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1 **Population dynamics of the brown alga *Himanthalia elongata* under harvesting pressure.**

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8 **Abstract**

9 Through experimental harvesting, followed by a 12-month monitoring of demographic attributes, we
10 tested the influence of harvesting on the population dynamics of *Himanthalia elongata*. We further
11 explore the data to test the hypothesis that the canopy would exert a negative effect on the other
12 developmental stages (intraspecific competition) throughout the recovery cycle of the population. This
13 showed that the *H. elongata* canopy plays a marked seasonal role not by precluding the presence of other
14 developmental stages but by delaying or preventing their growth and development. The removal of the
15 canopy facilitates the transition from one developmental stage to another, eventually permitting a fast
16 recovery of size structure in the population. This study allows us to integrate population dynamics and
17 intraspecific relationships in our understanding of macroalgal recovery patterns.

18 **Key-words:** intraspecific relationships, intertidal, management, population dynamics, restoration

19 **Introduction**

20 Canopy loss, for example through harvesting, is globally considered a threat to marine ecosystem,
21 seriously impacting biodiversity and functioning worldwide (Bruno and Bertness, 2001). Previous studies
22 have shown a wide range of responses to canopy removal, including reduction or loss of diversity and
23 reduction in primary productivity (Crowe et al., 2013). Fucoïds and other intertidal macroalgae are
24 recognized as foundation species (*sensu* Jones et al., 1994) that have an important effect on abiotic
25 conditions, community assembly and ecosystem functioning (Benedetti-Cecchi et al., 2001; Tait and
26 Schiel, 2011). Variations in their distribution may trigger changes in the whole system, such as shifts in
27 community composition (Lilley and Schiel, 2006) or changes in the height and structure of the canopy
28 itself (Golléty et al., 2008).

29 Among them is *Himanthalia elongata* (L.) S. F. Gray, a brown alga forming dense stands on temperate
30 rocky shores in the Northern hemisphere (Creed, 1995). Unlike other members of the Fucales, it has a
31 biennial life cycle with four identifiable phases: vegetative growth, reproductive growth, reproduction
32 (gametes are released and fuse to form zygotes) and a recruitment phase during which zygotes settle on
33 the substratum (Stengel et al., 1999). Growth usually occurs between September and May, with a growth
34 rate peak during spring when seawater temperatures are approx. 10-12°C (Stengel et al., 1999). The time
35 of reproduction is from June to December, and is strongly site dependent, probably due to water
36 temperature. This alga has a two-stage morphology: first, the ‘button-like’ stage is initially club-shaped,
37 becoming peltate (‘mushroom-shaped’) when mature, about 2-3 cm in height and 2-4 cm in diameter,
38 slightly dimpled in the middle, and attached to the substratum by a short stipe and discoid holdfast.
39 Second, the mature peltate stage typically produces two long (up to 3 m) thong-like reproductive
40 receptacles (Stengel et al., 1999), hereafter referred as ‘fronds’.

41 In addition to being ecologically important, *H. elongata* is also of commercial importance. It was
42 traditionally harvested for centuries along the eastern Atlantic in Norway, France, Spain, Scotland, and
43 Ireland for fertilizer, human food, and alginic acid extracts. *H. elongata* is currently harvested mainly as
44 edible seaweed for human consumption in France, Ireland and Spain. Due to the high food value of *H.*
45 *elongata* (Plaza et al., 2008), commercial harvesting of this species is likely to expand quickly. In France,
46 *H. elongata* can be harvested all-year round but most of the harvest occurs between March and June,
47 because after June large individuals are thick and grainy, thus less appealing for human consumption. In
48 Brittany, annual harvested quantities of *H. elongata* have increased by 35% between 2009 and 2013
49 (unpublished data). Despite the sustainably-oriented harvesting practices implemented for seaweeds in
50 Europe these past few years, concern has raised about the broader impacts of harvesting (Isabel et al.,
51 2011; Smale et al., 2013; Stagnol et al., 2016).

52 Demographic parameters have been used to examine the effect of harvesting in natural populations of
53 brown macroalgae (e.g. Arenas and Fernández, 2000; Rivera and Scrosati, 2006; Santos, 1995). Size

54 distributions result from differences in individual growth rates, consistent with the asymmetric
55 competition hypothesis of dominance and elimination of smaller individuals by larger ones (Hara, 1988;
56 Weiner and Thomas, 1986). The dynamics of size inequality as a function of plant size and density are
57 important to understand not only the population structure, but also the interactions between individuals
58 (Hara, 1988). Indeed, intraspecific facilitation (positive effects of density) is generally regarded as a major
59 determinant of the dynamics of seaweed populations (Arenas and Fernández, 2000; Courchamp et al.,
60 1999; Stephens and Sutherland, 1999). Creed (1995) confirmed the importance of density as a major
61 regulator in *H. elongata* populations. Despite this, intraspecific relationships in macroalgal populations
62 have usually been ignored (Paine, 1990) and their importance is poorly known. Besides, the development
63 of seaweed population depends largely on the survival and growth of early post-settlement stages (Steen
64 and Scrosati, 2004). In this context, demographic attributes, such as density, biomass, and size structure,
65 could serve as ecological indicators to monitor the population dynamics of commercially important brown
66 macroalgae.

67 One recent study realized on the same study site and at the same sampling dates as this study, found no or
68 little impact of the harvesting of *H. elongata* on its associated community, while its percentage cover was
69 significantly affected up to nine months after the disturbance (Stagnol et al., 2016). They showed,
70 however, that 12 months after the disturbance, the percentage cover of *H. elongata* on the impacted zone
71 had returned to a state comparable to the one observed on the undisturbed control zone.

72 Through experimental harvesting, followed by a 12-month monitoring, we tested the influence of the
73 harvesting on the population dynamics of *H. elongata* and the hypothesis that the canopy could exert an
74 effect on the other developmental stages (intraspecific relationships) throughout the recovery cycle of the
75 population. This strategy allowed us to integrate population dynamics and intraspecific relationships in
76 our understanding of macroalgal recovery patterns.

77 **Material and methods**

78 **Study site**

79 This study was performed in Brittany, the French region in which commercial seaweed harvesting is the

80 most important (> 90% of macroalgae harvested in France). Field work was carried out on a site where
81 *H. elongata* is commonly harvested, at Porspoder (48°N31.607', 4°W46.169'). This study site was also
82 chosen for its large *H. elongata* standing crop and accessibility. This site is dominated by rocky substrata
83 and presents a high water movement velocity.

84 **Experimental design and set-up**

85 The experimental design considered two treatments: one control (C) and one manipulated (M) where the
86 canopy was removed, with five replicates each. Regarding *H. elongata*, the French legislation states that
87 only individuals longer than 80 cm can be harvested. Harvest was realized in April 2012, by gathering by
88 hand all individuals longer than 80 cm on a 115 m² surface area. The fronds were cut at least 10 cm from
89 the mushroom-like base. Sampling was done just before frond removal (T0) and then one month later
90 (T1). Sampling frequency was then set to every two months, and then to every three months. Each sample
91 is hereafter referred to as T_n where *n* is the number of months since harvest. At each sampling date, five
92 0.1 m² random quadrats were sampled on each treatment zones (C and M)

93 **Density, length, biomass, and developmental stage**

94 Individuals were classified as early club-shaped stage, mature vegetative mushroom-shaped stage and
95 thong-like reproductive receptacles (fronds). Individuals of these developmental stages within the quadrats
96 were counted and the maximal length of each frond was measured. Maximal length was used as size
97 descriptor because length is probably crucial for survival and reproduction of individuals given that light
98 is the primary resource for algae and that longer thalli intercept more light (Carpenter, 1990). As length
99 and biomass were highly correlated in *H. elongata*, the relationship between frond length and dry weight
100 was examined using non-linear regressions. They were applied to fit parameters of the typical allometric
101 power equation:

$$102 \quad DW = a \times FL^b, \quad \text{equation 1}$$

103 where DW represents dry weight (g); FL, frond length (cm), and *a* and *b* are constants. To fit the
104 parameters, 36 individuals were collected in Roscoff (48°N43.686', 3°W59.282') in front of the Station

105 Biologique de Roscoff. An attempt was made to obtain samples representative of the full size range of the
106 species. For each individual, the maximal length and dry weight, obtained after drying at 60°C for 48 h,
107 were recorded. An allometric length-weight equation was obtained using a power law equation. Based on
108 density, the maximal length of each individual in the quadrats in each treatment at each sampling date was
109 converted to dry weight using this equation. The average dry weight per m² could then be estimated for
110 each treatment at each sampling date, to investigate the temporal variation of *H. elongata* biomass, as well
111 as stock recovery after harvesting.

112 **Size structure and inequality**

113 The frond size structure was determined for each zone and each sampling date, for which nine size classes
114 (SCs) were previously established on the basis of frond length: 0-25 cm, 26-50 cm, 51-75 cm, 76-100 cm,
115 101-125 cm, 126-150 cm, 151-175 cm, 176-200 cm and > 200 cm. Frond size (length) inequality was
116 determined for each zone and each sampling date by calculating the Gini coefficient using the length
117 values for all the fronds of the five quadrats of each zone. This size-structure descriptor was selected here
118 because it is the statistic that most accurately reflects the size hierarchy in populations (Weiner and
119 Solbrig, 1984). The Gini coefficient ranges from a minimum of zero, when all individuals are equal in size
120 (perfect equality), and a theoretical maximum of one in an infinite population in which every individual,
121 except one, has a size of zero (perfect inequality). The Gini coefficient is frequently used as a measure of
122 size inequality in seaweed populations (e.g. Arenas and Fernández, 2000; Rivera and Scrosati, 2006;
123 Santos, 1995).

124 **Data analysis**

125 Multivariate analyses were made to test the effect of the experimental harvest disturbance using a
126 permutational multivariate analysis of variance (PERMANOVA) design that included two factors: (i)
127 controls vs. manipulated (CsM: 2 levels, fixed), and (ii) time (T: 6 levels, fixed and crossed). We
128 examined biological responses to the harvesting disturbance for three demographic attributes (i.e. total
129 density, dry standing biomass, Gini coefficient). We also examined multivariate differences in the density

130 of the different developmental stages of *H. elongata* (i.e. adult fronds, button-like stages, and mushroom-
131 shaped stages), using the same design as above. Analyses were made with the PERMANOVA+ add-on
132 package for PRIMER v6 (Anderson et al., 2008).

133 **Results**

134 **Biomass, density and Gini coefficient**

135 The allometric relationship between frond length and dry weight was checked for 36 *H. elongata* fronds
136 ranging from 8 to 281 cm:

$$137 \text{ DW} = 0.0041 \times \text{FL}^{1.8744}, R^2 = 0.93, p < 0.001 \quad \text{equation 2}$$

138 The average dry weight varied over time in both zones (Fig. 1a), with the highest values occurring in
139 September (T5) on the control area. The temporal variation patterns were similar in both treatments, but
140 the biomass was lower on the M treatment than on the C treatment (PERMANOVA, $p < 0.05$, Table 1),
141 during the one-year period, except before harvesting (T0) and at the end of the study (T12) (Pairwise
142 comparison, $p > 0.05$). Highest values of dry standing biomass were observed at T5 on the C treatment
143 and at T12 on the M treatments. Total density varied significantly throughout the year from April 2012 to
144 April 2013 (Fig. 1b) in both treatments (PERMANOVA, $p < 0.05$, Table 1). The density significantly
145 decreased from T1 to T3 on the M treatment, and significantly increased from T8 to T12 on both
146 treatments (Pairwise comparison, $p < 0.05$). Lowest values were observed between T3 and T8 on both
147 treatments. The Gini coefficient varied significantly over time in both zones (Fig 1c, PERMANOVA, $p <$
148 0.05 , Table 1), with the highest values occurring at T3 and T5 for the C treatment and at T1 and T8 for the
149 M treatment.

150 **Developmental stages**

151 The temporal variation patterns of the frond density (Fig. 2a) were significantly different between the two
152 treatments (PERMANOVA, $p = 0.001$, Table 1). Thong-like reproductive receptacles (fronds), which
153 indicate the possible occurrence of sexual reproduction, reached their highest frequency in the population

154 at T3 in July in the C treatment (14%) and at T8 in December in the M treatment (78%). The peak of
155 fronds observed at T8 in the M treatment was due to a high number of small fronds ($n = 56$) shorter than
156 13 cm, except for 2 individuals. At the same time in the C treatment, the fronds ($n = 10$) consisted of 40%
157 new and young fronds shorter than 6 cm and 60% of old and reproductive fronds longer than 200 cm.
158 Once reproductive tissues were lost in the C treatment, resulting in a loss of biomass, senescent fronds
159 were observed at the end of the study (T12). In the M treatment, the biomass increased from T8 to T12 as
160 the result of the growth of the short fronds observed at T8 (Fig. 1a).

161 The density of the mushroom-shaped stage (Fig. 2b) did not vary significantly throughout the year in
162 either treatment zones and no significant differences were observed between them (PERMANOVA, $p >$
163 0.05, Table 1). The density of the club-shaped stage varied significantly over time in both treatments
164 (PERMANOVA, $p < 0.001$, Table 1). Finally, the density of the club-shaped stage (Fig. 2c) followed the
165 same temporal pattern as the total density: it significantly decreased from T1 to T3 on the M treatment,
166 and significantly increased from T8 to T12 on both treatments (Pairwise comparison, $p < 0.001$). Lowest
167 values were observed between T3 and T8 on both treatments.

168 **Size structure and inequalities**

169 Frond size structure varied seasonally during the study period (Fig. 3). The first sample (T0) was taken in
170 April 2012 during the reproductive growth phase of *H. elongata*. After the experimental harvest, two
171 different population dynamics were observed in the different treatments.

172 In the C treatment, we observed that during the phase of reproductive growth, in spring (T0-T1), the thalli
173 progressively shifted from smaller size classes to larger size classes, resulting in an increase in inequality
174 (Fig. 1c), reaching a peak at the beginning of autumn (T5) ($G = 0.89$). During this period, longer fronds ($>$
175 200 cm) were recorded, representing 100% of the frond population (Fig. 3a). Then, the beginning of
176 winter (T8) coincided with the start of the vegetative growth in the population and the emergence of
177 recruits in smaller size classes. By the end of the study (T12), senescence caused reduction of thalli from
178 the larger size classes to smaller size classes while the number of thalli from smaller size classes (0-25 cm

179 and 26-50 cm) increased, due to the early growth of recruits. Due to these changes, the control zone
180 reached its minimum inequality ($G = 0.36$).

181 In the M treatment, harvest removed the majority of thalli, resulting in only one medium thallus (66 cm)
182 observed at T1. The remaining thalli progressively increased in length while germlings (mushroom-shaped
183 stage) shifted to the thong-like receptacle stage, resulting in an increased number of thalli in the smaller
184 classes. The beginning of winter (T8) also coincided in the population with the emergence of recruits in
185 the smallest size class (0-25 cm), which constituted almost 100% of all plants. By the end of the study
186 (T12), the vegetative growth phase followed by the reproductive growth phase, resulted in the progressive
187 shift of thalli from the smallest size class to larger size classes.

188 **Discussion**

189 The regrowth of the canopy is expected to depend on newly recruited individuals and reproductive growth
190 of algae that survived the disturbance. The recovery process of the M treatment zone appeared to occur in
191 three steps: first, the reproductive fronds of algae that survived the disturbance could reproduce since
192 individuals shorter than 80 cm were not removed (T3). Second, the incomplete removal of the canopy may
193 have been favorable for the growth and development processes, allowing these remaining individuals, as
194 well as the early developmental stages (club-shaped and mushroom-shaped), to grow and occupy higher
195 size classes. Third, the transition of these early developmental stages to the final adult stage was clearly
196 visible in winter (T8) (Fig. 3b), possibly facilitated by the absence of a dense canopy of adults.

197 Eight months after removal, the number of fronds from the smallest size class [0-25 cm] was highest in the
198 M treatment ($112 \pm 12.5 \text{ ind.m}^{-2}$) than in the C treatment ($20 \pm 1.1 \text{ ind.m}^{-2}$), suggesting that transition of
199 these early developmental stages to the final adult stage, was more successful in the M treatment than in
200 the C treatment. This may be explained by a lower competition between the adult stage forming a dense
201 canopy and the early developmental stages living below the canopy. In the M treatment, the lack of a
202 protective structure from the adult canopy during recruitment led to the creation of such micro-habitats,
203 mainly with the rapid colonization of bare areas by red turf algae. It has been shown that the survival and

204 growth of young buttons were highest in red algal turfs that protect the recruits from wave action and
205 desiccation (Stengel et al., 1999). The role of these recruits in canopy recovery, however, was only visible
206 at the end of the study, with an increase in the number of individuals in higher size classes, similar to the
207 pattern observed in the C treatment. Canopy recovery was also linked with the recovery of the total
208 biomass of *H. elongata* fronds, whose values at T12 were not different between the two treatments and
209 were similar to those prior to the disturbance (T0). The stock renewal of *H. elongata* was, therefore,
210 effective one year after harvesting.

211 In summary, in the C treatment, cohorts present at the start of the study (T0) grew and ultimately exerted a
212 high intraspecific competition on the other developmental stages, by stopping further growth of juveniles.
213 On the other hand, M treatment seems to have reduced intraspecific competition, allowing juveniles to
214 grow. Then, the juveniles developed continuously, as seen in T8 with the high number of small fronds
215 (Fig. 3b), permitting a fast recovery of size structure in this dynamic population.

216 Although it is widely reported that the structure and dynamics of most ecological communities are
217 controlled partly by interactions between species (Bertness and Callaway, 1994; Bulleri, 2009; Edwards
218 and Connell, 2012), the role of intraspecific relationships is less often integrated in studies of population
219 dynamics. Recent research has emphasized the central role of positive species interactions as important
220 drivers of community structure and ecosystem functioning (Brooker et al., 2008; Bulleri, 2009). This
221 study showed negative intraspecific relationships (competition) in *H. elongata* in the undisturbed zone (C
222 treatment). Positive effects of high densities on growth have been reported mainly in furoid algae, where
223 high densities may offer some protection against physical stress related to wave action and desiccation
224 (Choi and Norton, 2005; Steen and Scrosati, 2004; Viejo and Aberg, 2001). In our work, although the
225 impact of adult fronds on juvenile stages (club-shaped and mushroom-shaped button) was not directly
226 measured, it seems likely that the presence of the canopy confers a disadvantage to the juvenile stage by
227 reducing the availability of space, light and/or nutrients and by competing for those limiting resources
228 (Carpenter, 1990). It appears that the *H. elongata* canopy plays a marked seasonal role, when the adult
229 fronds are highly developed (in summer at T3 and T5). At that time, adult fronds do not preclude the

230 presence of other developmental stages but somehow they delay or prevent their growth and development.
231 Therefore, the removal of the canopy facilitates the transition from one developmental stage to another.

232
233 Overall our results suggest that the incomplete removal of the canopy (since individuals smaller than 80
234 cm remained) may have ensured the continued recruitment and re-growth of *H. elongata*, facilitating the
235 regeneration of the exploited area. Growth and recruitment can be regulated by density-dependent
236 processes operating at small-scale during the early stages of substrate colonization. Furthermore, the
237 health and diversity of the surrounding macroalgal populations play an essential role in recovery, probably
238 through the recruitment process and the magnitude of herbivorous grazing. Moreover, *H. elongata* being a
239 seasonal canopy-forming species, its canopy loss on the impact sites was mediated by the natural and
240 seasonal reduction in the *H. elongata* canopy on the control sites (also see Stagnol et al., 2016). From a
241 conservation point of view, our results support the current legal harvesting techniques in France that
242 enforce minimum harvesting size for specific seaweed including *H. elongata*, to minimize their impact on
243 juvenile plants. Nowadays, *H. elongata* is also gathered by hand on shore in Ireland and Spain. Public
244 authorities from these countries should introduce and enforce minimum harvesting size guidelines for *H.*
245 *elongata* (if it is not already), and more generally, implement species specific regulations to ensure the
246 sustainability of the algae resources and harvesting activities. In addition, species specific management
247 requires ecological indicators sensitive to harvesting pressures and easy to measure by scientific observers
248 and/or fishermen. In this context, demographic attributes are easily obtainable indicators that can be used
249 as tools for stakeholders and policy makers.

250
251 The effects of other factors such as herbivory or extreme environmental conditions may also have
252 operated on the intraspecific relationships of *H. elongata*. Indeed, recovery is assumed to be higher in the
253 presence of herbivores (Aquilino and Stachowicz, 2012), which are thought to promote succession by
254 grazing on early-successional fast-growing ephemeral species that would otherwise prevent establishment
255 of perennial algae (Aquilino and Stachowicz, 2012). Understanding the balance between these factors is

256 important to understand how settlement patterns affect population dynamics, although understanding the
257 individual influences of each factor can be difficult (Stachowicz and Byrnes, 2006).

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265 **References**

- 266 Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to Software and
267 Statistical Methods. (PRIMER-E : Plymouth, UK.).
- 268 Aquilino, K.M., Stachowicz, J.J., 2012. Seaweed richness and herbivory increase rate of community
269 recovery from disturbance. *Ecology* 93, 879–890. doi.org/10.1890/11-0457.1
- 270 Arenas, F., Fernández, C., 2000. Size structure and dynamics in a population of *Sargassum muticum*
271 (Phaeophyceae). *J. Phycol.* 36, 1012–1020. doi:10.1046/j.1529-8817.2000.99235.x
- 272 Benedetti-Cecchi, L., Pannacciulli, F., Bulleri, F., Moschella, P.S., Airoldi, L., Relini, G., Cinelli, F.,
273 2001. Predicting the consequences of anthropogenic disturbance: large-scale effects of loss of
274 canopy algae on rocky shores. *Mar. Ecol. Prog. Ser.* 214, 137–150. doi:10.3354/meps214137
- 275 Bertness, M.D., Callaway, R., 1994. Positive interactions in communities. *Trends Ecol. Evol.* 9, 191–193.
276 doi:10.1016/0169-5347(94)90088-4
- 277 Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G., Liancourt, P.,
278 Tielbörger, K., Travis, J.M.J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey,
279 E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C.L., Saccone, P., Schiffers, K., Seifan, M.,
280 Touzard, B., Michalet, R., 2008. Facilitation in plant communities: the past, the present, and the
281 future. *J. Ecol.* 96, 18–34. doi:10.1111/j.1365-2745.2007.01295.x

- 282 Bruno, J.F., Bertness, M.D., 2001. Habitat modification and facilitation in benthic marine communities,
283 in: Marine Community Ecology (Bertness, M.D. et Al., Eds). Sinauer, pp. 201–218.
- 284 Bulleri, F., 2009. Facilitation research in marine systems: state of the art, emerging patterns and insights
285 for future developments. *J. Ecol.* 97, 1121–1130. doi:10.1111/j.1365-2745.2009.01567.x
- 286 Carpenter, R.C., 1990. Competition among marine macroalgae: a physiological perspective. *J. Phycol.* 26,
287 6–12. doi:10.1111/j.0022-3646.1990.00006.x
- 288 Choi, H.G., Norton, T.A., 2005. Competitive interactions between two furoid algae with different growth
289 forms, *Fucus serratus* and *Himanthalia elongata*. *Mar. Biol.* 146, 283–291. doi:10.1007/s00227-
290 004-1441-4
- 291 Courchamp, F., Clutton-Brock, T., Grenfell, B., 1999. Inverse density dependence and the Allee effect.
292 *Trends Ecol. Evol.* 14, 405–410. doi:10.1016/S0169-5347(99)01683-3
- 293 Creed, J.C., 1995. Spatial dynamics of a *Himanthalia elongata* (fucales, Phaeophyta) population. *J.*
294 *Phycol.* 31, 851–859. doi:10.1111/j.0022-3646.1995.00851.x
- 295 Crowe, T.P., Cusson, M., Bulleri, F., Davoult, D., Arenas, F., Aspden, R., Benedetti-Cecchi, L.,
296 Bevilacqua, S., Davidson, I., Defew, E., Fraschetti, S., Golléty, C., Griffin, J.N., Herkül, K.,
297 Kotta, J., Migné, A., Molis, M., Nicol, S.K., Noël, L.M.-L.J., Pinto, I.S., Valdivia, N., Vaselli, S.,
298 Jenkins, S.R., 2013. Large-scale variation in combined impacts of canopy loss and disturbance on
299 community structure and ecosystem functioning. *PLoS ONE* 8, e66238.
300 doi:10.1371/journal.pone.0066238
- 301 Duarte, L., Viejo, R.M., Martínez, B., deCastro, M., Gómez-Gesteira, M., Gallardo, T., 2013. Recent and
302 historical range shifts of two canopy-forming seaweeds in North Spain and the link with trends in
303 sea surface temperature. *Acta Oecologica* 51, 1–10. doi:10.1016/j.actao.2013.05.002
- 304 Edwards, M.S., Connell, S.D., 2012. Competition, a major factor structuring seaweed communities, in:
305 Wiencke, C., Bischof, K. (Eds.), *Seaweed Biology, Ecological Studies*. Springer Berlin
306 Heidelberg, pp. 135–156.

- 307 Golléty, C., Migné, A., Davoult, D., 2008. Benthic metabolism on a sheltered rocky shore: role of the
308 canopy in the carbon budget. *J. Phycol.* 44, 1146–1153. doi:10.1111/j.1529-8817.2008.00569.x
- 309 Halpern, B.S., Silliman, B.R., Olden, J.D., Bruno, J.P., Bertness, M.D., 2007. Incorporating positive
310 interactions in aquatic restoration and conservation. *Front. Ecol. Environ.* 5, 153–160.
311 doi:10.1890/1540-9295(2007)5[153:IPIIAR]2.0.CO;2
- 312 Hara, T., 1988. Dynamics of size structure in plant populations. *Trends Ecol. Evol.* 3, 129–133.
313 doi:10.1016/0169-5347(88)90175-9
- 314 Isabel, S.-P., Serrão, E.A., Per, Å., 2011. Recovery after trampling disturbance in a canopy-forming
315 seaweed population. *Mar. Biol.* 159, 697–707. doi:10.1007/s00227-011-1847-8
- 316 Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69, 373–386.
317 doi:10.2307/3545850
- 318 Lilley, S.A., Schiel, D.R., 2006. Community effects following the deletion of a habitat-forming alga from
319 rocky marine shores. *Oecologia* 148, 672–681. doi:10.1007/s00442-006-0411-6
- 320 Moss, B., 1969. Apical meristems and growth control in *Himantalia elongata* (S. F. Gray). *New Phytol.*
321 68, 387–397. doi:10.1111/j.1469-8137.1969.tb06451.x
- 322 Paine, R.T., 1990. Benthic macroalgal competition: complications and consequences. *J. Phycol.* 26, 12–
323 17. doi:10.1111/j.0022-3646.1990.00012.x
- 324 Plaza, M., Cifuentes, A., Ibáñez, E., 2008. In the search of new functional food ingredients from algae.
325 *Trends Food Sci. Technol.* 19, 31–39. doi:10.1016/j.tifs.2007.07.012
- 326 Rivera, M., Scrosati, R., 2006. Population dynamics of *Sargassum lapazeanum* (Fucales, Phaeophyta)
327 from the Gulf of California, Mexico. *Phycologia* 45, 178–189. doi:10.2216/05-47.1
- 328 Santos, R., 1995. Size structure and inequality in a commercial stand of the seaweed *Gelidium*
329 *sesquipedale*. *Mar. Ecol. Prog. Ser.* 119, 253–263. doi:10.3354/meps119253
- 330 Sauvageau, M.C., 1918. Sur la dissémination et la naturalisation de quelques algues marines. *Bull. Inst.*
331 *Océan. Monaco* 1–28.

- 332 Smale, D.A., Burrows, M.T., Moore, P., O'Connor, N., Hawkins, S.J., 2013. Threats and knowledge gaps
333 for ecosystem services provided by kelp forests: a northeast Atlantic perspective. *Ecol. Evol.* 3,
334 4016–4038. doi:10.1002/ece3.774
- 335 Stachowicz, J.J., Byrnes, J.E., 2006. Species diversity, invasion success, and ecosystem functioning:
336 disentangling the influence of resource competition, facilitation, and extrinsic factors. *Mar. Ecol.*
337 *Prog. Ser.* 311, 251–262. doi:10.3354/meps311251
- 338 Stagnol, D., Michel, R., Davoult, D., 2016. Unravelling the impact of harvesting pressure on canopy-
339 forming macroalgae. *Mar. Freshw. Res.* 67(1): 153-161 doi:10.1071/MF14198
- 340 Steen, H., Scrosati, R., 2004. Intraspecific competition in *Fucus serratus* and *F. evanescens*
341 (Phaeophyceae: Fucales) germlings: effects of settlement density, nutrient concentration, and
342 temperature. *Mar. Biol.* 144, 61–70. doi:10.1007/s00227-003-1175-8
- 343 Stengel, D., Wilkes, R., Guiry, M., 1999. Seasonal growth and recruitment of *Himantalia elongata*
344 (Fucales, Phaeophycota) in different habitats on the Irish west coast. *Eur. J. Phycol.* 34, 213–221.
345 doi:10.1080/09670269910001736272
- 346 Stephens, P.A., Sutherland, W.J., 1999. Consequences of the Allee effect for behaviour, ecology and
347 conservation. *Trends Ecol. Evol.* 14, 401–405. doi:10.1016/S0169-5347(99)01684-5
- 348 Tait, L.W., Schiel, D.R., 2011. Dynamics of productivity in naturally structured macroalgal assemblages:
349 importance of canopy structure on light-use efficiency. *Mar. Ecol. Prog. Ser.* 421, 97–107.
350 doi:10.3354/meps08909
- 351 Viejo, R.M., Aberg, P., 2001. Effects of density on the vital rates of a modular seaweed. *Mar. Ecol. Prog.*
352 *Ser.* 221, 105–115. doi:10.3354/meps221105
- 353 Weiner, J., Solbrig, O.T., 1984. The meaning and measurement of size hierarchies in plant populations.
354 *Oecologia* 61, 334–336. doi:10.1007/BF00379630
- 355 Weiner, J., Thomas, S.C., 1986. Size variability and competition in plant monocultures. *Oikos* 47, 211–
356 222. doi:10.2307/3566048
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Figures

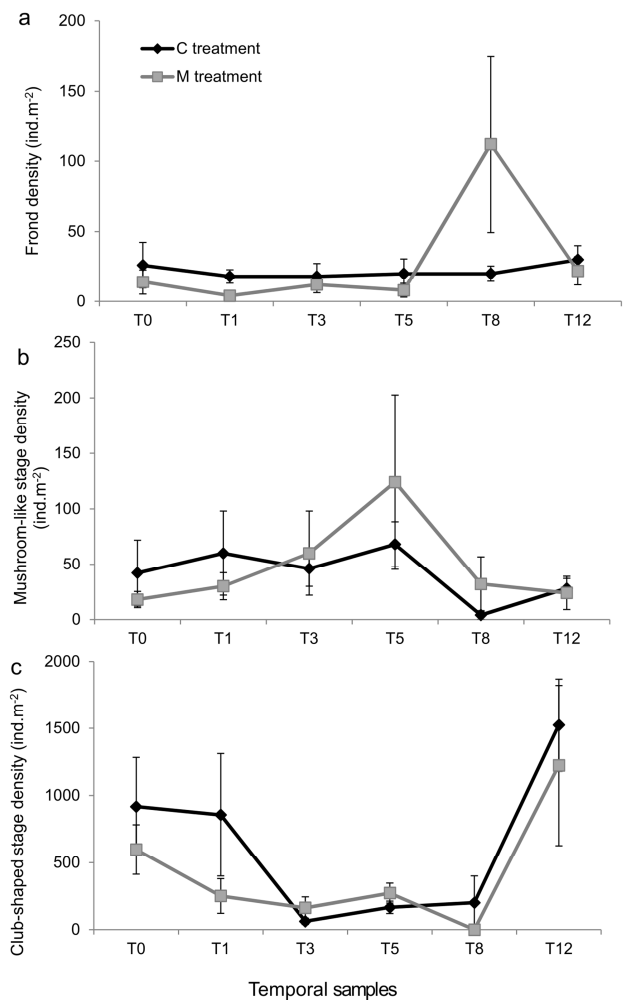
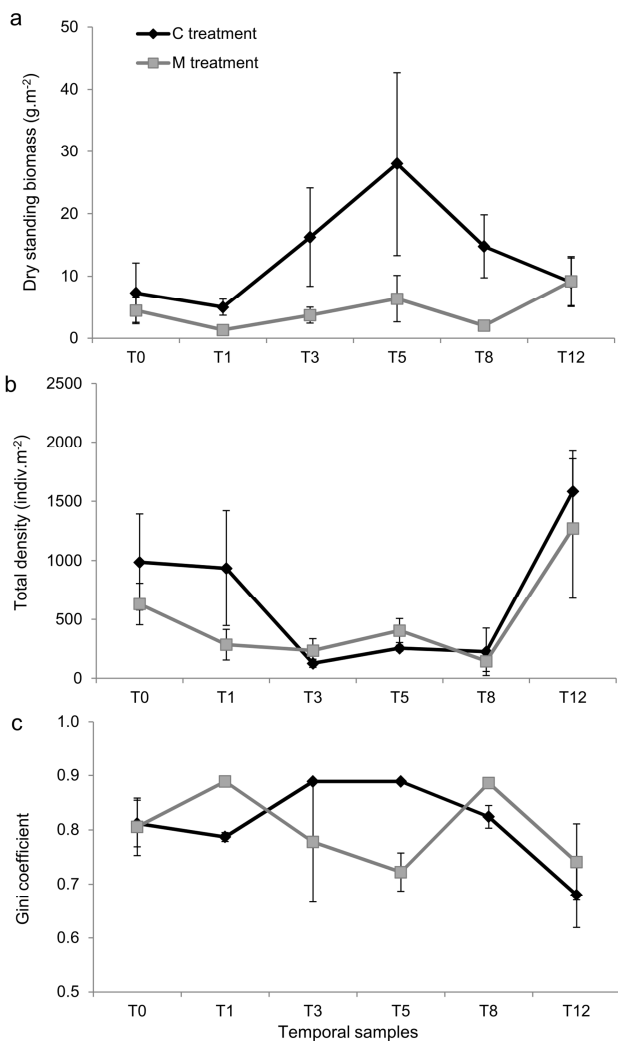


Fig. 1 Temporal variation (mean \pm SE) of dry standing biomass

Fig. 2 Temporal variation in densities ($\text{individual}\cdot\text{m}^{-2}$; mean

Table 1 Summary of Permutational Analysis of Variance (PERMANOVA) for demographic parameters and developmental stages of *Himantalia elongata* population. *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$. Factors: controls vs. manipulated (CsM: 2 levels, fixed), and time (T: 6 levels, fixed and crossed).

Demographic parameters							
Source of variation	df	Dry standing biomass		Total density		Gini coefficient	
		MS	F	MS	F	MS	F
CsM	1	8311.80	4.70 *	1348.80	0.74	348.79	1.85 ***
T	5	1625.40	0.92	7189.60	3.96 ***	227.24	1.21
CsMxT	5	2078.00	1.18	1238.40	0.68	193.77	1.03
Res	48	1767.70		1813.40		188.14	

Developmental stages							
Source of variation	df	Frond density		Club-shaped stage density		Mushroom-like stage density	
		MS	F	MS	F	MS	F
CsM	1	22559.00	13.91 ***	1978.10	0.78	1746.40	0.54
T	5	2126.10	1.31	9880.00	3.88 ***	4130.60	1.27
CsMxT	5	1587.50	0.98	2133.70	0.84	2626.10	0.81
Res	48	1622.10		2548.00		3254.20	

