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1 RUNNING PAGE HEAD: Facilitation under disturbance.

2 **Disturbance alters ecosystem engineering by a canopy-forming alga.**

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23

24 *Canopy-forming furoid algae have an important role as ecosystem engineers on rocky*
25 *intertidal shores, where they increase the abundance of species otherwise limited by*
26 *exposure during low tide. The facilitative relationship between *Ascophyllum nodosum**
27 *and associated organisms was explored using a frond breakage experiment (100%,*
28 *50%, 25%, 0% frond density) in southern England, to assess the consequences of*
29 *disturbance. Understorey substratum temperature was on average 3°C higher in 0%*
30 *and 25% treatments than in intact plots and 50% treatments. An increase of more than*
31 *200% light (as PAR during low tide) was recorded in 0% treatments in comparison to*
32 *other treatments and intact plots (which had similar light levels). Mobile invertebrate*
33 *species richness declined by on average 1 species per m² in the treatments with only 25*
34 *% and 0 % intact fronds, and the abundance of *Littorina obtusata* declined by 2.4-4.2*
35 *individuals per m² in the treatments with 25% and 0% intact fronds. Sessile species,*
36 *including *Osmundea pinnatifida* and encrusting coralline algae, declined by on average*
37 *half in the 0% frond treatments. These results suggest that the ability of *Ascophyllum* to*
38 *mediate environmental conditions to the understorey is the mechanism responsible for*
39 *species distributed in the understorey (autogenic ecosystem engineering). The results of*
40 *this study imply that a pulse disturbance resulting in a 50% breakage of *Ascophyllum**
41 *fronds significantly increases temperature and decreases the abundance of mobile*
42 *invertebrates usually associated with *Ascophyllum*. Sessile species associated with*
43 **Ascophyllum* can, however, withstand a breakage to 75% of *Ascophyllum* fronds.*

44 **KEYWORDS:** algae, *Ascophyllum nodosum*, community, marine, intertidal.

45

46 INTRODUCTION

47 Canopy-forming algae play important roles in habitat provision and primary
48 production in temperate coastal ecosystems worldwide (Littler & Murray, 1974;
49 Thompson *et al.*, 2002). They are, however, under threat from a variety of impacts at
50 local and regional scales including eutrophication (Bonsdorff *et al.*, 1997; Rönnerberg &
51 Bonsdorff, 2004), siltation resulting from urbanisation (Schiel *et al.* 2006; Airoldi &
52 Hawkins, 2007), harvesting (Ang *et al.*, 1996; Zemke-White & Masao, 1999; Ugarte *et*
53 *al.*, 2006), trampling (Povey & Keough, 1991; Keough & Quinn, 1998; Schiel &
54 Taylor, 1999; Araújo *et al.*, 2009) and point source pollution (Bellgrove *et al.*, 1997;
55 Keser *et al.*, 2005). Canopy species are being influenced by the overarching effects of
56 climate change interacting with local impacts, including rising and stormier seas
57 (Underwood, 1998, 1999; Hawkins *et al.*, 2009) and more frequent extreme high
58 temperatures (Thompson *et al.*, 2002; Keser *et al.*, 2005, Wernberg *et al.*, 2016),
59 perhaps exacerbated by greater grazing pressure (Davies *et al.*, 2007; Menge & Olson,
60 1990). Depending on the frequency of recurrence, these perturbations could act as either
61 pulse disturbances (e.g. unusual spike in grazing pressure Cervin & Åberg, 1997), or
62 long-term press disturbance (e.g. rising seas). Here we focus on the community
63 consequences of a pulse disturbance that reduced the density of fronds (simulating
64 breakage by herbivory or storm activity) of *Ascophyllum nodosum* (hereafter referred to
65 as *Ascophyllum*), the major long-lived, canopy-forming macroalga dominating intertidal
66 shores of the Northern Atlantic (Stephenson & Stephenson, 1972; Jenkins *et al.*, 2008) .
67 Observational (Davies *et al.*, 2007; Gollety *et al.*, 2011) and modelling studies
68 (Hawkins *et al.*, 2009) suggests *Ascophyllum* is likely to be increasingly disturbed over
69 the coming decades in response to climate change and local anthropogenic impacts.

70 Individual *Ascophyllum* plants proliferate vegetatively from long-lived holdfasts,
71 and stands are thought to last for centuries, with individual fronds lasting tens of years,
72 creating a perennial habitat for epiphytic and understory organisms (Araújo *et al.*,
73 2009). *Ascophyllum* communities recover slowly after experimental manipulation
74 (Jenkins *et al.* 2004; Ingólfsson & Hawkins, 2005) or harvesting (Ang *et al.*, 1996;
75 Zemke-White & Masao, 1999; Ugarte *et al.*, 2006), taking more than a decade to return
76 to their original state (Ingólfsson & Hawkins, 2008).

77 In contrast to previous studies that examined the impacts of complete canopy
78 removal (Bertness & Leonard, 1997; Jenkins *et al.*, 1999a; b; c; Petraitis & Dudgeon,
79 1999; Jenkins *et al.*, 2004), we were interested in the impacts of partial frond loss, as
80 might result from a pulse disturbance such as overgrazing, or an extreme weather event
81 (e.g. heat wave, storm). The impacts of pulse disturbances resulting in partial canopy
82 loss have been investigated for the fucoids *Hormosira banksii* (Schiel and Lilley 2007)
83 and *Fucus gardneri* (Speidel *et al.*, 2001), though have not previously been undertaken
84 on *Ascophyllum* canopies or fronds.

85 Much attention has been given to press disturbances such as increased
86 temperature due to climate change (Keser *et al.*, 2005; Mieszkowska *et al.*, 2007),
87 increases in grazing pressure (Pavia & Toth, 2000; Davies *et al.*, 2007), and trampling
88 (Araújo *et al.*, 2009), but a single pulse disturbance in full canopies can have long-term
89 consequences at a local scale (Ingólfsson & Hawkins, 2008; Wernberg *et al.*, 2016).

90 Whilst full canopies of *Ascophyllum* can play an autogenic ecosystem engineering
91 (*sensu* Jones *et al.*, 1994) role, we were interested in assessing the conditions under
92 which this role breaks down, or the threshold frond density beyond which *Ascophyllum*
93 ceases to be an effective ecosystem engineer. Specifically we tested the following
94 hypotheses: (1) Temperature and light on the substratum will increase in proportion to

95 frond reduction; (2) Changes in community composition will be proportional to frond
96 reduction. Alternatively, (3) there is a threshold density of intact fronds below which
97 *Ascophyllum* ceases to modulate temperature and light, with community composition
98 showing a similar threshold.

99 MATERIALS AND METHODS

100 **Spatial variation in assemblages associated with *Ascophyllum nodosum***

101 Three sites in southern England were initially surveyed in summer 2006: Batten
102 Bay (Turnchapel) within Plymouth Sound (50°21'27"N 4°07'38"W), and two sites near
103 the township of Looe (50°20'41"N, 4°27'08"W), hereafter referred to as 'Looe' and
104 'Hannafore Point'. All sites consisted of gently sloping wave-sheltered sedimentary
105 rock platforms dominated at the mid-shore level by extensive canopies of *Ascophyllum*,
106 inter-dispersed with patches of *Fucus serratus* and *Fucus vesiculosus*.

107 To assess the spatial variation in assemblages associated with a full canopy of
108 *Ascophyllum*, all three sites were surveyed. Thirty replicate, haphazardly-placed
109 quadrats (0.3 x 0.3 m, appropriate to the scale of the macrofauna) with > 95 %
110 *Ascophyllum* canopy cover (naturally lower cover canopies did not occur), were
111 quantitatively sampled at each site for percentage cover of algae and sessile animals
112 (using 49 point-intercepts, see Jenkins *et al.*, 2005) and the abundance of individual
113 mobile macroinvertebrates (defined as those > 5 mm length), which were counted
114 directly. Where algae and sessile animals occurred in quadrats but not under point-
115 intercepts, they were recorded as present to account for rare species. In contrast to
116 previous work that only examined a limited suite of species (Boaden & Dring, 1980;
117 Bertness & Leonard, 1997; Jenkins *et al.*, 1999a; 1999c; Leonard, 1999; Petraitis &
118 Dudgeon, 1999, Speidel *et al.*, 2001) or took a functional group response (e.g.
119 'understorey species' Araújo *et al.*, 2009), a complete inventory of the macrofauna and

120 understorey algae of *Ascophyllum* stands was made and whole community responses
121 measured (see also: Gollety *et al.*, 2011). The percentage covers of algal taxa were
122 recorded as two separate layers: the canopy layer, and the understorey layer, which was
123 revealed by gently moving the canopy aside.

124 **Effects of a pulse disturbance reducing densities of *Ascophyllum* fronds on the**
125 **physical environment and associated assemblages**

126 A manipulative field experiment was conducted to simultaneously test the
127 hypotheses that: (1) temperature and light on the substratum will increase in proportion
128 to frond reduction; (2) changes in community composition will be proportional to frond
129 reduction; or alternatively, (3) there is a threshold density of intact fronds below which
130 *Ascophyllum* ceases to modulate temperature and light, with community composition
131 showing a similar threshold. Hannafore Point was selected as the best site for
132 experimental manipulation as it had an extensive bed of *Ascophyllum*, allowing good
133 separation between sample plots, and it was easily accessible during low tide. Twenty,
134 haphazardly-placed, fixed 4-m² plots were established within a reef area of
135 approximately 2000 m², and labelled with plastic tags fixed with stainless steel screws
136 into bedrock. All plots initially had > 95 % *Ascophyllum* cover and five replicates (all
137 replicates are at the plot level) were assigned randomly to three frond reduction
138 treatments and one unmanipulated control. The *Ascophyllum* holdfast occurs as a
139 perennial basal disc from which multiple fronds arise directly in a clump, and can
140 regrow after disturbance (Ugarte *et al.*, 2006). The fronds are often very long (≥ 80 cm
141 at our sites) and can create different amounts of canopy cover during low tide
142 depending on where they have fallen on the receding tide. Therefore to allow a
143 consistent disturbance to be applied between plots (mimicking frond breakage e.g. due
144 to herbivory or storm activity) the frond density near the holdfast (rather than the

145 percentage canopy cover) was manipulated. In July 2006, fronds in each holdfast clump
146 were trimmed and removed to create the following treatments: 0 % intact fronds (all
147 fronds were removed), 25 % intact fronds (75 % of fronds were removed), 50 % intact
148 fronds (50 % of fronds were removed) and 100 % intact fronds (a control with
149 unmanipulated frond densities). It is important to emphasise that the treatments
150 represent the densities of intact fronds relative to the original frond densities and do not
151 necessarily correspond to a linear relationship with canopy percentage cover. For each
152 removal treatment, the fronds were cut at the base with garden secateurs to no more
153 than 10 cm above the rock surface, to reduce frond density whilst still allowing for
154 vegetative regeneration. Although these short fronds remained in all treatments
155 throughout the experiment, they did not grow above 10 cm in length and no
156 macroinvertebrates were recorded (unpublished data) using it as habitat. Any fronds
157 able to sweep into the treatment plots from outside plants were trimmed back to prevent
158 edge effects.

159 EFFECTS ON PHYSICAL ENVIRONMENT: TEMPERATURE AND LIGHT

160 Temperature was recorded on the substratum (under any canopy algae) of each
161 experimental plot using a standard waterproof aquarium thermometer to the nearest
162 0.1°C on all sampling visits. Underwater TidBit Stowaway temperature data loggers
163 (Onset, Bourne, Massachusetts, USA) were attached by bolts to the rock in 6 plots (6
164 loggers unevenly spread over 4 treatments, n = 1-2 due to limited availability) to
165 establish minimum and maximum temperatures within canopy treatments; these were
166 set to record every 10 minutes over a 3-week period (2/8/06-23/8/06, summer). Light
167 was recorded in all plots at sampling visits 7, 21 and 36 days as Photosynthetically
168 Active Radiation (PAR) under the canopy (or simply on the substratum in 0 % intact-
169 frond plots) using a LI-COR-250 (LI-COR, Lincoln, Nebraska, USA) meter with a

170 waterproof sensor. All sampling was undertaken during daylight hours at low tide
171 (summer sampling predominantly around midday). Further physical measurements were
172 not taken on other sampling dates due to logistical constraints.

173 EFFECTS ON ASSOCIATED ASSEMBLAGES: MOBILE AND SESSILE MACROINVERTEBRATES 174 AND MACROALGAE

175 The macroinvertebrate and macroalgal assemblages in each treatment were
176 sampled using two 0.3 x 0.3 m sub-quadrats placed in the centre of the plot (fixed
177 position, marked with a screw; randomised positioning was not possible without
178 introducing inconsistencies in substratum complexity). Abundances of macroalgae,
179 sessile and mobile macroinvertebrates in experimental plots were sampled 4 days before
180 the manipulation (half of the plots were sampled on one day, half the following day due
181 to logistical constraints, 19-20/6/2006) and 7, 21, 36, 69 and 272 days thereafter. Data
182 from sub-quadrats were averaged to give one value per plot (n = 5 per treatment) to
183 avoid pseudoreplication.

184 **Data analysis**

185 Multivariate analyses on species abundance and cover data (analysed separately)
186 were used to compare 1) assemblages across sites (> 95 % *Ascophyllum* cover quadrats)
187 at Hannafore Point (experiment site), Looe and Batten Bay; and 2) assemblages among
188 experimental treatments at Hannafore Point. Differences between groups were
189 visualised with nMDS based on Bray-Curtis similarities and ANOSIM identified the
190 relative range of dissimilarities between groups (Bonferroni correction was applied,
191 Quinn & Keough, 2002). SIMPER was applied to identify which taxa contributed most
192 to the patterns identified in the ANOSIM and nMDS (contributions > 10 % are
193 reported). All multivariate statistics were performed using Primer v7.

194 Univariate analyses comparing abundances of individual taxa in quadrats with
195 naturally < 95 % canopy-cover of *Ascophyllum* between sites involved a single-factor
196 ANOVA (Quinn & Keough, 2002) with Site as a random factor (Hannafore Point,
197 Looe, and Batten Bay). To determine which taxa and abiotic factors were affected by an
198 experimental reduction of *Ascophyllum* fronds, differences among experimental
199 treatments were analysed using a single-factor repeated-measures ANOVA (hereafter
200 rmANOVA) (Quinn & Keough, 2002) with Treatment as a fixed factor. Response
201 variables included species/taxon richness, individual species abundances, light and
202 temperature. Where treatment x time interactions were significant, a one-way ANOVA
203 and Tukey's test was undertaken for each sampling date to explain the differences
204 between canopy controls and treatments (Quinn & Keough, 2002). All univariate tests
205 were performed using SYSTAT v13.

206 Probability distribution plots were examined to visually test for normality of
207 data, and residual plots were examined for homogeneity of variance (Quinn & Keough,
208 2002). Data were transformed (invertebrate counts: square root; percentage cover: log
209 (x +1)) where necessary to meet these assumptions. Where sphericity was not met in
210 repeated-measures ANOVA, the Greenhouse-Geisser adjusted *P*-values were used
211 (Quinn & Keough, 2002).

212 RESULTS

213 **Spatial variation in assemblages associated with *Ascophyllum nodosum***

214 The assemblages of mobile invertebrates (ANOSIM, Global $R = 0.155$, $P =$
215 0.001) and sessile invertebrates and algae (Global $R = 0.463$, $P = 0.001$) differed
216 amongst sites and all three sites were distinct ($P = 0.001$ for all pairwise comparisons).
217 However, while statistically significant, the differences in the mobile invertebrate
218 assemblages among sites were only slight (indicated by Global R and pairwise R -values

219 < 0.2). The periwinkles *Littorina littorea* and *Littorina obtusata*, and the topshell
220 *Phorcus lineatus* differed amongst sites (ANOVA; $F_{2,87} = 15.991$, $P < 0.001$; $F_{2,87} =$
221 5.469 , $P = 0.006$; $F_{2,87} = 11.310$, $P < 0.001$; respectively). *Littorina littorea* accounted
222 for 19-23% of the variation in mobile invertebrate assemblages among sites (mean
223 \pm SEM: 1.94 ± 0.12 , 14.4 ± 0.35 , 11.1 ± 0.40 per m² at each of Hannafore Point, Looe and
224 Batten Bay, respectively; SIMPER). *Littorina obtusata* accounted for 18-19% of the
225 variation in mobile invertebrate assemblages among sites (mean \pm SEM: 13.3 ± 0.30 ,
226 13.7 ± 0.28 , 7.8 ± 0.21 per m² at each of Hannafore Point, Looe and Batten Bay,
227 respectively; SIMPER). *Phorcus lineatus* accounted for 11-12% of the variation in
228 mobile invertebrate assemblages when comparing Hannafore Point and Looe with
229 Batten Bay (mean \pm SEM: 0.56 ± 0.12 , 0.78 ± 0.10 , 5.9 ± 0.25 per m² at each of
230 Hannafore Point, Looe and Batten Bay, respectively; SIMPER). Variability in the
231 abundances of *Patella* spp., *Gibbula cinerera* and *Actinia equina* accounted for a further
232 13-19% of the variation in mobile invertebrate assemblages (SIMPER) but there were
233 no differences in their mean abundances among sites (ANOVA; $F_{2,87} = 0.329$, $P =$
234 0.720 ; $F_{2,87} = 0.841$, $P = 0.435$; $F_{2,87} = 0.602$, $P = 0.550$; respectively).

235 The differences in sessile invertebrate and algal assemblages among sites were
236 stronger than those for mobile invertebrates (indicated by Global R and pairwise R-
237 values between 0.3-0.6 for sessile species). Univariate analyses confirmed differences in
238 the abundances of these species among sites, with Hannafore Point having the highest
239 cover of *Spirorbis spirorbis* (ANOVA; $F_{2,87} = 17.3$, $P < 0.001$, mean 2.7 % \pm 0.75)
240 compared with Looe (mean 2 % \pm 0.70) and Batten Bay (mean 0.5 % \pm 0.30). *Osmundea*
241 *pinnatifida*, encrusting coralline algae and bare rock were less abundant at Hannafore
242 Point (mean 0.1 % \pm 0.12, < 0.1 % \pm 0.03 and < 0.25 % \pm 0.12, respectively) compared
243 with both Looe (mean 2.7 % \pm 0.39, 4.8 % \pm 0.42 and 2.8 % \pm 0.45, respectively) and

244 Batten Bay (mean 1.3 % \pm 0.37, 3.8 % \pm 0.46 and 2.3 % \pm 0.53, respectively; ANOVA;
245 $F_{2,87} = 16.4$, $P < 0.001$). Other sessile taxa accounted for less than 10 % of the
246 cumulative variation among sites (SIMPER) and were not investigated further.

247 **Effects of a pulse disturbance reducing densities of *Ascophyllum* fronds on the**
248 **physical environment and associated assemblages**

249 EFFECTS ON PHYSICAL ENVIRONMENT: TEMPERATURE AND LIGHT

250 Temperatures recorded in the 50 % intact-frond treatment did not differ from
251 those found in control 100 % intact-frond plots (mean 20°C \pm 0.7 and 19°C \pm 0.5
252 respectively, Table 1: $P > 0.05$, Figure 1). The 25 % intact-frond treatment had
253 increased mean temperatures, at least 1°C above that recorded in the 100 % intact-frond
254 control (Table 1: $P < 0.05$, Figure 1). The 0 % and 25 % intact-frond treatments did not
255 differ from each other with respect to temperature ($P > 0.05$) but both had increased
256 mean temperatures, at least 1°C above that recorded in the 100% intact-frond control.
257 The differences in average temperatures among treatments appear of a smaller
258 magnitude in autumn and winter, but this was not supported statistically
259 (time*treatment term Table 1, Figure 1). The variation in temperatures among
260 treatments was consistent over time with the maximum daily temperatures recorded in
261 plots over a three-week period (maximum, minimum and average temperatures are
262 illustrated in Appendix C; no analysis possible due to low replication). Maximum daily
263 temperatures recorded over this same period were lowest in 50 % and 100 % intact-
264 frond treatments, and highest in both the 0 % and 25 % intact-frond treatments
265 (Appendix C).

266 Available light (as PAR) in plots only increased after complete frond removal (0
267 % intact fronds) when compared with the 100 % intact-fronds control (Table 1, Figure
268 2). A trend towards increased light in the 25 % intact-fronds treatment (Figure 2)

269 relative to 100 % intact-fronds control was evident when examining the means, but was
270 not statistically significant ($P > 0.05$). Consistent with the patterns of variability in
271 temperature among treatments, there was greater variability in available light amongst
272 low frond-density treatments (0 % and 25 % intact fronds) compared to higher frond-
273 density treatments (50 % and 100% intact fronds) that had consistently low light levels
274 (Figure 2).

275 EFFECTS OF ASSOCIATED ASSEMBLAGES: MOBILE AND SESSILE MACROINVERTEBRATES
276 AND MACROALGAE

277 Manipulation of the density of *Ascophyllum* fronds resulted in variable levels of
278 canopy cover at low tide over time and the degree of disturbance to the fronds did not
279 directly correspond with percentage cover (Table 1, Figure 3). The 50 % and 100 %
280 intact-fronds treatments had similar *Ascophyllum* cover throughout the experiment
281 (Table 1, Figure 3). From 7 to 36 days post-thinning, the 50 % and 100% intact-fronds
282 treatments had an average 85 % *Ascophyllum* cover (Figure 3). Sixty-nine days post-
283 thinning *Ascophyllum* declined to an average 77 % cover in both treatments. The 25 %
284 intact-fronds treatment had lower *Ascophyllum* cover than both the 50 % and 100%
285 intact-fronds treatments, except at day 272 when a decline of *Ascophyllum* in the control
286 and 50 % intact-fronds treatment resulted in similar percentage cover (Table 1, Figure
287 3). The 25 % intact-fronds treatment had much higher (mean ~60 % throughout)
288 *Ascophyllum* cover than the 0 % intact-fronds treatment which had the lowest
289 *Ascophyllum* cover (0 %) of all treatments (Table 1, Figure 3)

290 The assemblages of mobile and sessile taxa found in all plots were similar prior
291 to experimental reductions of *Ascophyllum* (ANOSIM; Global $R < 0$, $P > 0.6$). Between
292 21 and 69 days after manipulation, assemblages of mobile or sessile taxa in the 50 %
293 intact-fronds treatment did not differ from those in the 100 % intact-fronds control

294 (Tables 2 & 3, Appendices A, B, D & E). Up to 70 days post-removal, the 25 % and 0
295 % intact-fronds treatments had different assemblages of mobile and sessile taxa
296 compared with controls (Tables 2 & 3, Appendices A, B, D & E). On the final sampling
297 visit (Day 272, approximately 9 months after the pulse disturbance, 16th April 2007,
298 spring) the mobile invertebrate species assemblages were not different among
299 treatments (Table 3). This reflected partial recovery of *Ascophyllum* in the 0 % intact-
300 fronds treatments (to approximately 25 % canopy cover, Figure 3), and an increase in
301 the percentage cover of the mid-canopy species *Fucus serratus* across all plots
302 (approximately 50% canopy cover, Figure 5C). There were, however, still significant
303 differences after 9 months in the assemblages of sessile taxa in the 0 % intact-fronds
304 treatment compared to both the 25 % and 100 % intact-fronds treatments but the
305 assemblages of sessile taxa in the 50 % intact-fronds treatment did not differ from any
306 other treatments (Appendix A).

307 All of the ten mobile invertebrate species recorded (for full list see Appendix D)
308 were found to contribute to differences identified in the ANOSIM analysis between the
309 treatment types, although average abundances among treatment types and at different
310 visits varied (further explained by univariate analyses below). Of all the sessile taxa
311 (and/or cover components) sampled, *Fucus serratus*, encrusting corallines, bare rock,
312 *Spirorbis spirorbis*, *Osmundea pinnatifida*, sand-covered rock, *Mastocarpus stellatus*,
313 *Ulva* spp., *Cladophora rupestris*, *Lomentaria articulata*, unidentified red turf and the
314 barnacle *Perforatus perforatus*, were found to contribute to the differences identified
315 between canopy treatments (SIMPER). These individual species and habitat types were
316 analysed using univariate techniques (when they occurred in sufficient abundances) to
317 further identify responses to reduction of *Ascophyllum* (Table 1, Figures 4 & 5).

318 Invertebrate species richness in the 50 % and 100 % intact-fronds treatments
319 were similar on day 7 and 21, with higher average species richness than both the 25 %
320 and 0 % intact-fronds treatments (Table 1, Figure 4A, Tukey's $P < 0.05$). On day 36
321 only the 50 % intact-fronds treatment differed from other treatments, with higher
322 species richness (Table 1, Figure 4A, Tukey's $P < 0.05$). On day 69, the 100 %, 50 %
323 and 25 % intact-fronds treatments had similar average species richness, all higher than
324 the 0 % intact-fronds treatment (Table 1, Figure 4A, Tukey's $P < 0.05$). At the end of
325 the experiment, the 0 % intact-fronds treatment had lower species richness than the 50
326 % and 100 % intact-fronds treatments (Table 1, Figure 4A, Tukey's $P < 0.05$), but did
327 not differ from the 25 % intact-fronds treatment. The 25 % intact-fronds treatment had
328 similar species richness to the 50 % intact-fronds treatment, but remained lower than the
329 100% intact-frond control (Table 1, Figure 4A, Tukey's $P < 0.05$).

330 *Species-specific responses to disturbance*

331 The abundance of the periwinkle *Littorina obtusata* differed among treatments
332 throughout the study (Table 1, Figure 4B). On day 7 the 25 % and 0 % intact-fronds
333 treatments had less than half the abundance ($\sim 1/0.09 \text{ m}^2$ c.f. $\sim 4/0.09 \text{ m}^2$) of *L. obtusata*
334 found in the 50 % intact treatments and less than a quarter of that found in the 100 %
335 intact-fronds control ($\sim 10/0.09 \text{ m}^2$, Figure 4B, Tukey's $P < 0.05$). On days 21 and 69,
336 the 50 % and 100 % intact-fronds treatments had similar abundances of *L. obtusata*,
337 which were higher than those recorded in both the 0 % and 25 % intact-fronds
338 treatments (Figure 4B, Tukey's $P < 0.05$). The same pattern was evident on day 36,
339 although not statistically significant (Table 1, Figure 4B). *Littorina obtusata* was more
340 commonly observed on the fronds and holdfasts of *Ascophyllum* than under the canopy
341 on the rock surface. In contrast, the abundance of the congeneric, largely rock-surface-
342 dwelling, *Littorina littorea* did not respond to frond reductions but varied over time

343 (Table 1, Figure 4C). The top shell *Phorcus lineatus* differed in abundance among
344 treatments at different times throughout the study (Table 1, Figure 4D). The abundance
345 of *P. lineatus* in the 0 % intact-fronds treatment was higher than in the 100 % intact-
346 fronds control on days 21 and 36 and higher than that in all other treatments on day 69
347 (Figure 4D, Tukey's $P < 0.05$). The abundance of the top shell *Gibbula umbilicalis*
348 varied among treatments on different sampling visits (Table 1, Figure 4E). On days 7
349 and 21 there were fewer *G. umbilicalis* in the 0 % intact-fronds treatment compared to
350 other treatments; although no differences were identified on other sampling visits (Table
351 1, Figure 4E, Tukey's $P < 0.05$).

352 Encrusting coralline algae did not differ ($P = 0.066$) in cover among treatments,
353 though varied temporally, with a decline occurring on days 69 and 272 in all treatments
354 (Table 1, Figure 5A). Although not quantified, a decline of the integrity of the
355 encrusting coralline algae was observed in the 0 % intact-fronds treatment, with a loss
356 of pigment and surface peeling. Similarly, the cover of the turf-forming alga *Osmundea*
357 *pinnatifida* did not vary among treatments, but varied over time, increasing in
358 abundance on day 272 in the 100 %, 50 % and 25 % intact-fronds treatments (Table 1,
359 Figure 5B). The differences in abundance of the furoid alga, *Fucus serratus*, among
360 treatments and the control were not consistent over time (Table 1, Figure 5C). *Fucus*
361 *serratus* had a higher percentage cover in the 100 % intact-fronds control during day 7
362 compared to all other treatments; but no difference in percentage cover among
363 treatments on other days (Table 1, Figure 5C, Tukey's $P < 0.05$). On day 272 a decline
364 in abundance of *F. serratus* occurred in the control and 25 % intact-fronds treatment
365 and an increase occurred in the 0 % intact-frond treatment (Table 1, Figure 5C). The
366 percentage cover of the algae *Ulva* spp. only differed among treatments and the control
367 plots on day 69 (Table 1, Figure 5D), with greater cover in the 100 % intact-fronds

368 control (average 33 %) compared with the 50 % and 25 % intact-fronds treatments (both
369 average 16 %, Tukey's $P < 0.05$), *Ulva* spp. were not recorded in the control plots. *Ulva*
370 spp. remained below 5 % cover throughout the rest of the study. Univariate analyses of
371 additional taxa found during the study were not possible due to low abundances.

372 DISCUSSION

373 Theory predicts that the importance or role of a species as an ecosystem
374 engineer will depend on interactions and thresholds between environmental stress and a
375 suite of morphological and ecological traits (Bruno and Bertness, 2001, Crain and
376 Bertness, 2006, Jones et al. 1994, 1997). Thus whilst a species may be considered to be
377 an autogenic ecosystem engineer under one set of conditions (e.g. full canopy cover), it
378 may cease to do so if these conditions break down. Intertidal rocky shores are
379 particularly stressful environments with tidal cycles of emersion and gradients in
380 physiological stress (e.g. desiccation, temperature, UV). Whilst full canopies of
381 *Ascophyllum* have been demonstrated to act as autogenic ecosystem engineers and
382 facilitate understorey biodiversity (Jenkins *et al.* 1999a; b; c; Jenkins & Hawkins 2003;
383 Jenkins *et al.* 2004), we have demonstrated that this engineering role can be
384 compromised by a pulse disturbance that reduces frond density and the ability of the
385 canopy to modulate the physical environment. For *Ascophyllum* to act effectively as an
386 autogenic ecosystem engineer at Hannafore Point, we found that at least 50 % of the
387 fronds (corresponding with 70-98 % *Ascophyllum* cover) need to remain in order for
388 temperature to remain cooler and for the associated invertebrate community to persist.
389 With only 25 % intact-fronds remaining (corresponding with 50-70 % *Ascophyllum*
390 cover), macroalgae and sessile invertebrates could persist at Hannafore Point but at
391 reduced abundances.

392 *Ascophyllum* altered the physical environment by reducing light and temperature
393 within the understorey, but the effect varied amongst pulse disturbance treatments and
394 was not proportional to frond densities. *Ascophyllum* reduced temperature in the 50 %
395 and 100 % intact-fronds treatments. The maximum temperatures recorded using the
396 continuous data loggers also suggest that the canopy may buffer from temperature
397 extremes since the 50 % and 100 % intact-fronds treatments had the least variation in
398 temperature. This more stable temperature is likely to exert less physical stress on
399 species associating with the canopy and improve survival (Crisp 1964). *Ascophyllum*
400 also filtered light to the understorey in all plots except those in which fronds were
401 completely removed (0 % intact-fronds treatment). Even the 25 % intact-fronds
402 treatment had an average light intensity six times lower than in the 0 % intact-fronds
403 treatment. Unexpectedly, percentage cover of *Ascophyllum* was not directly
404 proportional to the density of fronds, and declined in all treatments with intact fronds
405 over time. Throughout the experiment the percentage cover of *Ascophyllum* in the 50 %
406 and 100 % intact-fronds treatments were similarly high, suggesting that *Ascophyllum*
407 can withstand high levels of frond breakage whilst still maintaining a high canopy
408 percentage cover and its ecosystem engineering function. This pattern tracked an
409 ongoing decline in canopy cover in 100 % intact-frond controls, suggesting additional
410 natural influences on canopy cover occurring at this site, which may influence
411 ecosystem engineering function.

412 A marked short-term disturbance effect was observed seven days after the
413 treatments were applied with species assemblages varying between all treatments and
414 the control. Changes in species assemblages related to stable temperatures in controls
415 compared with increased temperatures in all treatments. Light intensity to the
416 understorey increased as fronds were reduced, although the 50 % and 25 % intact-

417 fronds treatments had similar light intensities, and the 0 % intact-fronds treatment had
418 the highest light intensity (more than double the highest recorded in the 25-50 %
419 treatments). This short-term response for all data suggests the assemblage needs
420 somewhere between 7 and 21 days to recover from a single disturbance. This contrasts
421 with the findings of Speidel *et al.* (2001) in Washington where abundances of
422 littorinids, limpets and ephemeral algae did not differ among canopy reductions of
423 *Fucus gardneri* despite rock temperatures being reduced by up to 7°C in all plots
424 containing canopy algae. The differences in responses amongst these studies (Speidel *et*
425 *al.* 2001 & this study) suggest that either particular species in Washington and the UK
426 respond differently to canopy presence and/or rock temperature, or that rock
427 temperature is not the driver of macroinvertebrate species patterns.

428 Our investigation found general similarities in responses of the community to
429 those in *Ascophyllum* complete canopy-removal studies undertaken by Jenkins *et al.* on
430 the Isle of Man (Jenkins *et al.* 1999a; b; c; Jenkins *et al.* 2004). In addition, we found
431 that taxon richness was higher in the 100 % and 50 % intact-fronds treatments when
432 compared with the 25 % and 0 % intact-fronds treatments. This pattern may also be
433 related to differences in temperature amongst treatments. The algal turfs (e.g.
434 *Osmundea pinnatifida*, *Chondrus crispus*) in the understorey of removed canopies on
435 the Isle of Man (Jenkins *et al.*, 1999b) were found to degrade once the canopy was lost.
436 We also found this at Hannafore Point (*Lomentaria* sp. and *Cladophora* sp), but the
437 species differed. Ingolfsson and Hawkins (2008) also found *Cladophora* sp. was lost
438 following *Ascophyllum* removal in Iceland, and this loss persisted for 17 years despite
439 canopy recovery. These studies in multiple locations suggest that a decline of turf-
440 forming algae is a common response to *Ascophyllum* canopy loss and is likely a
441 response to increased light and temperature when the canopy is removed (this study).

442 Although differences in abundance of *Littorina obtusata* occurred immediately
443 after removal, subsequently abundances did not differ between the 50 % and 100 %
444 intact-fronds treatments, but *L. obtusata* was much less common in the 25 % and 0 %
445 intact-fronds treatments. *L. obtusata* occurs on the *Ascophyllum* canopy (Watson &
446 Norton, 1987; Williams, 1992) and even displays a facilitative relationship with its
447 ‘host’, as its grazing of tissue causes the alga to produce phlorotannins, reducing its
448 susceptibility to grazing by other invertebrates (Pavia & Toth, 2000). Observations at all
449 sites sampled in this study found a high number of *L. obtusata* attached to the fronds of
450 *Ascophyllum* and since thinning and removal directly reduced fronds, this may explain
451 lower abundances in the 25 % and 0 % intact-fronds treatments, especially at the
452 beginning of the experiment.

453 Many of the taxa with reduced abundances in the 0 % intact-fronds treatment
454 were algae, suggesting that either higher light levels (Wiencke & Davenport, 1988; see
455 Kubler & Raven, 1994; Irving *et al.*, 2004), or increased herbivory by grazers such as
456 *Phorcus lineatus* (Mieszkowska *et al.*, 2007), impacted their survival in areas where the
457 density of fronds was greatly reduced. Figueiredo *et al.* (2000) reported that crustose
458 corallines are common under algal canopies on rocky shores and in our study encrusting
459 corallines bleached and peeled away from the surface in the 0 % intact-fronds treatment,
460 suggesting they are sensitive to high light, drying, temperature exposure or a
461 combination.

462 Disturbances that may result in thinning of *Ascophyllum* canopy include
463 increased grazing intensity (species introductions or range shifts, Davies *et al.*, 2007),
464 climate change (reduced growth and recruitment), and trampling and harvesting
465 (Boaden & Dring, 1980; Keser *et al.*, 2005; Araújo *et al.*, 2009; Hawkins *et al.*, 2009).
466 Climate change is likely to affect *Ascophyllum* (Davies *et al.*, 2007) and shore

467 communities in a multitude of ways such as increased sea and air temperatures stressing
468 its physiological processes (Svensson *et al.*, 2009), increased storm activity causing
469 physical damage, and the immigration and emigration of species that may compete or
470 alter species interactions as local conditions change (e.g. increased grazer diversity and
471 abundance, Hawkins *et al.*, 2009). The only published studies to examine thinning of
472 *Ascophyllum* canopies were undertaken in Portugal and examined press disturbances by
473 human trampling (Araújo *et al.*, 2009; Bertocci *et al.*, 2011; Araújo *et al.*, 2012). Araújo
474 *et al.* (2009) found trampling (at disturbance levels resulting in similar *Ascophyllum*
475 cover to our 25 % intact-fronds treatment) negatively impacted the community
476 associated with *Ascophyllum*. Consistent with these studies (Araújo *et al.*, 2009;
477 Bertocci *et al.*, 2011, Araújo *et al.*, 2012), we found a decreased abundance of some
478 understory species, but did not find increased *Ulva* spp. recruiting into 0 % intact-
479 fronds plots as seen in Portugal (Araújo *et al.*, 2009). In contrast, *Ulva* spp. were in low
480 abundance throughout the study at Hannafore Point with the exception of September
481 2006 (summer) where abundance spiked in all treatments except the 0 % intact-fronds
482 treatment. This is likely to be due to differences between sites and times of disturbance.
483 Thinning of perennial intertidal furoid algae was also investigated in New Zealand by
484 Schiel and Lilley (2007) on the Australasian species *Hormosira banksii*. Schiel and
485 Lilley (2007) found significant stepwise responses when comparing 0 %, 25 % and 50
486 % canopy cover treatments to the 75 % canopy and unmanipulated control plots. This
487 matches with our findings at Hannafore Point where the macroinvertebrate assemblages
488 found in our 100 % and 50 % intact-fronds treatments (which correspond, in terms of
489 *Ascophyllum* canopy cover, with their 0 % reduction) differed from those found in the
490 25 % and 0 % intact-fronds treatments (which correspond, in terms of *Ascophyllum*
491 canopy cover, with their 75 % and 100 % reductions). Given the similarities between

492 our findings and other studies, management (e.g. restricted site access for sensitive
493 locations) may be necessary to maintain the ecosystem engineering function of
494 *Ascophyllum*, especially as frond breakage due to multiple climate change impacts (e.g.
495 increased desiccation/grazing pressure/storms) is predicted to increase (Hawkins *et al.*
496 2009).

497 Despite the spatial variation in species assemblages from undisturbed canopies
498 detected between our study sites, other thinning studies with spatially variable
499 assemblages have shown similar general patterns within the understory including the
500 loss of sensitive algae (e.g. non-geniculate corallines, Lilley, 2004), a decline in species
501 richness (Araújo *et al.*, 2009), and replacement with other species (Jenkins *et al.*, 1999c;
502 Araújo *et al.*, 2009).

503 The results of this study support the general findings of other studies
504 investigating the consequence of *Ascophyllum* canopy disturbance to shore ecology
505 (Jenkins *et al.* 1999a; b; c; Jenkins & Hawkins 2003; Jenkins *et al.* 2004; Ingólfsson &
506 Hawkins 2008), but additionally demonstrate that there is a threshold of disturbance
507 beyond which the autogenic engineering role of *Ascophyllum* is compromised.
508 Reduction of more than 50 % of fronds near the holdfast will reduce its ability to
509 modulate temperature, light and support the understory community assemblage. Given
510 that intact *Ascophyllum* canopies have been shown to support high levels of biodiversity
511 elsewhere (Black & Miller, 1991; Jenkins *et al.*, 1999b; Jenkins *et al.*, 2004; Keser *et*
512 *al.*, 2005; Davies *et al.*, 2008; Ingólfsson & Hawkins, 2008; Watt & Scrosati, 2013)
513 disturbance resulting in frond loss is likely to have widespread consequences, with slow
514 recovery times when less than 50 % of fronds remain intact. Our work demonstrates the
515 values of investigating the conditions under which habitat-forming species may

516 modulate the physical environment and act as autogenic ecosystem engineers to better
517 manage the assemblages and biodiversity that they facilitate.

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697

698 FIGURE LABELS

699 **Fig. 1.** Average temperature \pm SE recorded on substratum beneath canopy layer (where
700 present) within plots through time, n = 5. ● 100 % intact-fronds, ○ 50 % intact-fronds, □
701 25 % intact-fronds, ■ 0 % intact-fronds.

702

703 **Fig. 2.** Average Photosynthetically Active Radiation (PAR) \pm SE recorded on
704 substratum beneath canopy layer (where present) within plots through time, n = 5. ●
705 100 % intact-fronds, ○ 50 % intact-fronds, □ 25 % intact-fronds, ■ 0 % intact-fronds.

706

707 **Fig. 3.** Average percentage cover \pm SE of *Ascophyllum* canopy through time (not
708 including holdfast fronds < 10 cm), n = 5. ● 100 % intact-fronds, ○ 50 % intact-fronds,
709 □ 25 % intact-fronds, ■ 0 % intact-fronds.

710

711 **Fig. 4.** Average abundances of invertebrates \pm SE found in treatment plots through time
712 (per m²), n = 5: (A) species richness; (B) *Littorina obtusata*; (C) *Littorina littorea*; (D)
713 *Phorcus lineatus*; (E) *Gibbula umbilicalis*. ● 100 % intact-fronds, ○ 50 % intact-fronds,
714 □ 25 % intact-fronds, ■ 0 % intact- fronds.

715

716 **Fig. 5.** Average percentage cover of associated algae \pm SE found in treatment plots
717 through time, n = 5: (A) encrusting coralline algae; (B) *Osmondea pinnatifida*; (C)
718 *Fucus serratus*; (D) *Ulva* spp. ● 100 % intact-fronds, ○ 50 % intact-fronds, □ 25 %
719 intact-fronds, ■ 0 % intact-fronds.

TABLES

Table 1. Repeated measures ANOVA comparing changes following disturbance to *Ascophyllum* canopy at Hannafore Point for time, treatment and time x treatment, n = 5. All df are: Treatment = 3(16), Time = 4, Treatment*Time = 12(64); unless indicated beside p-value.

Only Factors with significant p-values are shown. MS_{Residual} and degrees of freedom are provided to allow reconstruction of the full ANOVA table. Statistical significance is indicated in bold, * indicates p-values adjusted to Greenhouse-Geisser Epsilon, ^a indicates significant Tukey’s test (pairwise details described in results text). Algal data are Log (x+1) transformed and Invertebrate data are square root transformed to meet assumptions of normality where necessary.

VARIABLE	MS _{Residual}		P-value		
	Treatment	Time	Time x Treat	Treatment	Time
<i>Ascophyllum</i> canopy cover	293.193	95.897	0.0001 ; df = 15(80)	0.0001	0.0001 ; df = 5(80)
Number of Invertebrate Species	1.231	0.727	0.750	0.002^a	0.008
<i>Littorina obtusata</i>	9.996	4.194	0.189	0.0001^a	0.234
<i>Littorina littorea</i>	0.318	0.084	0.550	0.442	0.0001
<i>Phorcus lineatus</i>	0.044	0.107	0.003^a	0.0001	0.0001
<i>Gibbula umbilicalis</i>	0.240	0.165	0.010^a	0.021	0.001*
Encrusting Coralline Algae	417.910	144.874	0.946	0.066	0.045*
<i>Osmundea pinnatifida</i>	139.083	37.906	0.065*	0.222	0.0001*
<i>Fucus serratus</i>	7.832	2.029	0.033^a	0.303	0.001
<i>Ulva</i> spp.	11.390	133.680	0.0001^a	0.001	0.0001*
Temperature (°C)	2.736	3.182	0.169	0.0001*	0.0001*
PAR (μmol m ⁻² s ⁻¹)	75555.481	37660.959	0.311; df=6	0.002* ;df = 3	0.252;df = 2

Table 2. Pairwise ANOSIM comparing assemblages of sessile taxa (as percentage cover) among treatments (average for 2 sub plots in each treatment area) at each sampling date, n = 5. Data log (x+1) transformed. Statistical significance (indicated by *) adjustment of alpha (Bonferonni correction) to 0.008, relative difference using R is indicated in bold.

Treatments	Day 7		Day 21		Day 36		Day 69		Day 272	
	R	P	R	P	R	P	R	P	R	P
control, F50	0.332	0.024	0	0.460	0.036	0.373	0.228	0.079	0.128	0.159
control, F25	0.316	0.048	0.096	0.239	0.196	0.063	0.064	0.31	0.176	0.135
control, F0	0.556	0.016	0.396	0.024	0.340	0.024	0.904	0.008*	0.7	0.008*
F50, F25	0.012	0.429	-0.228	0.960	-0.012	0.476	-0.016	0.524	-0.048	0.508
F50, F0	0.092	0.246	0.052	0.286	0.052	0.333	0.636	0.008*	0.24	0.063
F25, F0	0.492	0.016	0.26	0.079	0.20	0.175	0.504	0.016	0.388	0.024
GLOBAL R	0.271	0.001	0.1	0.132	0.131	0.066	0.403	0.001	0.252	0.004

Table 3. Pairwise ANOSIM comparing assemblages of mobile invertebrate species (invertebrate assemblage) among treatments (average for 2 sub plots in each treatment area) at each sampling date, n = 5. Data square root transformed. Statistical significance (indicated by*) adjustment of alpha (Bonferonni correction) to 0.008, relative difference using R is indicated in bold.

Treatments	Day 7		Day 21		Day 36		Day 69		Day 272	
	R	P	R	P	R	P	R	P	R	P
control, F50	-0.056	0.611	-0.072	0.651	-0.048	0.635	0.04	0.357	-0.104	0.254
control, F25	0.34	0.008*	0.312	0.024	0.608	0.008*	0.636	0.008*	-0.06	0.635
control, F0	0.628	0.008*	0.648	0.008*	0.368	0.032	0.656	0.008*	0.164	0.183
F50, F25	0.184	0.063	0.264	0.056	0.452	0.016	0.488	0.024	0.004	0.460
F50, F0	0.656	0.008*	0.708	0.008*	0.24	0.071	0.472	0.008*	0.268	0.079
F25, F0	-0.004	0.556	0.396	0.016	-0.06	0.659	0.396	0.016	0.104	0.254
GLOBAL R	0.294	0.005	0.369	0.001	0.256	0.007	0.442	0.001	0.066	0.177

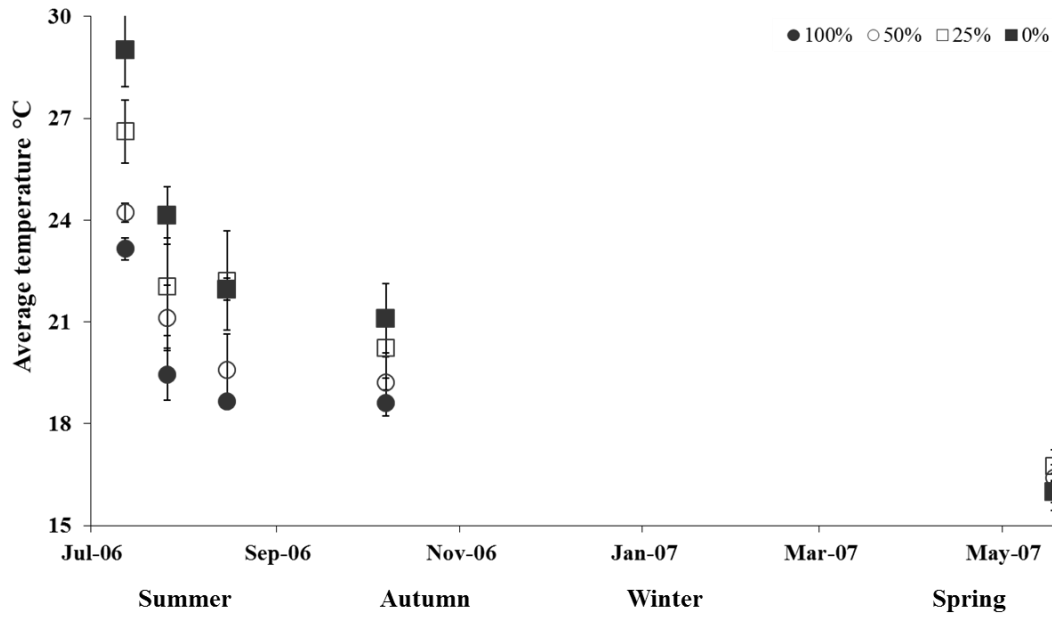


Fig. 1. Average temperature \pm SEM recorded on substratum beneath canopy layer (where present) within plots through time, n = 5.

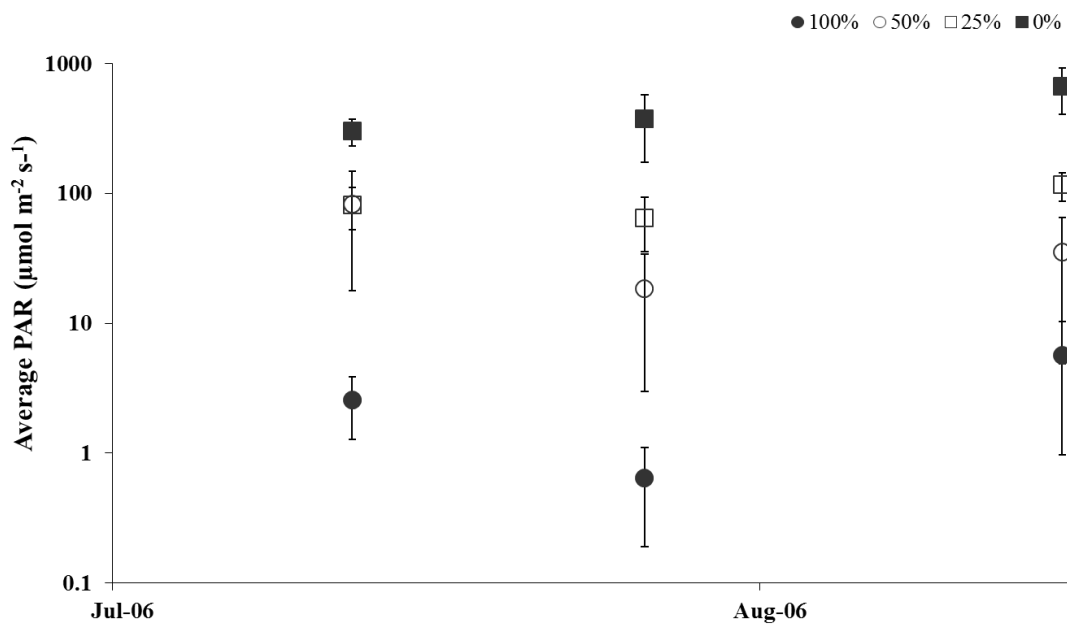


Fig. 2. Average Photosynthetically Active Radiation (PAR) \pm SEM recorded on substratum beneath canopy layer (where present) within plots through time, n = 5.

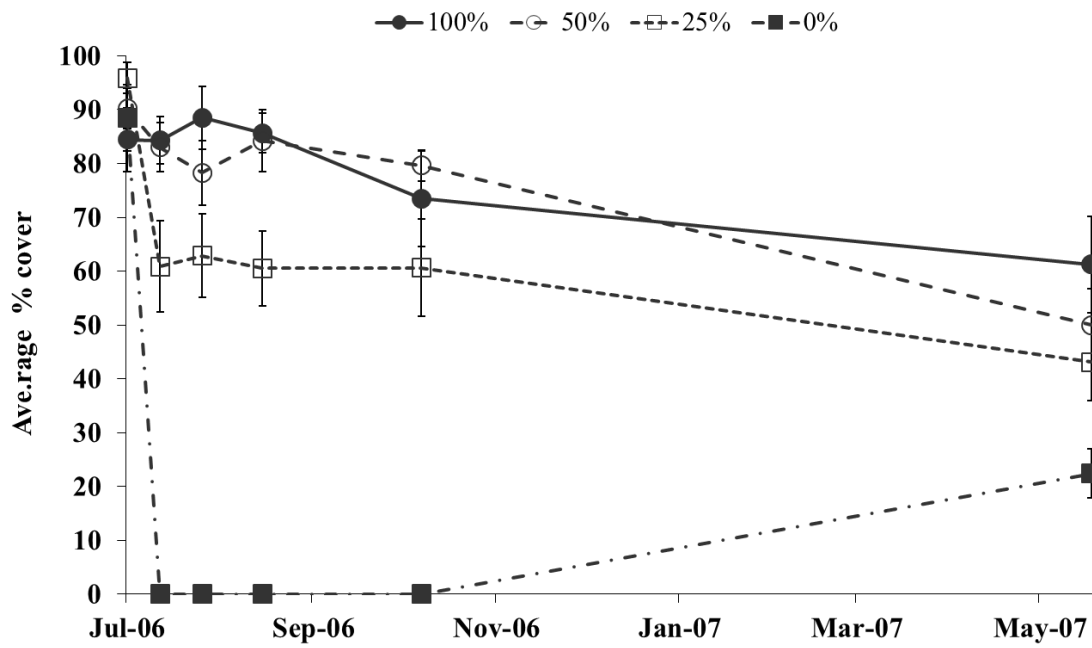


Fig. 3. Average percentage cover \pm SEM of *Ascophyllum* canopy found in plots through time (per 0.09 m²), n = 5.

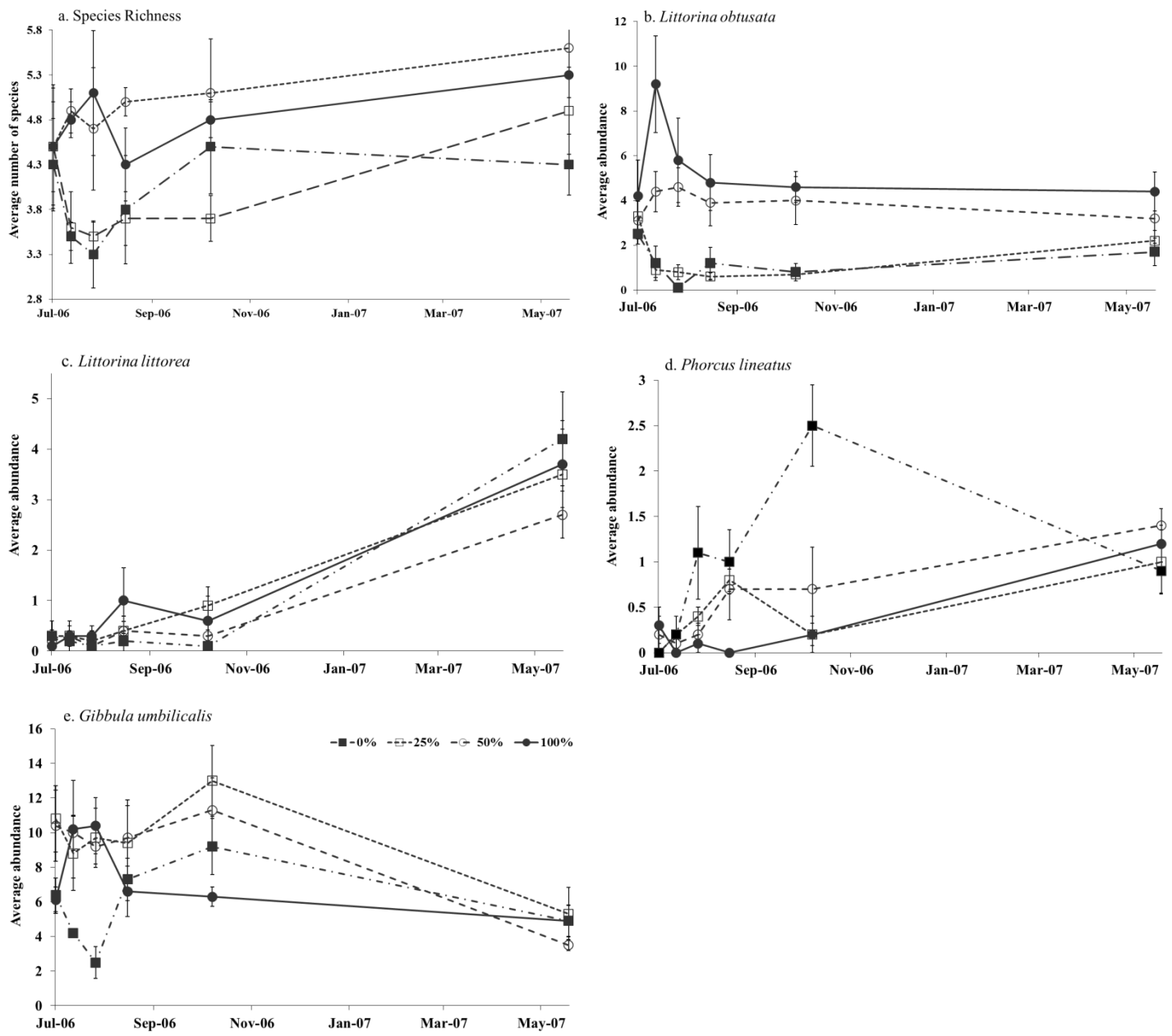


Fig. 4. Average abundances of invertebrates \pm SEM found in plots through time (per 0.09 m²), n = 5.

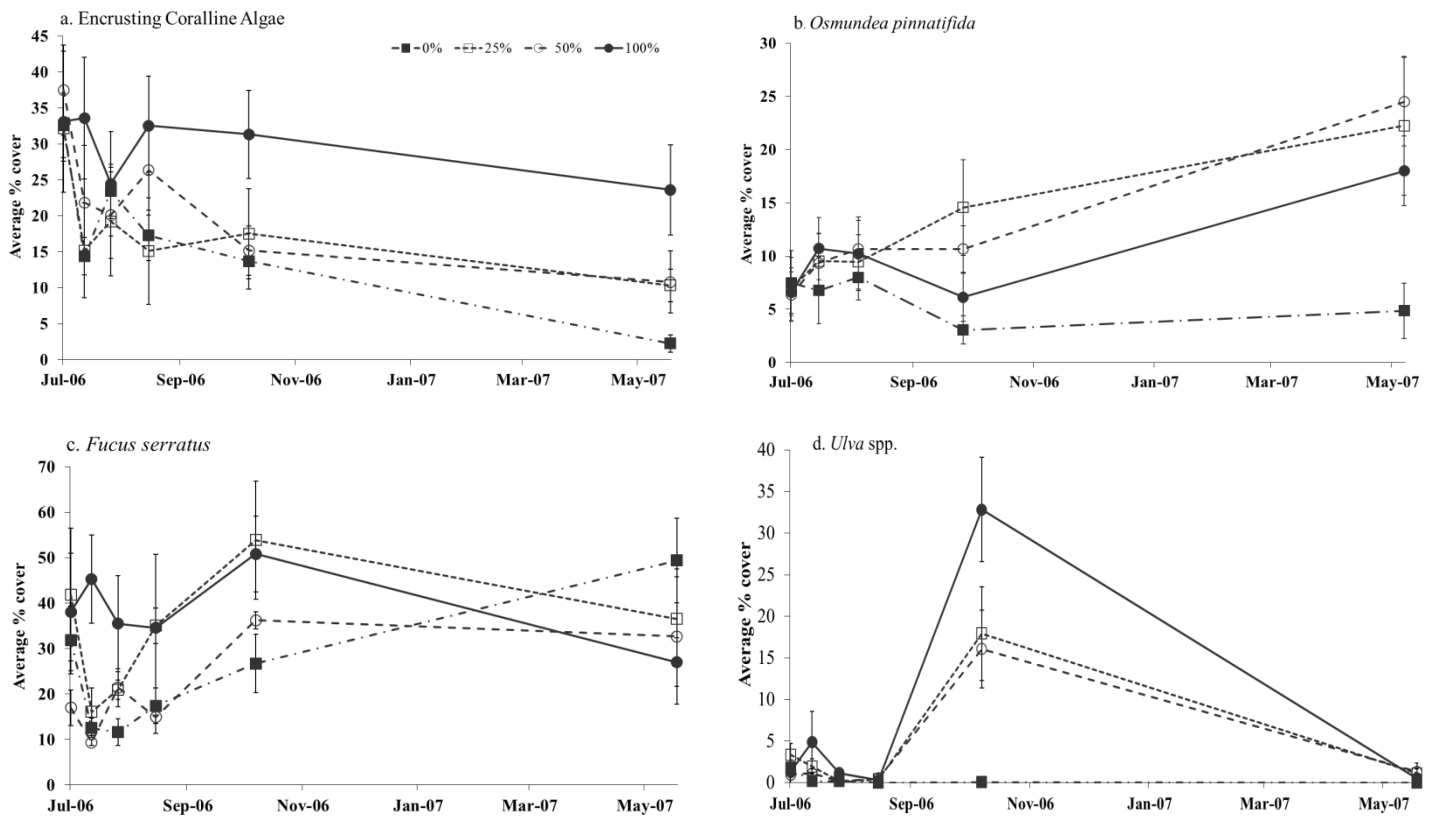
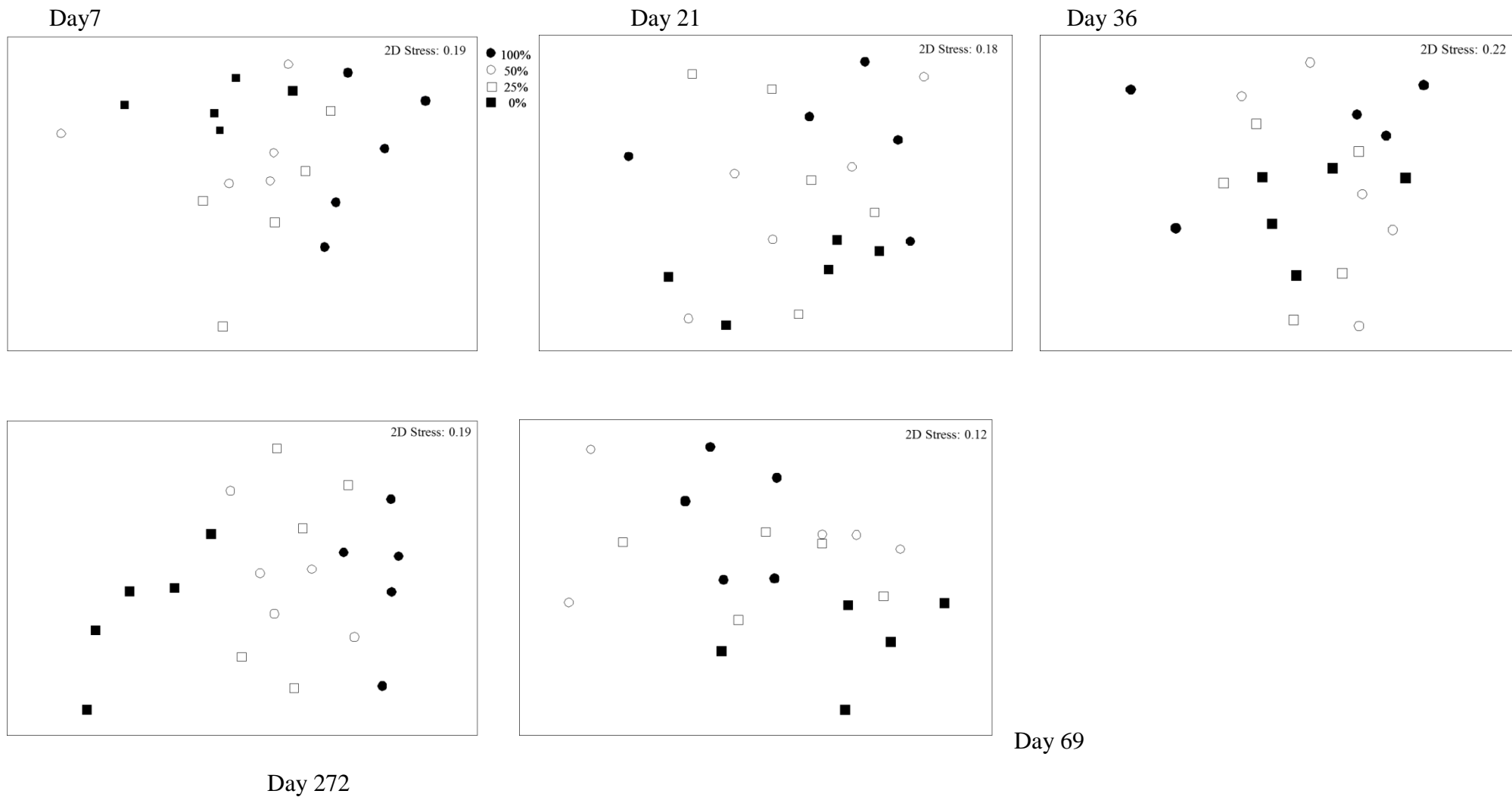
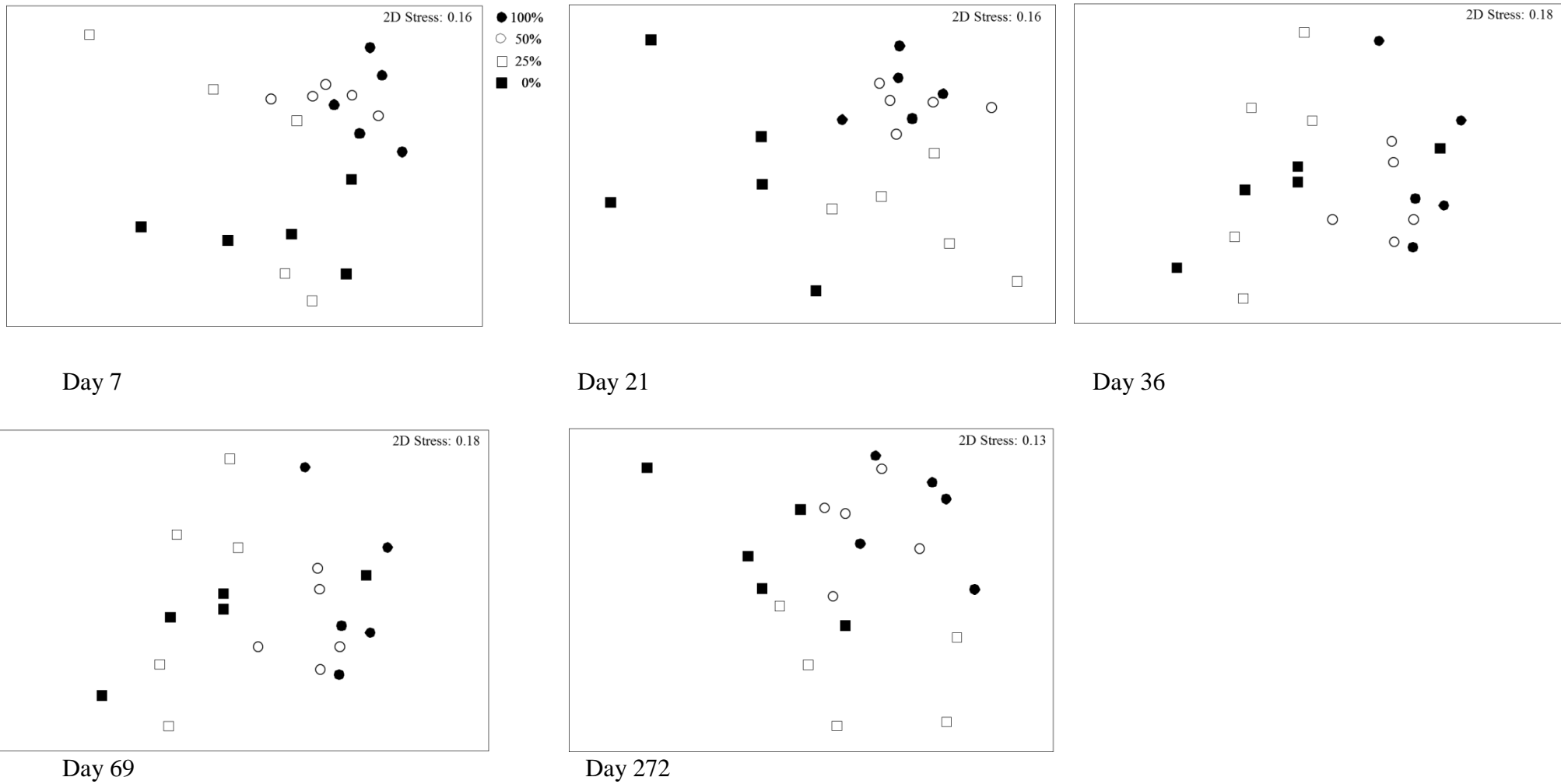


Fig. 5. Average abundances of algae \pm SEM found in plots through time (per 0.09 m²), n = 5.

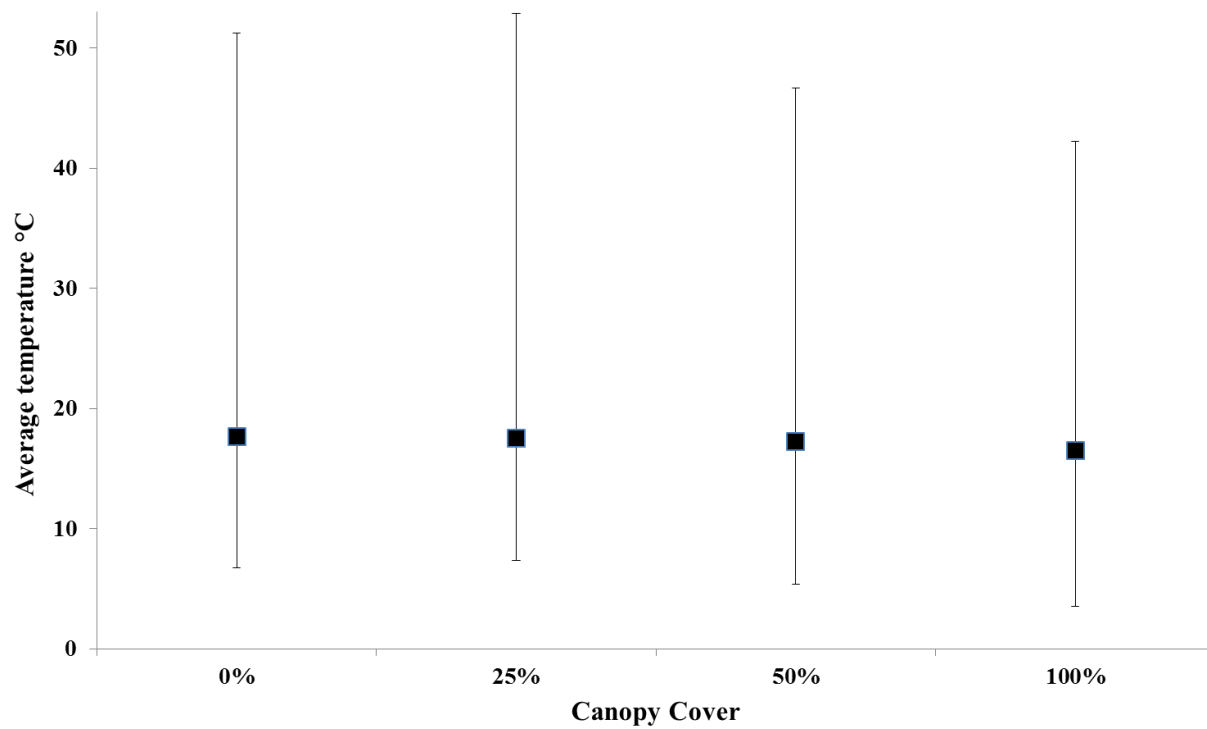
APPENDICES



A. Ordination plots of sessile species assemblages associated with canopy cover (legend shows treatment) treatments at each visit since the manipulation of the canopy.



B. Ordination plots of mobile invertebrate species assemblages associated with canopy cover treatments (legend shows treatment) at each visit since the manipulation of the canopy



C. Average temperatures recorded over a three-week period (in summer) within plots (Canopy Cover), error bars indicate maximum and minimum temperatures, n=1 (0%, 100%), n=2(25%, 50%).

D. Full species list from Hannafore Point.

Algae/Sessile species:

Furoid algae

Ascophyllum nodosum

Fucus serratus

Fucus vesiculosus

Barnacles

Balanus perforatus

Semibalanus balanoides

Polychaete

Spirorbis spirorbis

Sponges

Halichondria panicea

Hymeniacidon perleve

Foliose algae

Ceramium rubrum

Chondrus crispus

Cladophora rupestris

Corallina officinalis

Lomentaria articulata

Mastocarpus stellatus

Osmundea pinnatifida

Plumaria elegans

Ulva intestinalis

Ulva lactuca

Unidentified red turf

Epiphyte

Vertebrata lanosa

Encrusting algae

Hildenbrandia rubra

Encrusting coralline (e.g. *Lithothamnion* spp. and

Lithophyllum)

Ralfsia verrucosa

Mobile invertebrates:

Anemones

Actinia equina

Anemonia viridis

Crabs

Carcinus maenas

Gastropods

Gibbula umbilicalis

Littorina littorea

Littorina obtusata

Nucella lapillus

Patella vulgata

Phorcus lineatus

APPENDIX LABELS

Appendix A. Ordination plots of assemblages of sessile taxa associated with treatments at each visit since the manipulation of the canopy, $n = 5$. ● 100 % intact-fronds, ○ 50 % intact-fronds, □ 25 % intact-fronds, ■ 0 % intact-fronds.

Appendix B. Ordination plots of assemblages of mobile invertebrate species associated with canopy cover treatments at each visit since the manipulation of the canopy, $n = 5$. ● 100 % intact-fronds, ○ 50 % intact-fronds, □ 25 % intact-fronds, ■ 0 % intact-fronds.

Appendix C. Average temperatures recorded over a three-week period (in summer) within plots, error bars indicate maximum and minimum temperatures, $n = 1$ (100 %, 0 % intact-fronds), $n = 2$ (50 % fronds, 25 % intact fronds). ■ average temperature.

Appendix D. Full species list from Hannafore Point.

D

Algae/Sessile taxa:

Fucoid algae

Ascophyllum nodosum (Linnaeus) Le Jolis

Fucus serratus Linnaeus

Fucus vesiculosus Linnaeus

Barnacles

Perforatus perforatus (Bruguère, 1789)

Semibalanus balanoides (Linnaeus, 1767)

Polychaete

Spirorbis spirorbis (Linnaeus, 1758)

Sponges

Halichondria panacea (Pallas, 1766)

Hymeniacidon perlevis (Montagu, 1814)

Foliose algae

Ceramium virgatum Roth

Chondrus crispus Stackhouse

Cladophora rupestris (Linnaeus) Kützing

Corallina officinalis Linnaeus

Lomentaria articulate (Hudson) Lyngbye

Mastocarpus stellatus (Stackhouse) Guiry

Osmundea pinnatifida (Hudson) Stackhouse

Plumaria elegans (Bonnemaison) F.Schmitz

Ulva intestinalis Linnaeus

Ulva lactuca Linnaeus

Unidentified red turf

Epiphyte

Vertebrata lanosa (Linnaeus) T.A.Christensen

Encrusting algae

Hildenbrandia rubra (Sommerfelt) Meneghini

Encrusting coralline (e.g. *Lithothamnion* spp. Heydrich,
and *Lithophyllum* spp. Philippi)

Ralfsia verrucosa (Areschoug) Areschoug

Mobile invertebrates:

Anemones

Actinia equina (Linnaeus, 1758)

Anemonia viridis (Forskål, 1775)

Crabs

Carcinus maenas (Linnaeus, 1758)

Gastropods

Gibbula umbilicalis (da Costa, 1778)

Littorina littorea (Linnaeus, 1758)

Littorina obtusata (Linnaeus, 1758)

Nucella lapillus (Linnaeus, 1758)

Patella vulgata Linnaeus, 1758

Phorcus lineatus (da Costa, 1778)