhabiting the kelp *Laminaria hyperborea*. *J. Mar. Biol. Assoc. UK* 82, 243–  
775 247. doi:10.1017/S0025315402005416

776 Toth, G.B., Pavia, H., 2002b. Lack of phlorotannin induction in the kelp *Laminaria*  
777 *hyperborea* in response to grazing by two gastropod herbivores. *Mar. Biol.* 140, 403–  
778 409. doi:10.1007/s002270100707

779 Vahl, O., 1972. On the position of *Patina pellucida* (L.) (gastropoda) on the frond of *Laminaria*  
780 *hyperborea*. *Ophelia* 10, 1–9. doi:10.1080/00785326.1972.10430096

781 Vahl, O., 1971. Growth and density of *Patina pellucida* (L.) (Gastropoda: Prosobranchiata)  
782 on *Laminaria hyperborea* (Gunnerus) from Western Norway. *Ophelia* 9, 31–50.  
783 doi:10.1080/00785326.1971.10430089

784 Van Alstyne, K.L., 1988. Herbivore grazing increases polyphenolic defenses in the intertidal  
785 brown alga *Fucus distichus*. *Ecology*. doi:10.2307/1941014

786 Vanderklift, M.A., Kendrick, G.A., 2004. Variation in abundances of herbivorous  
787 invertebrates in temperate subtidal rocky reef habitats. *Mar. Freshw. Res.* 55, 93–103.  
788 doi:10.1071/MF03057

789 Vanderklift, M.A., Wernberg, T., 2008. Detached kelps from distant sources are a food  
790 subsidy for sea urchins. *Oecologia* 157, 327–335. doi:10.1007/s00442-008-1061-7

791 Vasquez, J.A., Vega, J.M.A., Buschmann, A.H., 2006. Long term variability in the structure  
792 of kelp communities in northern Chile and the 1997-98 ENSO. *J. Appl. Phycol.* 18, 505–  
793 519. doi:10.1007/s10811-006-9056-4

794 Velimirov, B., Field, J.G., Griffiths, C.L., Zoutendyk, P., 1977. The ecology of kelp bed  
795 communities in the Benguela upwelling system - Analysis of biomass and spatial  
796 distribution. *Helgoländer Wissenschaftliche Meeresuntersuchungen* 30, 495–518.  
797 doi:10.1007/BF02207857

798 Wernberg, T., Russell, B., Moore, P., 2011. Impacts of climate change in a global hotspot for  
799 temperate marine biodiversity and ocean warming. *J. Exp. Mar. Bio. Ecol.* 400, 7–16.  
800 doi:10.1016/j.jembe.2011.02.021

801 Wilson, K.L., Kay, L.M., Schmidt, A.L., Lotze, H.K., 2015. Effects of increasing water  
802 temperatures on survival and growth of ecologically and economically important

803 seaweeds in Atlantic Canada: implications for climate change. *Mar. Biol.* 162, 2431–  
804 2444. doi:10.1007/s00227-015-2769-7

805 Yesson, C., Bush, L.E., Davies, A.J., Maggs, C.A., Brodie, J., 2015. The distribution and  
806 environmental requirements of large brown seaweeds in the British Isles. *J. Mar. Biol.*  
807 *Assoc. United* 155, 167–175. doi:10.1016/j.ecss.2015.01.008

808 Young, E.B., Dring, M.J., Savidge, G., Birkett, D.A., Berges, J.A., 2007. Seasonal variations  
809 in nitrate reductase activity and internal N pools in intertidal brown algae are correlated  
810 with ambient nitrate concentrations. *Plant, Cell Environ.* 30, 764–774.  
811 doi:10.1111/j.1365-3040.2007.01666.x

812

Table 1. Results of univariate PERMANOVAs to examine the effects of Season (fixed), Site (fixed) and the Season x Site interaction on C:N values and phenol concentrations in both basal and distal blade tissue. Degrees of freedom associated with each factor are shown in parentheses. An asterisk (\*) with an F value indicates that PERMDISP detected significant differences in within-group dispersion between levels of that factor and significance of PERMANOVA was reduced to  $P < 0.01$ .

Response	Season (3)			Site (1)			Season x Site (3)			Residual (33)
	MS	F	<i>P</i> (perm)	MS	F	<i>P</i> (perm)	MS	F	<i>P</i> (perm)	MS
Basal C:N	656.64	217.68	<b>0.001</b>	5.58	1.85	0.186	2.07	0.68	0.545	3.01
Distal C:N	373.48	93.89	<b>0.001</b>	2.56	0.64	0.420	13.07	3.28	<b>0.033</b>	3.97
Basal phenol	0.007	5.28*	<b>0.007</b>	0.006	4.46*	0.050	0.004	3.11	<b>0.038</b>	0.001
Distal phenol	0.005	1.43	0.253	0.001	0.30*	0.618	0.001	0.084	0.976	0.003

Table 2. Results of univariate PERMANOVAs to examine the effects of Month (fixed), Site (fixed) and the Month x Site interaction on the total percentage area of grazing scars, total number of grazing scars and average size of grazing scars on *Laminaria digitata* blades grazed by *Patella pellucida*. Degrees of freedom associated with each factor are shown in parentheses. F values marked with an asterisk (\*) indicates that PERMDISP detected significant differences in within-group dispersion between levels of that factor and significance of PERMANOVA was reduced to  $P < 0.01$ .

Response	Month (11)			Site (1)			Month x Site (11)			Residual (215)
	MS	F	<i>P</i> (perm)	MS	F	<i>P</i> (perm)	MS	F	<i>P</i> (perm)	MS
Tot. % area grazed	15.73	9.69*	<b>0.001</b>	13.94	8.58*	<b>0.002</b>	0.98	0.60	0.836	1.62
Tot. no. scars	776.22	7.78*	<b>0.001</b>	17.04	0.17	0.703	47.22	0.47	0.928	99.74
Av. size scars	2.09	1.83	<b>0.044</b>	0.21	0.18	0.675	1.63	1.43	0.132	1.14



## Figure Legends

Figure 1. (A) Location of main study sites within the UK, with top inset indicating specific locations of Lynmouth Bay (blue star) and Wringcliff Bay (green star) on the North Devon coastline and bottom inset depicting the blue rayed limpet *Patella pellucida* and the kelp *Laminaria digitata*, which were the focus of the current study. (B) *In situ* temperature (Lynmouth = black line, Wringcliff = orange line) and light availability (Lynmouth = blue line, Wringcliff = green line) data for the period March 2016-March 2017 at both study sites. Measurements were obtained with a 'Hobo Tidbit' logger and a 'Hobo light and temperature pendant' logger, which were attached to the rocky substratum at each site and recorded hourly measurements. (C) Also shown are average daily significant wave height obtained for Bideford Bay (data courtesy of Channel Coastal Observatory, [www.channelcoast.org](http://www.channelcoast.org)) (January 2016 – March 2017) and monthly total sunshine hours obtained for Bude (Met Office, June 2017) (January 2016 – March 2017).

Figure 2. *Laminaria digitata* population dynamics in North Devon, UK. Plots show seasonal trends in (A) density (n = 10), (B) percentage cover (n = 12), (C) plant length (n = 10), (D) plant biomass (n = 10) and (E) standing biomass (n = 12). Where n = per site, per month. Additionally, at Lynmouth Bay only, seasonal trends in (F) elongation and erosion rates were measured. The number labels on plots indicate the number of replicate kelp individuals. At both sites, (G) winter dislodgement rates were quantified. NB. Black \* = no data collected at both sites, Orange \* = no data collected at one site.

Figure 3. Biochemical analysis of *Laminaria digitata* blades collected from the two study sites (Lynmouth Bay and Wringcliff Bay) in North Devon, UK. C:N ratio in (A) basal and (B) distal blade tissue and phenol content in (C) basal and (D) distal tissue for the four seasons of observation (n = 5 for all sampling events and sites).

Figure 4. *Patella pellucida* population dynamics in North Devon, UK. Plots indicate limpet abundances associated with the (A) blade, (B) stipe and (C) holdfast. Also shown are the length of limpets associated with the (D) blade, (E) stipe and (F) holdfast (F) and biomass (fresh weight) of limpets associated with the (G) blade, (H) stipe and (I) holdfast. All values are mean averages ( $\pm$  SE). NB: Numbers refer to the number of individual *P. pellucida* measured, "0" = no limpets found in the area of the kelp for that month (colour coded to the sites).

Figure 5. Micro-habitat preference of *Patella pellucida* associated with *Laminaria digitata*. Stacked bars indicate the relative occurrence of limpets on each section of the kelp plants,

for each survey month. Data from both sites pooled; numbers refer to the total number of individual *P. pellucida* found across the kelp plant.

Figure 6. Evidence of grazing on *Laminaria digitata* by *Patella pellucida* in North Devon, UK. (A) average total area grazed (as a percentage of blade area), (B) average area of newly-formed tissue grazed, (C) average number of grazing scars and (D) average grazing scar size. All values are mean averages ( $\pm$  SE).

Figure 7. (A) Map of southwest UK indicating additional survey sites (with insets a&b showing specific locations of North Devon and Plymouth sites). The abundances of *Patella pellucida* on *Laminaria digitata* blades at the two main sites in North Devon were compared with: (B) routine monthly surveys at two sites in south Devon; (C) autumn survey data from three sites along the south coasts of Devon and Cornwall; and (D) summer survey data from one site in Aberystwyth, Wales. The number of replicate kelp blades examined per site/month ranged from 8 to >50.

Figures

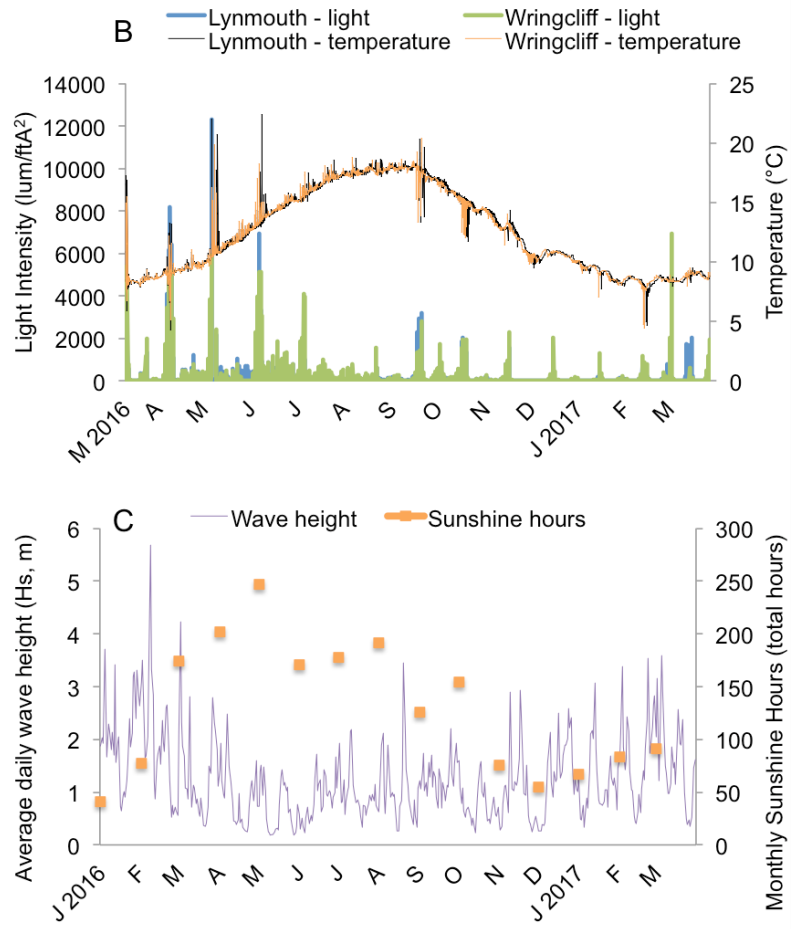
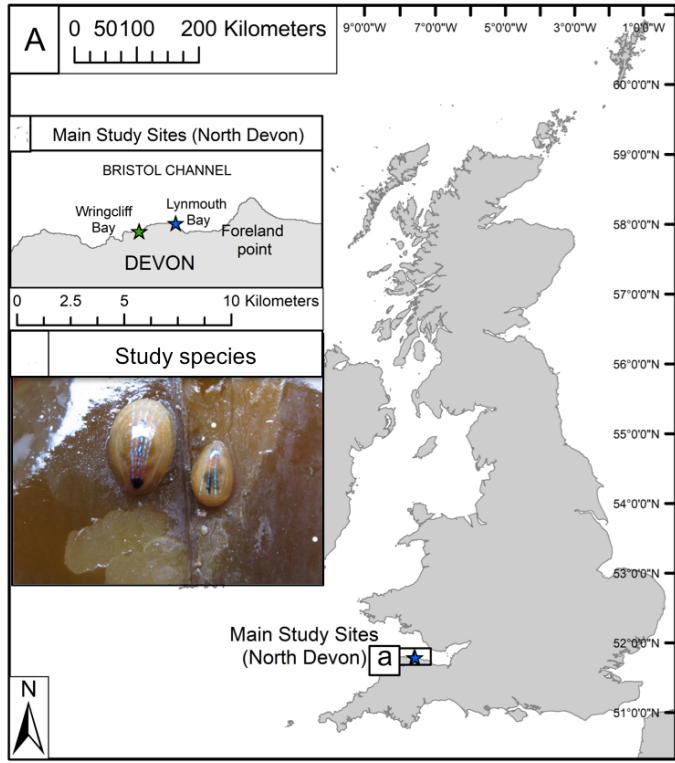


Fig. 1

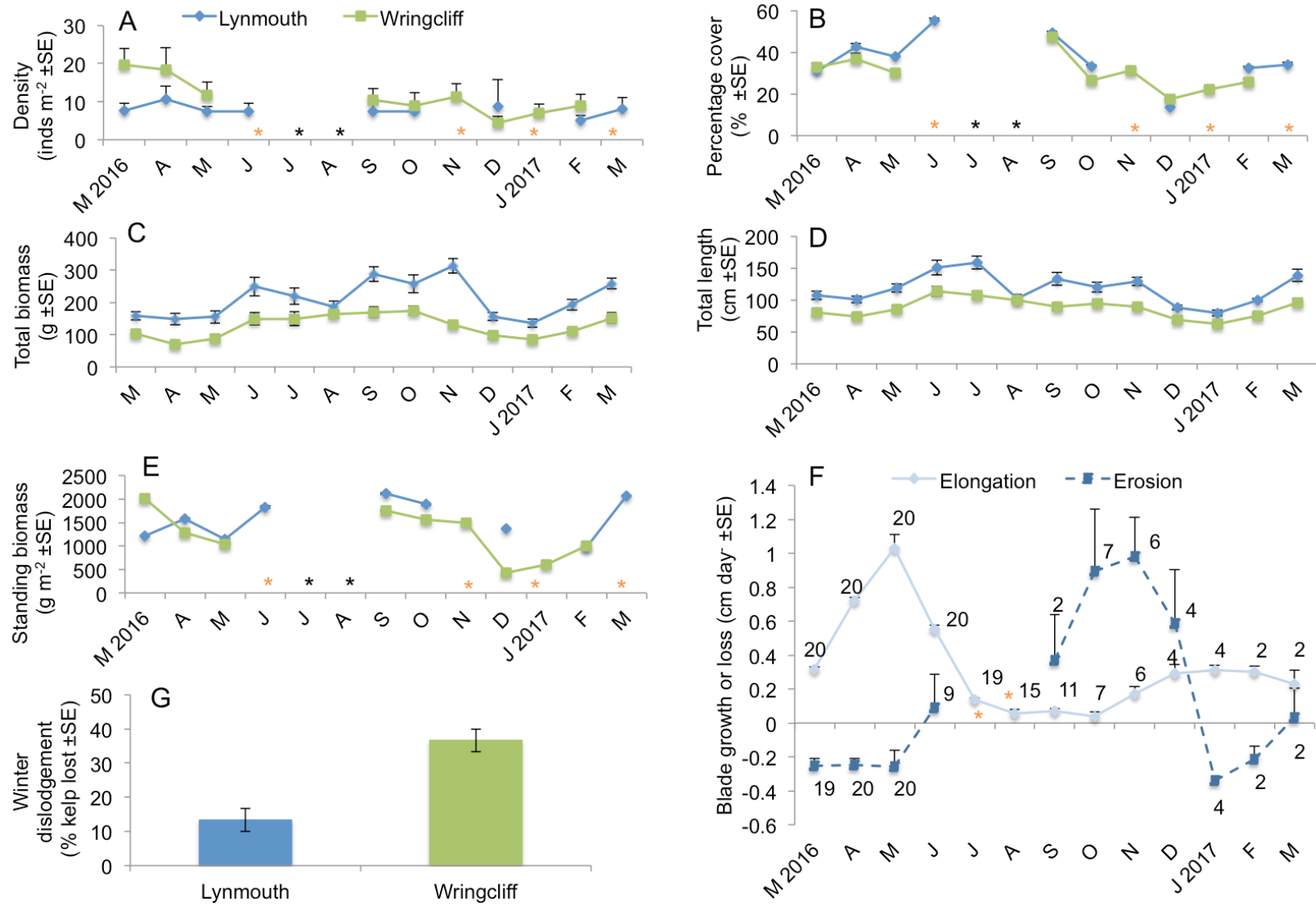


Fig. 2

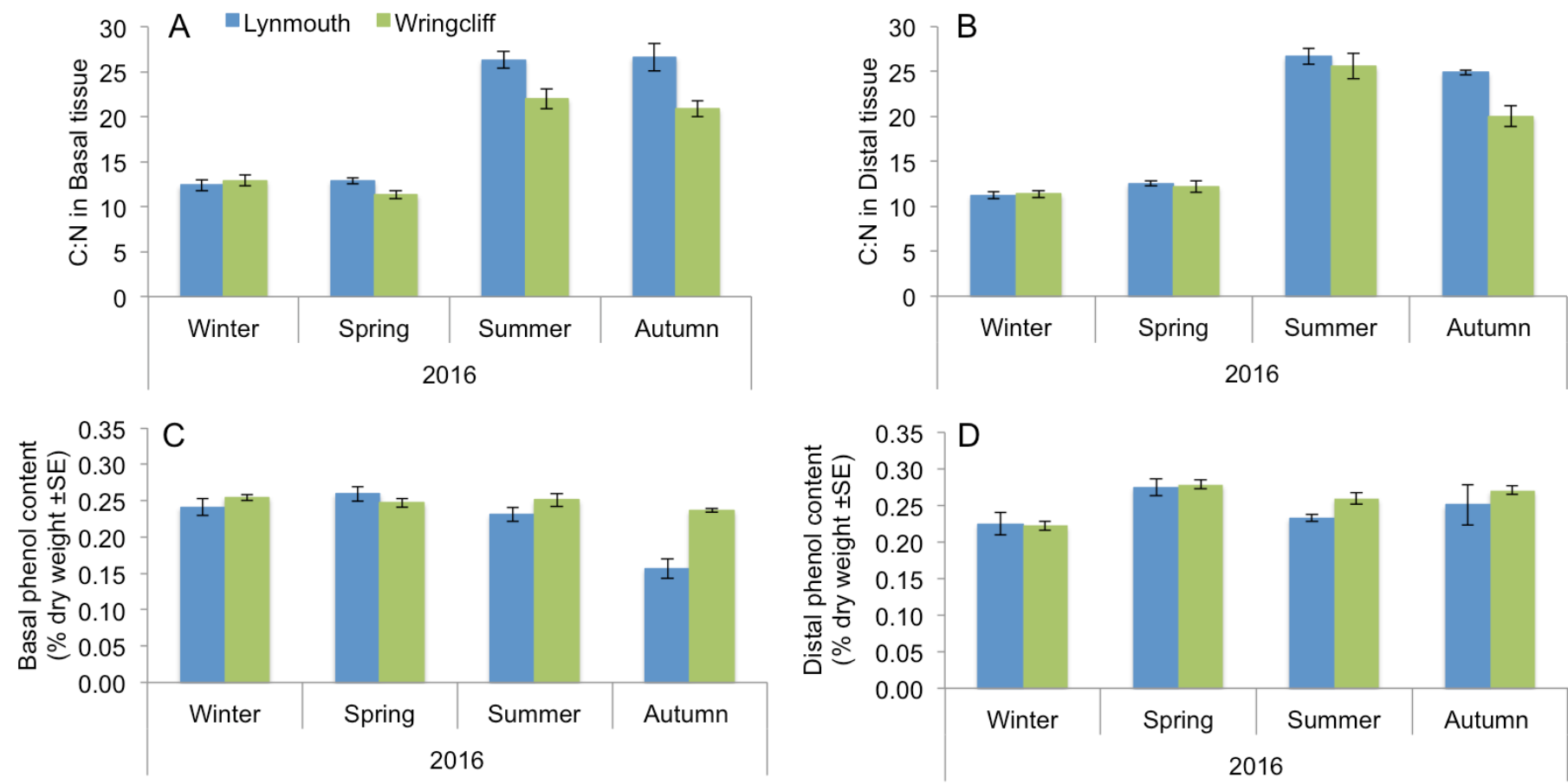


Fig. 3

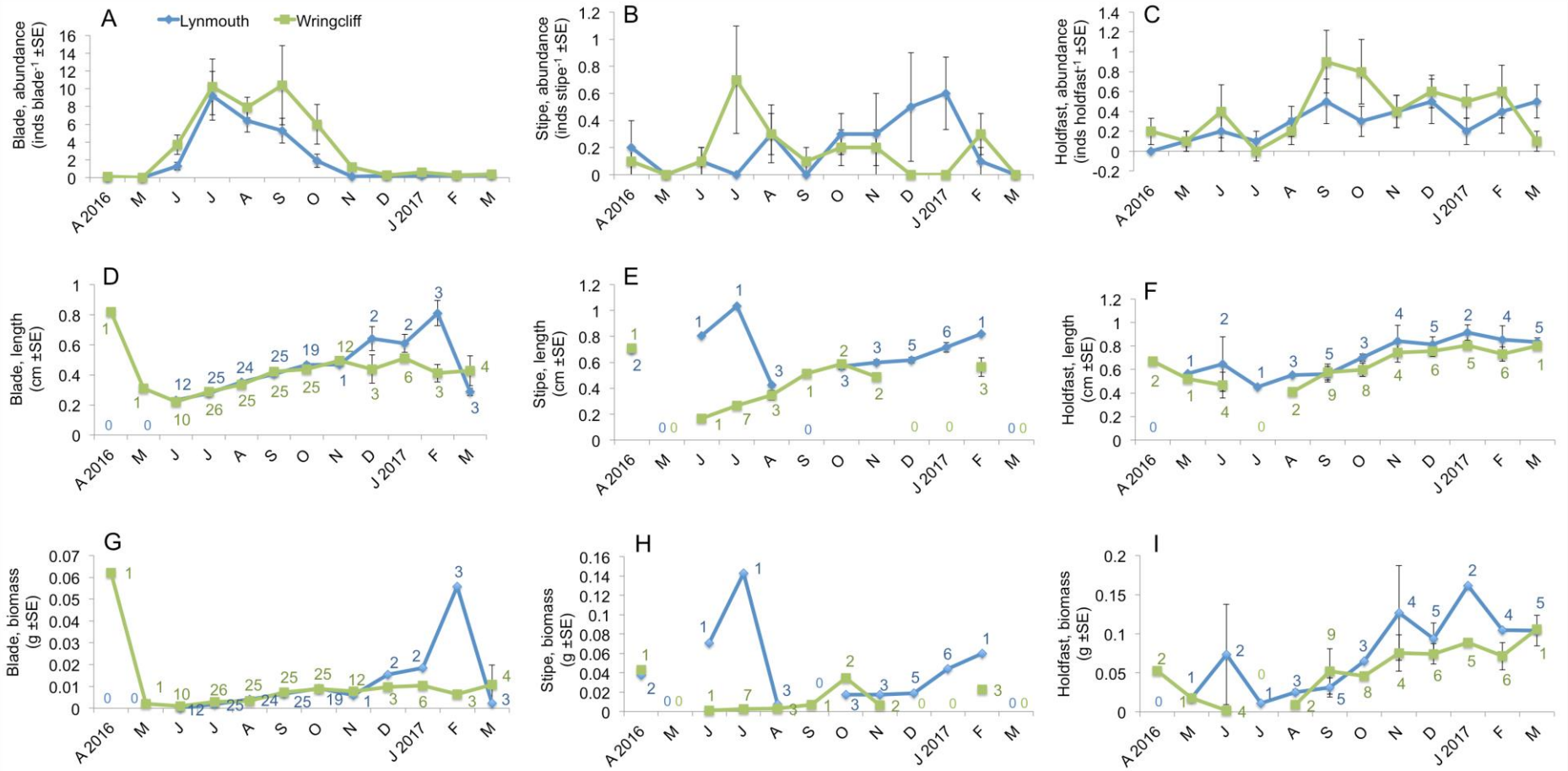


Fig. 4

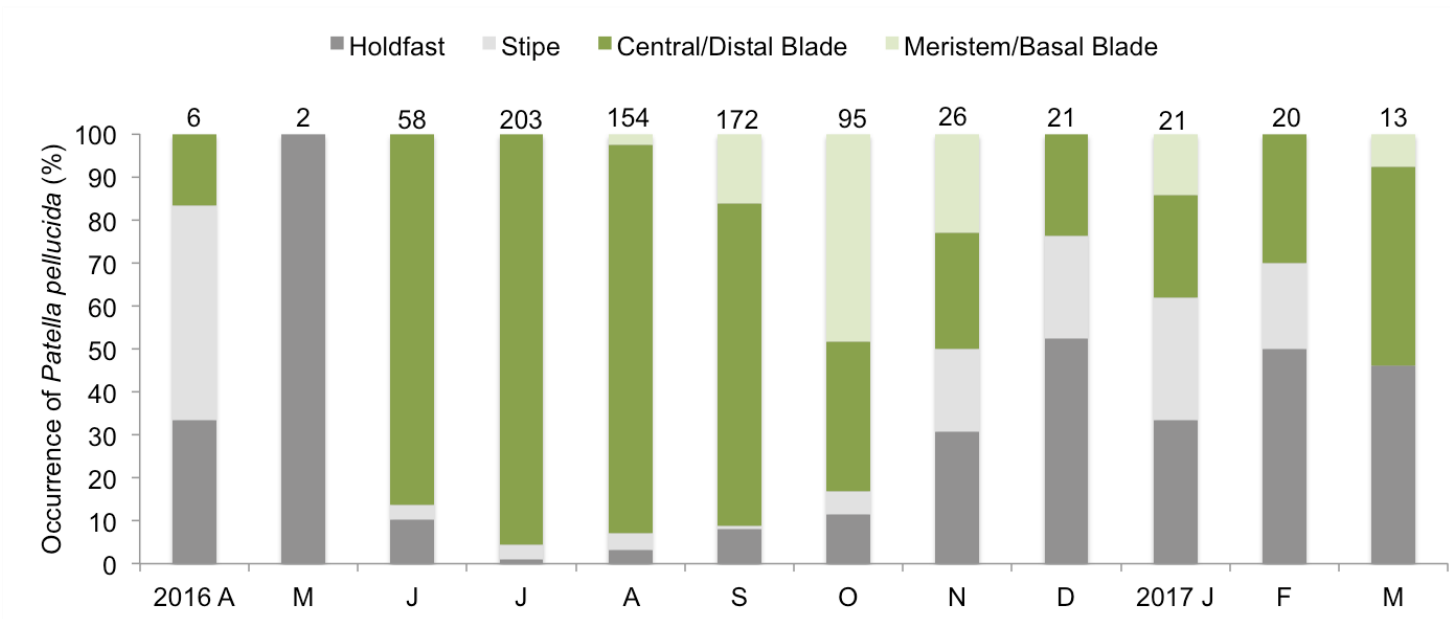


Fig. 5

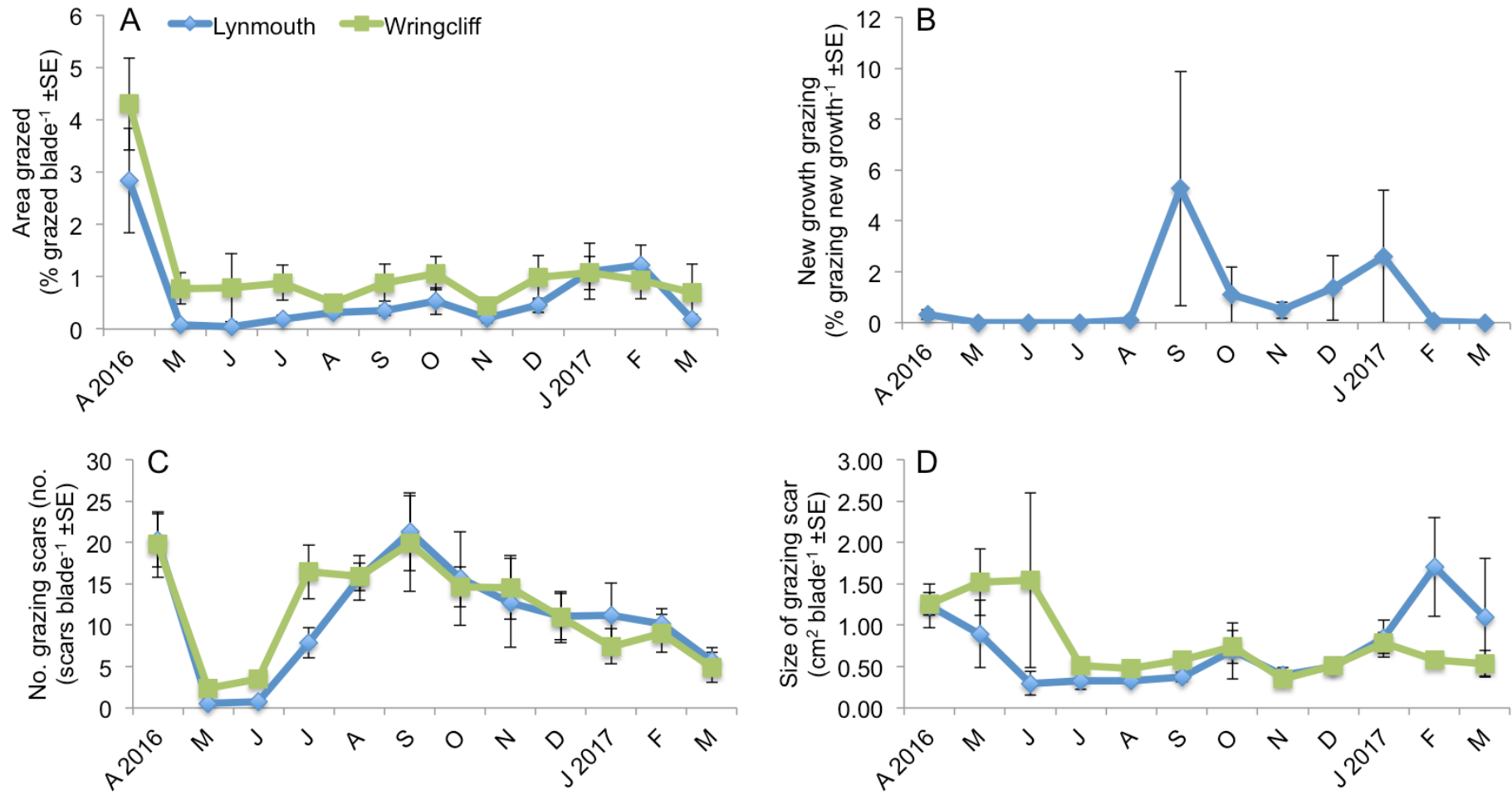


Fig. 6



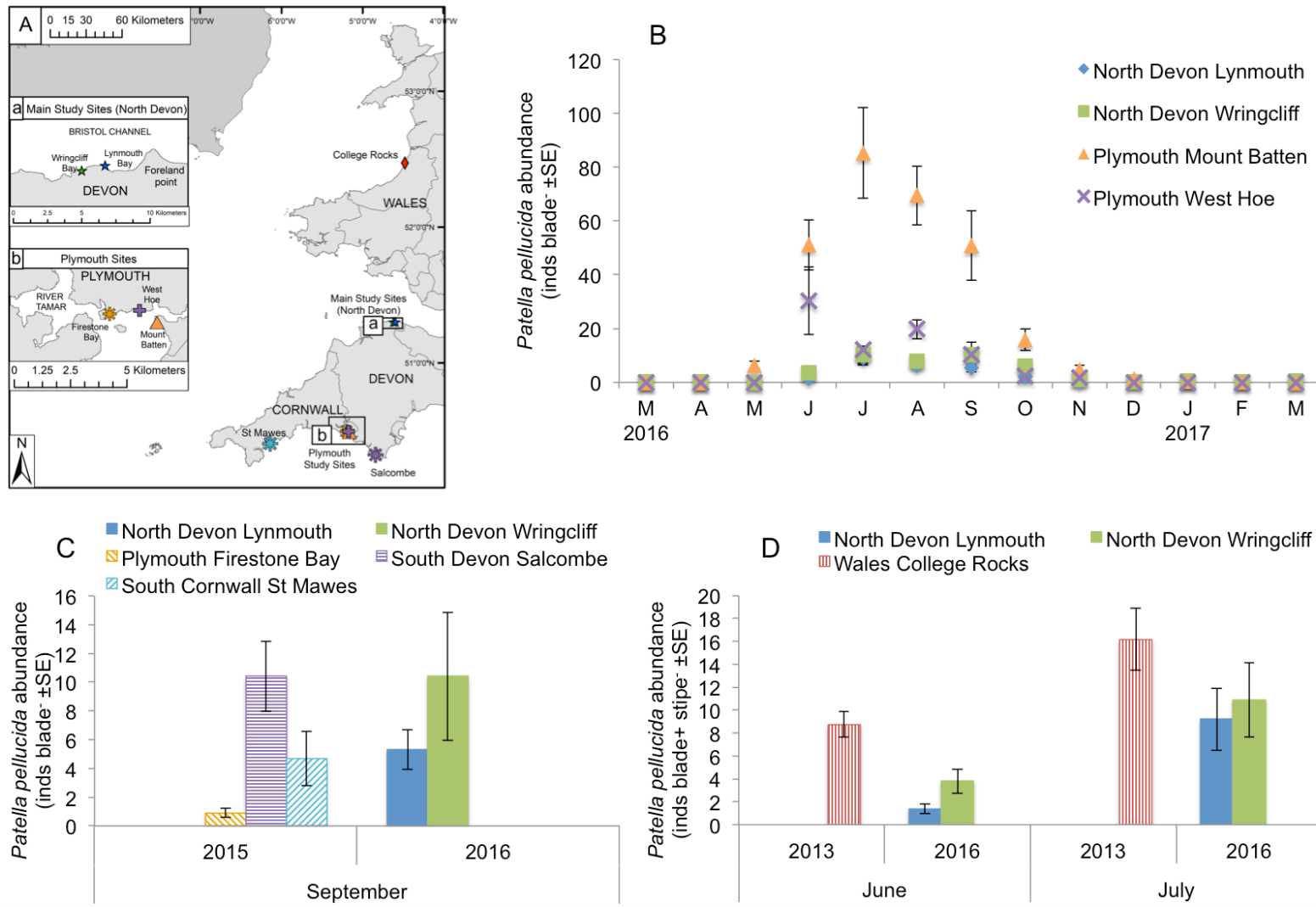


Fig. 7