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**Ecological feedback mechanisms and variable disturbance regimes:  
the uncertain future of Mediterranean macroalgal forests**

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19 **Abstract**

20 Loss of algal canopies can result in a shift towards a turf-dominated state, where variability in  
21 species life-history traits can determine new mechanisms of feedback, and influence the degraded  
22 system under variable regimes of disturbance. By focusing on rockpools dominated by *Cystoseira*  
23 *brachycarpa*, we tested the hypothesis that the alga *Dictyopteris polypodioides* could take  
24 advantage of extreme regimes of disturbance related to storms, and outcompete other turfs through  
25 a distinctive combination of life traits. Replacement of the canopy was initially driven by a mix of  
26 taxon-specific life-traits and resulting assemblages were susceptible to intense events of  
27 disturbance. Subsequently, *D. polypodioides* dominated removal quadrats, favored by density-  
28 dependent abilities to intercept more light and reach larger size than the rest of turf. These new  
29 positive feedbacks may contribute to maintain the modified state of the system and influence its  
30 ability to withstand extreme abiotic conditions.

31 **Keywords:** loss of canopy; turf; multiple life traits; feedback mechanisms; extreme events;  
32 disturbance regimes; Mediterranean macroalgal forests.

33

## 34 **1. Introduction**

35 Marine environments are currently subjected to increasing anthropogenic disturbances, which  
36 undermine the diversity, structure and functioning of ecosystems through additive or synergistic  
37 effects (Halpern et al. 2007; Crain et al. 2009; Claudet and Fraschetti 2010). Some of the most  
38 pervasive and widespread threats to these systems are represented by habitat loss (Airoldi and Beck  
39 2007), which can exacerbate the effects of both local and global stressors to natural environments  
40 (e.g. overfishing, global warming) (Thomas et al. 2004; Newton et al. 2007). This scenario is  
41 further complicated by the predicted fluctuations in the mean and variance of climate variables, as  
42 well as the increase in extreme events (Easterling et al. 2000; Gutschick and BassiriRad 2003),  
43 which can dramatically affect natural assemblages (Benedetti-Cecchi et al. 2006; Maggi et al. 2012;  
44 Wernberg et al. 2016).

45 Along temperate coasts, forests of brown algae belonging to Laminariales or Fucales are  
46 particularly at risk, due to their susceptibility to anthropogenic sources of stress, which has led to a  
47 global loss of these algal stands in proximity of urban areas (Benedetti-Cecchi et al. 2001; Steneck  
48 et al. 2002; Airoldi and Beck 2007; Connell et al. 2008; Smale and Wernberg 2013; Thibaut et al.  
49 2014). During the last decade, marine heat waves and exceptional storms further contributed to  
50 erode macroalgal forests' distribution worldwide (Navarro et al. 2011; Smale and Vance 2016;  
51 Wernberg et al. 2016). Under pristine conditions, these canopy-forming algae create a biogenic  
52 habitat for a plethora of organisms, by regulating light availability, water flow and sedimentation  
53 rates, as well as representing a protection from physical disturbance (Eckman et al. 1989; Wernberg  
54 et al. 2005; Rosman et al. 2007; Bertocci et al. 2010; Bulleri et al. 2012). As such, these bioengineer  
55 species are responsible for maintaining a highly diversified and productive ecosystem (Crowe et al.  
56 2013; Smale et al. 2013). Their loss can result in a shift towards the dominance of turf-forming  
57 algae or barren grounds (Benedetti-Cecchi et al. 2015; Wernberg et al. 2016; Filbee-Dexter and  
58 Wernberg 2018; O'Brien and Scheibling 2018), with a net decrease in the ecological, aesthetic and

59 economic value of the habitat. Once established, algal turfs can persist preventing the recovery of  
60 an algal canopy, resulting in turf- and canopy-dominated assemblages to be considered as  
61 alternative states in temperate rocky reefs (Benedetti-Cecchi et al. 2015; Rindi et al. 2017).

62 In ecological systems, positive and negative feedback mechanisms between biotic factors and  
63 abiotic conditions play a key role in maintaining alternative states (Scheffer et al. 2001). Turfs  
64 include numerous low-lying opportunistic species that can reproduce multiple times during the year  
65 and are characterized by fast growth. These traits, in addition to the ability of trapping sediment,  
66 have been associated to negative effects on recruitment of canopies and on the persistence of a  
67 degraded state (BenedettiCecchi and Cinelli 1996; Airoidi 1998; Perkol-Finkel and Airoidi 2010).  
68 Turfs comprise numerous species, which are usually not clearly defined (Connell et al. 2014), as  
69 they were a set of non-interacting species that respond homogeneously to environmental changes.  
70 However, differences in life-history traits (e.g., frequency and period of reproduction, growth rate,  
71 morphology, resource uptake, chemical defenses against herbivores) may exist within the same  
72 assemblage and affect how algal turfs as a whole interact with algal canopies under variable abiotic  
73 conditions (Bertocci et al. 2017). For example, a species with distinctive competitive features may  
74 take advantage of an (extreme) abiotic disturbance and establish new positive feedbacks, which can  
75 contribute to the ecological resilience (or resistance) of the modified system (Suding et al. 2004).  
76 Understanding how variation in species life-history traits within the turf assemblage affect  
77 interactions with algal canopies, and how disturbance moderates these interactions are key, yet  
78 largely unexplored questions that need to be addressed, to better understand the balance between  
79 turf- and canopy-dominated assemblages on temperate reefs.

80 This study focused on rockpools located in the northwestern Mediterranean, dominated by dense  
81 monospecific stands of the canopy-forming *Cystoseira brachycarpa* var. *balearica* (Sauvageau)  
82 Giaccone (Fucales) (hereafter *Cystoseira*), characterized by fronds up to 15 cm long. Rolling of  
83 boulders on the sloping sides during intense storm events is one of the main causes of mechanical

84 disturbance in these rockpools (Benedetti-Cecchi and Cinelli 1996), able to reduce *Cystoseira*  
85 coverage and facilitate the proliferation of turf (a mix a low-lying species, up to 2-3cm tall, with  
86 variable morphologies) (Maggi et al. 2012). Starting from late 2008, some rockpools at the study  
87 location have experienced a significant increase in coverage of the seaweed *Dictyopteris*  
88 *polypodioides* (A.P.De Candolle) J.V.Lamouroux (hereafter *Dictyopteris*), a frondose brown alga  
89 with a sheet-like thallus and a relatively small holdfast. Within these rockpools, *Dictyopteris* (both  
90 as juvenile and adult thalli) was initially present at low density and small size under the canopy of  
91 *Cystoseira*, and thus considered part of the turf matrix. While increasing in coverage, however,  
92 *Dictyopteris* became larger, finally resulting in dense patches of fronds up to 8 cm long, which  
93 partially replaced *Cystoseira* (E. Maggi pers. obs).

94 We hypothesized that *Dictyopteris* took advantage of extreme events of disturbance that removed  
95 the canopy and associated assemblage, and overcame the rest of the turf matrix (hereafter turf) due  
96 to a peculiar combination of life traits. In particular, we suggest that *Dictyopteris* was favored by its  
97 morphology, high growth rate and chemical defenses against herbivores (Schnitzler et al. 2001),  
98 which resulted in a faster growth and ability to intercept more light and reach larger size, in  
99 comparison to the rest of turf. This might result in a strong mechanism of competition, internally  
100 reinforced through density-dependent positive feedbacks. To test this model, we manipulated the  
101 presence/absence of either *Cystoseira* or *Dictyopteris*, under different temporal regimes and  
102 intensities of disturbance related to storm events, including an extreme scenario of aggregated and  
103 largely intense events. We monitored temporal changes in abundance of both manipulated species  
104 and turf, and finally estimated the percentage of reduction of photosynthetic active radiation (PAR)  
105 linked to the presence of adult thalli of *Cystoseira* or *Dictyopteris*. We expected 1) a dominance of  
106 *Dictyopteris* with largely intense or extreme regimes of disturbance, able to impact *Cystoseira* (if  
107 present) and the rest of assemblage (including turf); 2) a dominance of turf only where *Dictyopteris*  
108 was continuously removed; 3) a significant reduction of PAR at increasing abundance of adult thalli  
109 of either *Cystoseira* or *Dictyopteris*. Turf was considered either as a whole or by selecting most

110 abundant taxa differing in morphology to identify potential direct competitors of *Dictyopteris*. We  
111 compared the multivariate structure of assemblages under different experimental conditions, to  
112 estimate changes under crossed conditions of variable regimes of disturbance and dominance (i.e.  
113 *Cystoseira*, *Dictyopteris* or turf).

## 114 **2. Materials and Methods**

### 115 2.1. Study system

116 The experiment was conducted from October 2009 to June 2010 along a sandstone rocky shore (3.5  
117 km in length), located in the Province of Livorno, northwest Mediterranean (43°47'N, 10°33'E).  
118 This area is characterized by the presence of several low-shore rockpool formations, located from  
119 0.1 to 0.3 m above the mean low-water level and with a surface area ranging from 1.4 to 8 m<sup>2</sup>  
120 (mean depth  $\pm$  SD: 40  $\pm$  14.4 cm). Most rockpools were dominated by homogeneous canopy stands  
121 of *Cystoseira*, with fronds up to 15 cm long. Associated assemblages were made of a complex  
122 matrix of algal turf (filamentous forms such as *Ceramium* spp. and *Cladophora* spp., coarsely  
123 branched algae such as *Gelidium* sp., *Hypnea musciformis*, *Laurencia obtusa*, *Rytiphloea tinctoria*,  
124 sheet-like algae such as *Dictyota* spp., *Dictyopteris polypodioides*, *Padina pavonica*, and articulated  
125 corallines such as *Ellisolandia elongata* and *Jania* sp.; Maggi et al. 2012, Rindi et al 2017),  
126 encrusting algae, other erect algae (among others, *Halopteris scoparia*, *Sargassum vulgare*,  
127 *Sphaerococcus coronopifolius* and the invasive *Caulerpa cylindracea*) and sessile invertebrates  
128 (such as barnacles, polychaetes and gastropods). Herbivores were also present in the form of sea  
129 urchins and limpets (see Benedetti-Cecchi & Cinelli 1996 and Maggi et al. 2012 for details on  
130 species composition). Starting from late 2008, it was observed that stands of *Cystoseira* within  
131 some rockpools were partially replaced by dense patches of *Dictyopteris*, which was formerly  
132 present at low density and in small size under the canopy (thus included within the turf) (E.Maggi  
133 pers. obs.).

### 134 2.2. Experimental design

135 Temporal regime and intensity of events of disturbance by boulders were manipulated in a crossed  
136 design. We assumed that changes in the temporal regime of disturbance generated by the scouring  
137 of boulders inside rockpools would realistically simulate the effects of changes in temporal regime  
138 of disturbance linked to large storm events. To manipulate the temporal regime, we created two  
139 different temporal sequences of presence/absence of boulders inside rockpools: continuous presence  
140 (eight months; press regime), or temporarily limited presence where boulders were present for only  
141 two months of the experiment (from mid-November until mid-January, that is  $\frac{1}{4}$  of the temporal  
142 extent of the experiment; pulse regime). The first sequence reflected events of disturbance regularly  
143 distributed across the entire duration of the experiment; while the second sequence reflected  
144 temporarily aggregated disturbance events. As events of disturbance due to rolling of boulders  
145 occurred only in association with rough sea conditions, the pulse sequence was applied during  
146 months where we expected bad weather conditions. Four rockpools were randomly assigned to each  
147 of the two sequences of temporal regime. Within each temporal regime, two of the four rockpools  
148 were randomly assigned to each of two levels of intensity of disturbance, defined as the weight of  
149 boulders per unit area:  $I_{SMALL}$  and  $I_{LARGE}$ . In the pulse sequence they consisted, respectively, of 8 kg  
150  $m^{-2}$  and 16 kg  $m^{-2}$  (8 kg  $m^{-2}$  represented the median of the observed distribution of weights of  
151 boulders per unit area; Maggi et al. 2012). To obtain a total intensity of disturbance which could be  
152 compared between sequences, for each level of intensity, the two levels of intensity were reduced to  
153  $\frac{1}{4}$  in the press level, since boulders were present four times as long in this treatment. This resulted  
154 in 2 and 4 kg  $m^{-2}$ , respectively (Table 1). To avoid confounding effects due to a different probability  
155 of being overturned during storms (Sousa 1979; McGuinness 1984), care was taken in minimizing  
156 differences in weight among boulders (we always chose boulders of about 4 to 7 kg in weight). To  
157 verify that total intensity of disturbance was comparable between sequences, we calculated *a*  
158 *posteriori* the duration of rough sea events during the study period (Table 1). Data for the study site  
159 were collected from ISPRA (Istituto Superiore per la Protezione e Ricerca Ambientale;  
160 [www.idromare.it](http://www.idromare.it); meteorological station located in Livorno). We considered the occurrence of on-

161 shore winds (with an orientation between 180° and 360°) with daily average speed  $>5.5 \text{ m s}^{-1}$   
 162 (corresponding to waves at least 1 m in height and to a Beaufort scale of 4; the waves were  
 163 considered strong enough to move boulders inside rockpools) for at least two consecutive days, or  
 164  $>12 \text{ m s}^{-1}$  (Boufort scale of 6) when the wind was blowing only for one day. A total of nine events  
 165 occurred throughout the study and impacted on assemblages in the pools ascribed to the press  
 166 treatment, and five of these events impacted the pools assigned to the pulse treatment (Table 1, Fig.  
 167 1).

168

	press		pulse	
	I <sub>SMALL</sub>	I <sub>LARGE</sub>	I <sub>SMALL</sub>	I <sub>LARGE</sub>
Weight of boulders per unit area ( $\text{kg m}^{-2}$ )	2	4	8	16
No. of days of storm acting on assemblages	43	43	12	12
Realized total intensity of disturbance ( $\text{kg m}^{-2} \times \text{no. of days}$ )	86	172	96	192

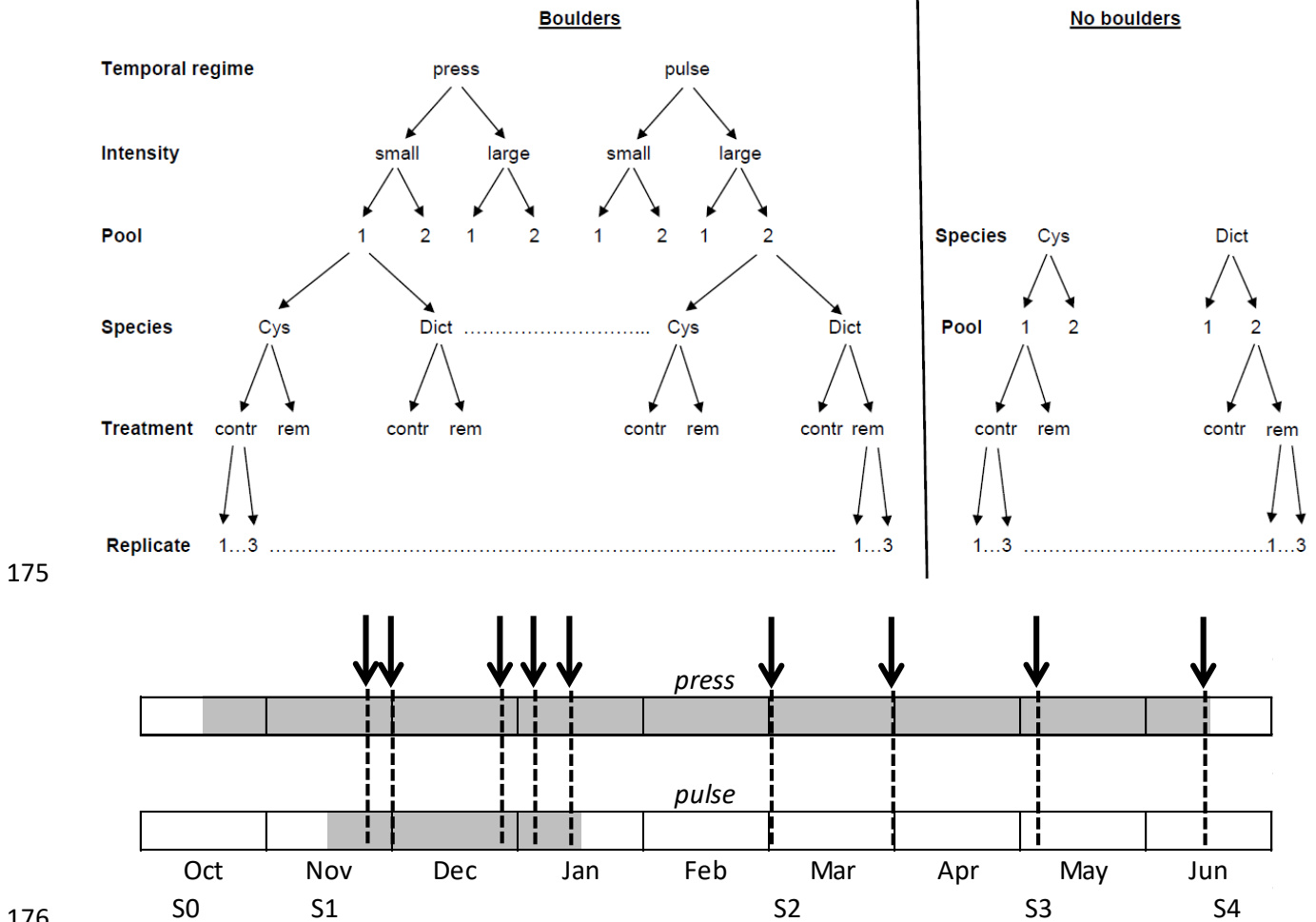
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170 **Table 1.** Applied disturbance in rockpools with a continuous (press) or temporally limited (pulse;  
 171 from mid-November to mid-January) presence of boulders. I<sub>SMALL</sub> and I<sub>LARGE</sub>: small and large  
 172 intensity of disturbance.

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177 **Figure 1.** Diagrammatic representation of the experimental design and distribution of disturbance  
 178 events over the course of the experiment (from mid-October 2009 to mid-June 2010), for each  
 179 sequence of press or pulse presence of boulders (grey). The black arrows indicate storm events  
 180 able to move boulders inside pools. S0 (set up) to S4: sampling dates.  
 181

182 Storm events lasted for a total of 12 days between mid-November and mid-January and for 31 days  
 183 during the rest of the period, resulting in comparable levels of disturbance intensity (scouring days  
 184 by boulders) between the two temporal regimes (Table 1). In order to represent the entire range of  
 185 natural intensities of disturbance, boulders were also removed from 4 additional rockpools  
 186 throughout the duration of the experiment (*No boulders* rockpools). Due to a lack of enough  
 187 rockpools where *Dictyopterus* and *Cystoseira* co-occurred, the control pools, where disturbance was  
 188 not applied, were represented by rockpools completely dominated by *Cystoseira* stands (with  
 189 *Dictyopterus* present only in the understory; n=2) or by *Dictyopterus* (where *Cystoseira* was almost

190 absent; n=2). Experimental treatments were checked and re-established after each storm event,  
191 when necessary.

192 In each of the eight rockpools assigned to press or pulse regimes of disturbance, six 9 x 9 cm  
193 quadrats 10s of cm apart, were randomly identified within the canopy of *Cystoseira* and additional  
194 six quadrats within *Dictyopteris* stands, for a total of 12 quadrats in each rockpool. Quadrats were  
195 marked at their corners with epoxy-putty (Subcoat S, Veneziani) to facilitate subsequent location.  
196 For both species, three randomly chosen quadrats were left untouched (control treatment), while  
197 axes, ramifications and holdfast of the dominant species were removed from the others throughout  
198 the study period, using a paint scraper and a knife (removal treatment). Care was taken to avoid  
199 damaging understory organisms or altering the topography of the substratum. In each of the four  
200 rockpools where boulders were continuously removed (No boulders), control and removal  
201 treatments were applied to a total of six quadrats dominated by the only species present (i.e.  
202 *Cystoseira* or *Dictyopteris*; Fig. 1).

### 203 2.3. Sampling and analyses of data

204 Rockpools were sampled at the start of the experiment (S0: set up) and four times during the  
205 experiment (S1 to S4; Fig. 1). An additional sampling was carried out in August 2011, 14 months  
206 after the end of the experimental manipulations, to check for potential long-term changes in the  
207 structure of assemblages (including identity of dominant taxa), under natural conditions of  
208 disturbance, recruitment and growth of macroalgae.

209 Percentage covers of organisms were estimated using a plastic frame of 8 × 8 cm (smaller than the  
210 marked plots, to avoid edge effects) divided into 16 sub-quadrats of 2 × 2 cm that were given a  
211 score from 0 to 4 (0 ≈ 0% coverage, 1 ≈ 25%, 2 ≈ 50%, 3 ≈ 75%, 4 ≈ 100%) for each taxon in each  
212 sub-quadrat. Final covers were obtained by summing scores over the 16 sub-quadrats (Dethier et al.  
213 1993), for a maximum score of 64. Values were then expressed as percentages. Organisms were

214 identified to the highest level of taxonomic resolution achievable in the field. Finally, diversity of  
215 species was estimated as the total number of non-manipulated taxa in each  $8 \times 8$  cm quadrat.  
216 Since experimental levels of intensity of disturbance were comparable between temporal regimes  
217 only over the entire duration of the study (Table 1), univariate data were analyzed as temporal  
218 means over the four sampling dates (ANOVA). In particular, to identify potential direct competitors  
219 of *Dictyopteris*, the percentage cover of turf was firstly analyzed as a whole and subsequently, the  
220 most abundant turf species, which differed in morphological traits, were analyzed separately. We  
221 identified filamentous algae (a set of species hardly distinguishable in the field), sheet-like algae  
222 (mostly represented by *Dictyota* spp.) and the articulated coralline *Ellisolandia elongata*. Each  
223 taxon was characterized by a mean temporal cover not lower than 5% per replicate plot. Univariate  
224 data included temporal means of diversity estimates, calculated as the total number of taxa within  
225 each quadrat (both algae and invertebrates).

226 For multivariate analyses, we first obtained the principal coordinates (PCO) (Gower 1966) from the  
227 Bray-Curtis dissimilarity matrix to place all the observations into a Euclidean space, without  
228 altering the original distances based on Bray-Curtis index. Then, for each replicate quadrat and each  
229 PCO, we averaged the values from the four sampling dates to obtain centroids of each replicate  
230 assemblage over the study period (Anderson 2001). The new multivariate dataset was analyzed  
231 through permutational multivariate analysis of variance (PERMANOVA), by applying Euclidean  
232 distances to calculate the dissimilarity matrix.

233 Rockpools with boulders were analyzed following a 5-ways design, with ‘Pool’ (random, 2 levels)  
234 nested within the interaction between ‘Intensity’ and ‘Temporal Regime’ (both fixed, 2 levels) and  
235 all factors crossed with ‘Species’ (fixed, 2 levels: *Cystoseira* and *Dictyopteris*) and ‘Treatment’  
236 (fixed, 2 levels: control and removal). To evaluate possible effects of ‘Intensity’ or ‘Temporal  
237 regime’ of disturbance (i.e. a memory of past experimental manipulations of disturbance), the data  
238 from August 2011 were firstly analyzed with the same experimental design. We then applied a  
239 simplified design with ‘Pool’, ‘Species’ and ‘Treatment’ as 3 crossed factors. Univariate and

240 multivariate data of assemblages from rockpools assigned to the No boulders treatment were  
241 analyzed separately, following a 3-ways design, with Pool nested within Species and crossed with  
242 Treatment (same levels as above). The same design was applied for the analysis of data from  
243 August 2011. Results from No boulders rockpools are described in a separate paragraph, for clarity  
244 purposes.

245 Analyses were run using the GAD package (R v 3.3.2, R Development Core Team 2016) and the  
246 ‘PRIMER 6 and PERMANOVA+’ program (©PRIMER-E 2007). Multivariate data were visualized  
247 through Canonical Analysis of Principal Coordinates (CAP) (©PRIMER-E 2007), by grouping data  
248 against significant factors detected by PERMANOVA.

249 At the end of the experimental manipulations (S4), we estimated the percentage of reduction of  
250 photosynthetic active radiation (PAR) related to the presence of *Cystoseira* or *Dictyopteris*. The  
251 percentage of reduction was calculated as the mean difference between PAR above the brown  
252 macroalga (either *Cystoseira* or *Dictyopteris*) and that above the understory assemblage (n=3 within  
253 each plot). Measures were taken by means of a light sensor mounted on a Diving PAM (WALZ).  
254 We excluded plots where the two species attained comparable coverages. Data were analyzed by  
255 regressing percentage of reduction of PAR and percentage cover of the alga, separately for  
256 *Cystoseira* and *Dictyopteris*.

### 257 **3. Results**

#### 258 3.1. Manipulated species

259 ANOVAs on percentage cover of *Cystoseira* and *Dictyopteris* confirmed that the removal treatment  
260 significantly reduced the abundance of both species (*Cystoseira*: ‘Species x Treatment’:  $F_{1,4} =$   
261 263.65,  $p < 0.001$ . *Dictyopteris*: ‘Species x Treatment’:  $F_{1,4} = 47$ ,  $p < 0.01$ ), although *Dictyopteris*  
262 reached mean values of about 20% where it was experimentally removed. Similar values of  
263 coverage of *Dictyopteris* were observed within quadrats where *Cystoseira* was removed. On the

264 contrary, *Cystoseira* did not attain more than 5% of cover within removal quadrats (Fig 2 A-B).  
265 Neither an increase in intensity nor in temporal regime of disturbance (or their interaction)  
266 significantly affected the coverage of any of the manipulated species. After 14 months since the end  
267 of experimental manipulations, coverage of *Cystoseira* was still affected by the interaction ‘Species  
268 x Treatment’ ( $F_{1,7} = 47.41, p < 0.001$ ), despite an increase in cover where it was initially removed.  
269 On the contrary, *Dictyopteris* attained comparable coverages where it was experimentally removed  
270 and left intact; it maintained larger values in removal than control quadrats within *Cystoseira* stands  
271 (‘Species x Treatment’:  $F_{1,7} = 6.16, p < 0.05$ ) (Fig. 2 D-E).

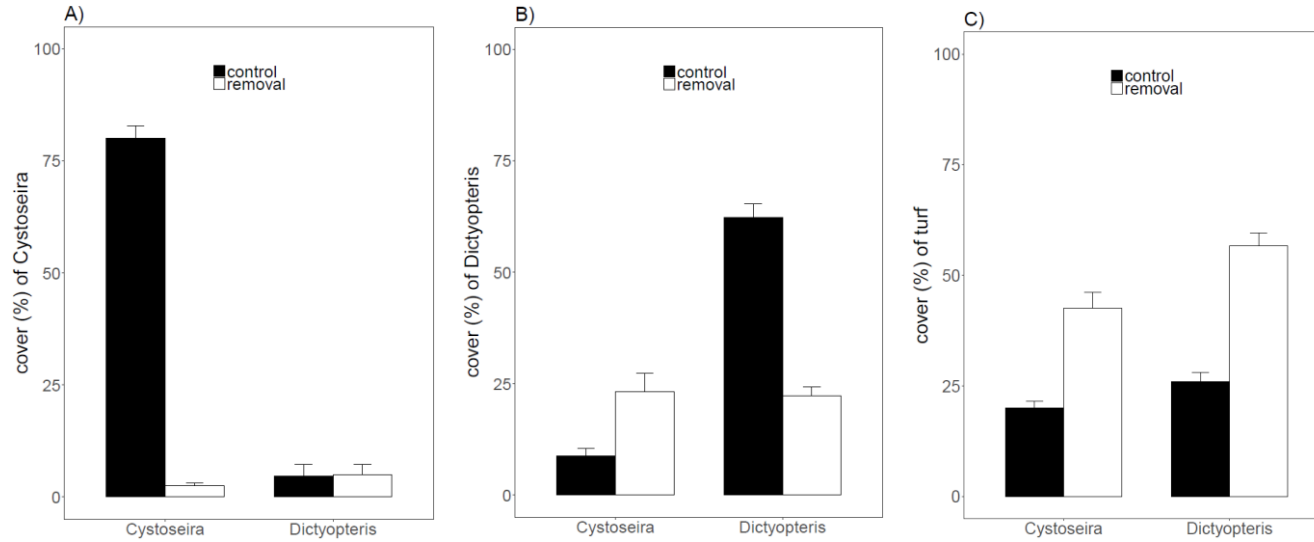
### 272 3.2. Turf

273 Total percentage cover of turf was significantly higher in quadrats within stands of *Dictyopteris*  
274 (mean percentage cover  $\pm$  1SE:  $41.38 \pm 2.83$ ) than of *Cystoseira* ( $31.33 \pm 2.52$ ) (‘Species’:  $F_{1,4} =$   
275  $8.16, p < 0.05$ ), independently of any intensity or temporal regime of disturbance. Turf coverage also  
276 increased after the removal of dominant species (‘Treatment’:  $F_{1,4} = 98.29, p < 0.001$ ) (control:  $23.05$   
277  $\pm 1.34$ ; removal:  $49.66 \pm 2.47$ ), despite large variability among rockpools (‘Pool’:  $F_{4,64} = 2.59,$   
278  $p < 0.05$ ) (Fig 2C). After 14 months, total cover of turf was not influenced by any factor, despite a  
279 trend for larger abundance in removal than control quadrats (‘Treatment’:  $F_{1,7} = 4.34, 0.05 < p < 0.1$ )  
280 (control:  $18.98 \pm 2.31$ ; removal:  $21.82 \pm 2.18$ ) (Fig. 2F).

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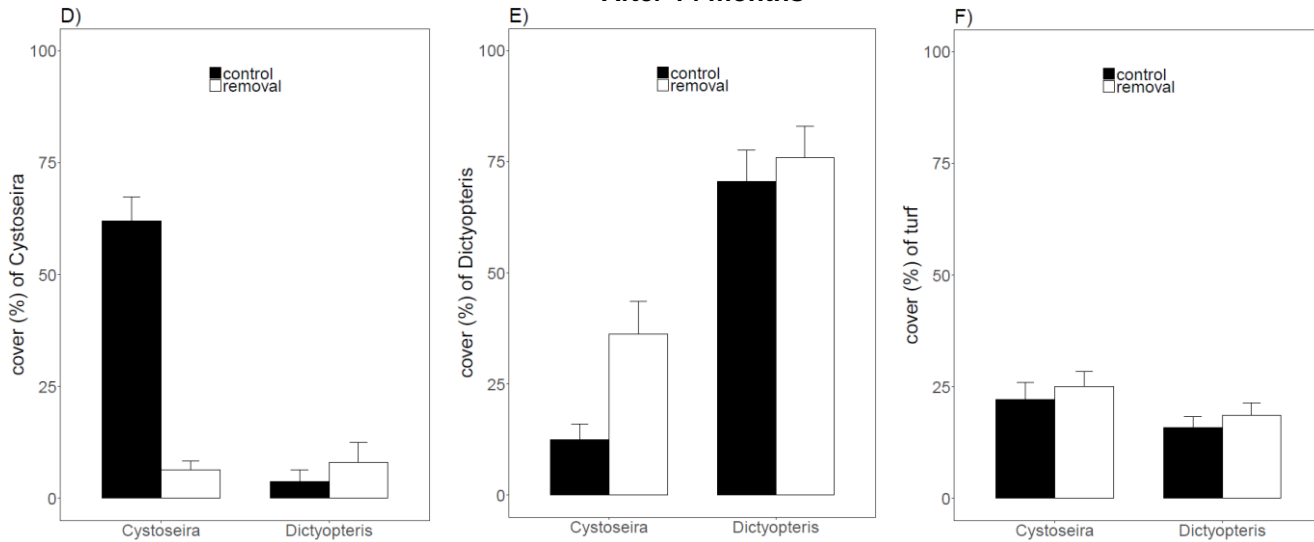
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During the study period



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After 14 months



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**Figure 2.** Mean percentage cover (+1SE) of *Cystoseira* (A, D), *Dictyopteris* (B, E) and turf (C, F), in control and removal quadrats within *Cystoseira* and *Dictyopteris* stands, across the study period (A-C; n=96) and after 14 months since the end of the experiment (D-F; n=24).

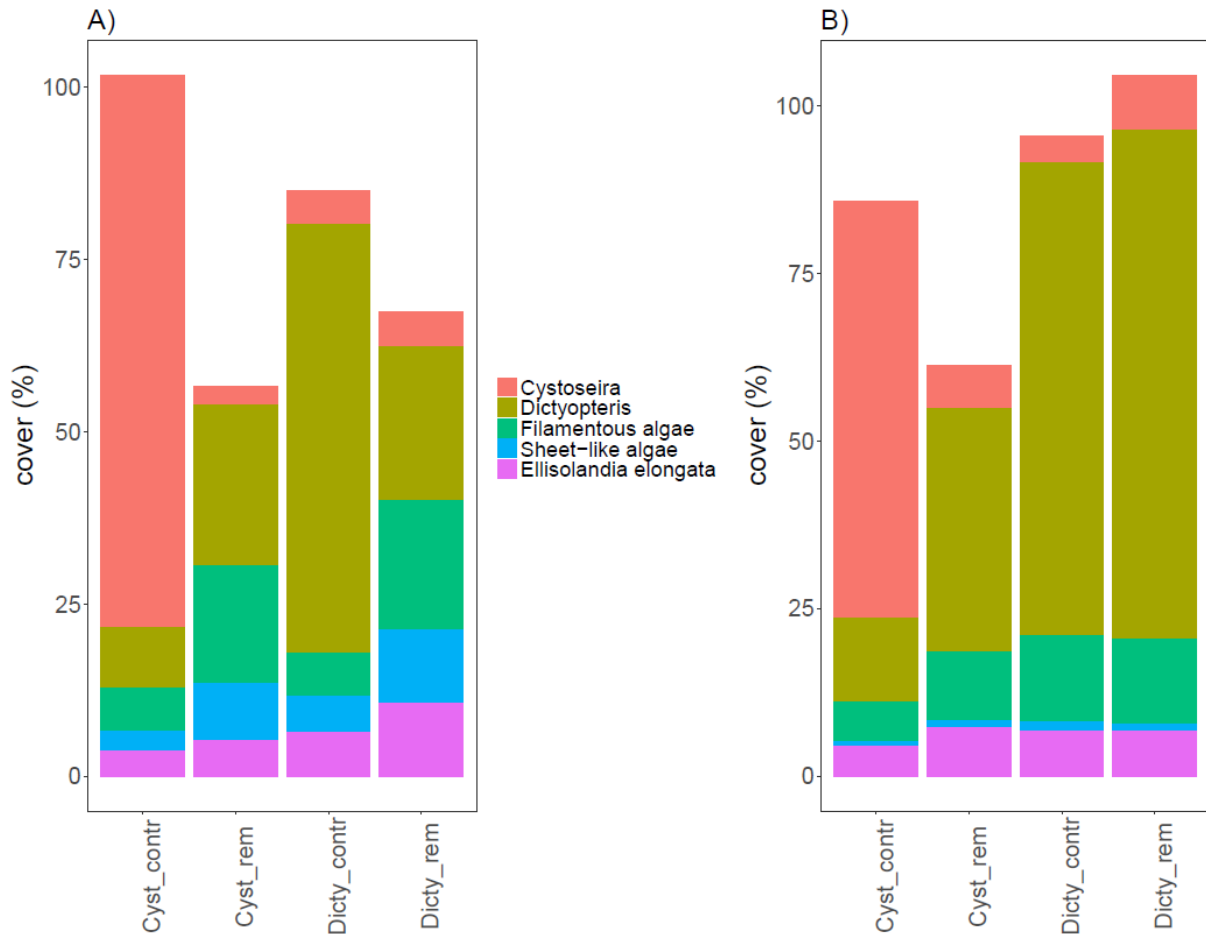
290 Among the most abundant taxa within turf, filamentous algae significantly increased when  
291 dominant species were removed ('Treatment':  $F_{1,4}=27.72$ ,  $p<0.01$ ) (control:  $6.18 \pm 0.59$ ; removal:  
292  $17.98 \pm 1.7$ ). Results also showed a significant interaction 'Pool x Species' ( $F_{4,64}=2.66$ ,  $p<0.05$ ); *a*  
293 *posteriori* analyses showed a contrasting pattern in abundance between plots within *Cystoseira* and  
294 *Dictyopteris* stands in two out of eight rockpools (press\_ISMALL\_pool a: *Cystoseira*>*Dictyopteris*;  
295 pulse\_ILARGE\_pool a: *Dictyopteris*>*Cystoseira*). After 14 months since the end of experimental  
296 manipulations, abundance of filamentous algae varied only among rockpools ('Pool':  $F_{7,64}=8.53$ ,  
297  $p<0.001$ ) (Fig. 3 A-B).

298 Analyses on sheet-like algae (mostly *D. dichotoma*) showed a significant interaction 'Temporal  
299 regime x Species x Treatment' ( $F_{1,4}=29.44$ ,  $p<0.01$ ). In particular, these algae were consistently  
300 more abundant in *removal* than *control* plots under every combination of Temporal regime and  
301 identity of Species (overall control:  $4.09 \pm 0.58$ ; overall removal:  $9.45 \pm 1.35$ ). Additional *a*  
302 *posteriori* comparison showed more variable results (*Cystoseira*\_control: pulse>press;  
303 *Cystoseira*\_removal: press>pulse; press\_control and pulse\_control: *Dictyopteris*>*Cystoseira*;  
304 press\_removal: *Cystoseira*>*Dictyopteris*). After 14 months, abundance of these algae was very low  
305 (mean cover per quadrat ~ 1%) and values were not analyzed (Fig. 3 A-B).

306 Similarly to sheet-like algae, analyses on coverage of *E. elongata* showed a significant interaction  
307 'Temporal regime x Species x Treatment' ( $F_{1,4}=9.57$ ,  $p<0.05$ ). This articulated coralline, however,  
308 was significantly more abundant in removal than control quadrats only within *Dictyopteris* stands  
309 under a *press* regime of disturbance (press\_*Dictyopteris*: removal>control). *A posteriori* comparison  
310 also showed larger covers within *Dictyopteris* than *Cystoseira* stands in two out of four  
311 combinations of Temporal regime and Treatment (press\_removal and pulse\_control:  
312 *Dictyopteris*>*Cystoseira*), as well as larger abundances under press than pulse regime of  
313 disturbance where *Dictyopteris* was removed (*Dictyopteris*\_removal: press>pulse). After 14 months

314 since the end of experimental manipulations, analysis detected only a significant variability among  
 315 rockpools ('Pool':  $F_{7,64}=2.57$ ,  $p<0.05$ ) (Fig. 3 A-B).

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318

319 **Figure 3.** Stacked bar charts showing mean percentage covers of *Cystoseira*, *Dictyopteris*,  
 320 filamentous algae, sheet-like algae (mostly *Dictyota* spp.) and *E. elongata*, in control and removal  
 321 quadrats within *Cystoseira* and *Dictyopteris* stands, across the study period (A, n=96) and after 14  
 322 months since the end of the experiment (B; n=24).

323

### 3.3. Associated assemblages

324

ANOVA showed no significant differences in diversity of associated taxa, neither before

325

experimental manipulations nor across the study period. After 14 months since the end of the

326

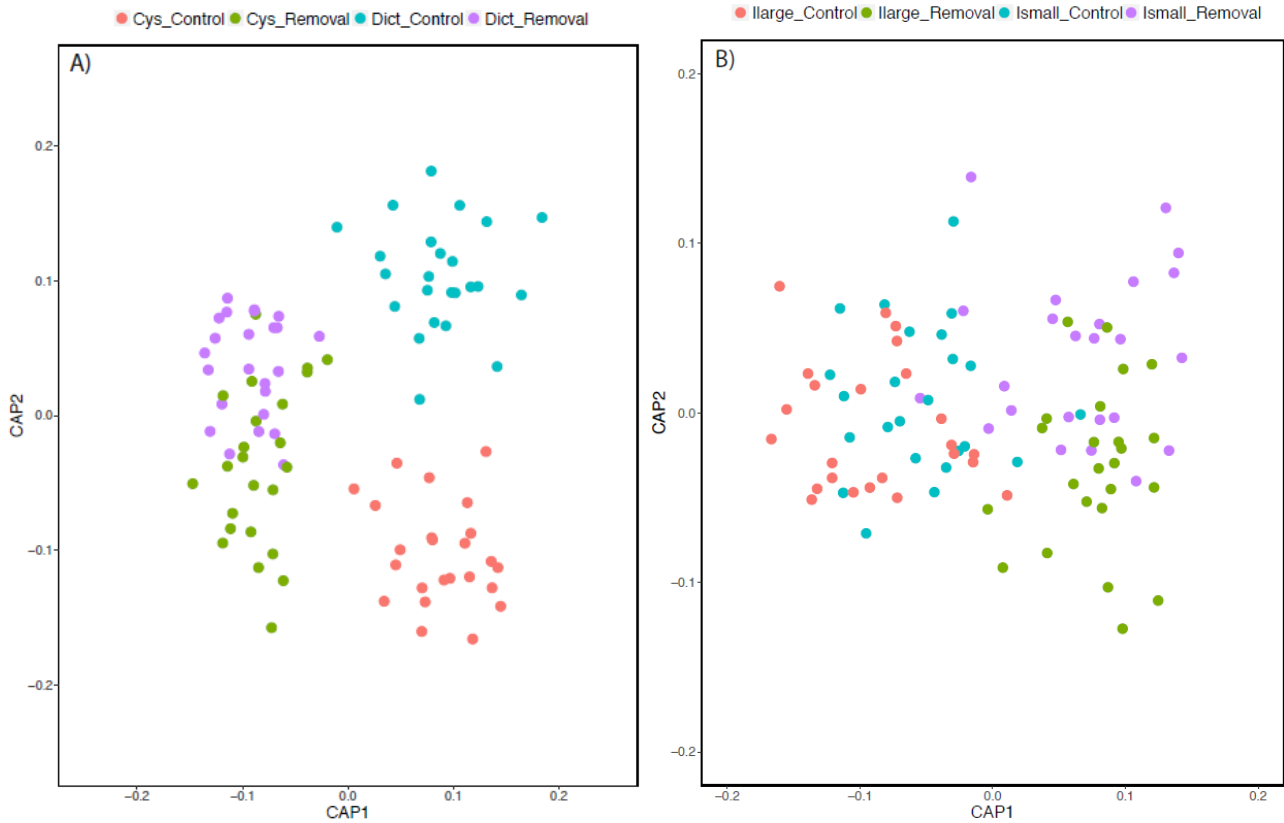
experiment, diversity was higher in removal than control quadrats only in one out of eight rockpools

327

('Pool x Treatment':  $F_{7,64} = 2.92$ ,  $p<0.05$ ).



328 PERMANOVA showed a significant difference between assemblages associated to *Cystoseira* or  
329 *Dictyopteris* (pseudo- $F_{1,4} = 3.345$ ,  $p = 0.004$ ) as well as among rockpools (pseudo- $F_{6,64} = 3.666$ ,  $p =$   
330  $0.001$ ) before the start of the experimental manipulations. Analyses on data collected during  
331 experimental manipulations showed significant interactions ‘Species x Treatment’ (pseudo- $F_{1,4} =$   
332  $1.714$ ,  $p = 0.02$ ) and ‘Intensity x Treatment’ (pseudo- $F_{1,4} = 1.611$ ,  $p = 0.028$ ), as well as differences  
333 among rockpools (pseudo- $F_{6,64} = 2.31$ ,  $p = 0.001$ ). *A posteriori* comparisons revealed that  
334 assemblages in control and removal treatments differed from each other independently of the  
335 dominant species, while assemblages dominated by *Cystoseira* differed from those dominated by  
336 *Dictyopteris* only in control quadrats (Fig 4A). Comparisons also revealed that an increase in  
337 intensity of disturbance caused no significant changes in assemblages either in control or removal  
338 quadrats, although CAP analysis showed some differentiation between  $I_{SMALL}$  and  $I_{LARGE}$   
339 assemblages in the removal treatment; on the contrary, removal and control quadrats differed from  
340 each other both with small and large intensity of disturbance (Fig 4B). After 14 months,  
341 PERMANOVA showed a significant difference in assemblages between *Cystoseira* and  
342 *Dictyopteris* stands only in three out of eight rockpools (‘Pool x Species’: pseudo- $F_{7,64} = 1.517$ ,  $p =$   
343  $0.004$ ).



344

345 **Figure 4.** Canonical Analysis on Principal coordinates (CAP) on assemblages from control and  
 346 removal quadrats associated to *Cystoseira* or *Dictyopteris* stands (A), or to small and large intensity  
 347 of disturbance (B). Each point represents the average assemblage across the 4 sampling dates,  
 348 calculated as centroids from a PCOs matrix (see Materials and Methods for further details).  
 349

349

### 350 3.4. 'No boulders' rockpools

351 Analyses on abundance of *Cystoseira* confirmed a significant reduction where it was experimentally  
 352 removed ('Species x Treatment':  $F_{1,2} = 67.43$ ,  $p < 0.05$ ); this effect persisted after 14 months since  
 353 the end of the manipulations only in one out of two rockpools ('Pool x Treatment':  $F_{2,16} = 2.855$ ,  
 354  $0.05 < p < 0.1$ ). The removal treatment was effective on *Dictyopteris* only in one out of two rockpools  
 355 during the experiment ( $F_{2,16} = 7.33$ ,  $p < 0.01$ ); after 14 months *Dictyopteris* attained comparable  
 356 coverage in its control and removal quadrats in both rockpools (Fig. A1).

357 Turf coverage increased after the removal of the dominant species ('Treatment':  $F_{1,2} = 77.77$ ,  
 358  $p < 0.05$ ); in addition, it was more abundant within rockpools dominated by *Cystoseira* compared to  
 359 those with *Dictyopteris* ('Species':  $F_{1,2} = 81.65$ ,  $p < 0.05$ ). Abundance of filamentous algae increased  
 360 following the removal treatment ('Treatment':  $F_{1,2} = 26.426$ ,  $p < 0.05$ ). A trend for a similar effect

361 was detected on sheet-like algae ('Pool x Treatment':  $F_{2,16} = 3.124$ ,  $0.05 < p < 0.1$ ; SNK:  
362 removal > control in one out of two rockpools dominated by *Cystoseira*). *E. elongata* was  
363 significantly more abundant within *Dictyopteris* than *Cystoseira* stands ('Species':  $F_{1,2} = 264.83$ ,  
364  $p < 0.01$ ). After 14 months, significant effects on filamentous algae and total turf disappeared (Fig.  
365 A2); cover of sheet-like algae and *E. elongata* was very low and data were not analyzed.

366 Diversity was significantly larger within rockpools dominated by *Cystoseira* in comparison to those  
367 dominated by *Dictyopteris* ('Species':  $F_{1,2} = 21.926$ ,  $p < 0.05$ ). In addition, the removal of  
368 *Cystoseira* increased the diversity of the associated assemblages, while the removal of *Dictyopteris*  
369 exerted the same effect only in one of the two rockpools ('Pool x Treatment':  $F_{2,16} = 3.83$ ,  $p < 0.05$ ).  
370 After 14 months, diversity varied between *Dictyopteris*-dominated rockpools ('Pool':  $F_{2,16} = 17.78$ ,  
371  $p < 0.001$ ) (Fig A3\_A-B). PERMANOVA showed significant differences in assemblages between  
372 *Cystoseira* and *Dictyopteris* stands ('Species': pseudo- $F_{1,2} = 1.824$ ,  $p = 0.037$ ), between removal  
373 and control treatments ('Treatment': pseudo- $F_{1,2} = 3.362$ ,  $p = 0.002$ ) and between rockpools  
374 ('Pool': pseudo- $F_{2,16} = 2.2$ ,  $p = 0.001$ ). After 14 months, factor 'Species' was not significant,  
375 although CAP analysis still showed a separation between plots within stands of *Cystoseira* and  
376 *Dictyopteris* ('Treatment': pseudo- $F_{1,2} = 3.575$ ,  $p = 0.021$ ; 'Pool': pseudo- $F_{2,16} = 2.63$ ,  $p = 0.002$ )  
377 (Fig. A3\_C).

### 378 3.5. Photosynthetic active radiation (PAR)

379 Sampling of PAR at the end of experimental manipulations showed a significant increase in  
380 percentage of reduction of PAR at increasing abundance of *Dictyopteris* ( $R^2=0.48$ ,  $F_{1,39}=37.15$ ,  
381  $p < 0.001$ ;  $n=42$ ). The canopy of *Cystoseira* also reduced PAR reaching the substrate. In this case,  
382 however, there was not a significant relationship with percentage cover ( $R^2=0.03$ ,  $F_{1,21} = 0.658$ ,  
383  $p=0.426$ ;  $n=24$ ); in fact, PAR was either highly (up to 99%) or moderately reduced (40-50%)  
384 independently of canopy cover.

#### 385 4. Discussion

386 Results did not detect any combination of intensity and temporal regime of disturbances able to  
387 reduce the abundance of *Cystoseira*, not even in case of extremely intense events aggregated in  
388 time. In the short term, *Dictyopteris* did not overcome turf where *Cystoseira* was experimentally  
389 eliminated under any regime of disturbance. In fact, turf attained consistent large coverages (around  
390 50%) in quadrats where either *Cystoseira* or *Dictyopteris* was removed; analyses on most abundant  
391 turf taxa revealed that *Dictyopteris* reached similar percentage covers as filamentous algae, and both  
392 were followed in abundance by other sheet-like algae (mostly *Dictyota* spp.) and the articulated *E.*  
393 *elongata*. Only under these conditions, assemblages were susceptible to an increase in intensity of  
394 events of disturbance. Dominance by *Dictyopteris* over turf was observed in the long term (i.e. after  
395 more than a year since the end of manipulations) under all removal conditions; nevertheless, it was  
396 more evident in removal plots within *Dictyopteris* than *Cystoseira* stands.

397 The Mediterranean Basin is considered a hot spot for *Cystoseira* species, but the impact of human  
398 activities were directly and/or indirectly responsible for significant declines of *Cystoseira* beds from  
399 infra-littoral and subtidal habitats (Benedetti-Cecchi et al. 2001; Hereu et al. 2008; Mangialajo et al.  
400 2008; Thibaut et al. 2014). Extreme climatic events can potentially contribute to erode these algal  
401 forests, as shown by the significant effects exerted by an exceptional storm event on deep-water  
402 populations of *Cystoseria zosteroides* (Navarro et al. 2011). A previous experiment conducted at the  
403 same location as the present study showed that *Cystoseira* could be affected by highly intense  
404 disturbance events due to rolling of boulders inside rockpools, during regularly distributed storm  
405 events; this effect was likely due to insufficient time for the species to recover among disturbance  
406 events (Maggi et al. 2012). The lack of effects under similar conditions in the present study could  
407 be explained by differences in the weight of boulders per unit area that were used to characterize the  
408 high intensity press disturbance events in the two studies. In the first study the authors used  $8 \text{ kg m}^{-2}$

409 while we used 4 kg m<sup>-2</sup>. Therefore, we cannot exclude that highly intense storm events might  
410 contribute to the future decline of shallow patchy forests of *Cystoseira* along Mediterranean coasts.

411 Turf- and canopy-dominated assemblages are considered as alternative states on temperate rocky  
412 reefs (Benedetti-Cecchi et al 2015, Rindi et al 2017). At small spatial scale, turfs are expected to  
413 dominate if *Cystoseira* is removed by events of disturbance acting at any time, except during the  
414 reproductive event of the canopy-forming alga (Benedetti-Cecchi 2000). Fast growth and multiple  
415 reproductive events, as well as the ability of trapping sediment, have been recognized as key  
416 mechanisms involved in the maintenance of a turf-dominated state along temperate Mediterranean  
417 coast (e.g. Benedetti-Cecchi and Cinelli 1996, Airoidi 1998). Nonetheless, the abundance of single  
418 turf species may vary at small spatial and temporal scales (Benedetti-Cecchi 2000) and differences  
419 in distinctive life-history traits within the same assemblage (e.g., morphology, frequency and period  
420 of reproduction, growth rate, resource uptake, chemical defenses against herbivores) might affect  
421 how algal turf as a whole interact with algal canopies under variable regimes of disturbance  
422 (Bertocci et al. 2017). In fact, this may determine changes in relative abundances of species and  
423 even dominance, driven and reinforced by new feedback mechanisms (Suding et al. 2004). Short  
424 term results did not confirm our expectations, as neither *Dictyopteris* nor other singular turf taxa  
425 dominated removal plots under any disturbance conditions. In this study, short-term dynamics  
426 driving the overall dominance of turf over canopy-forming species are likely linked to a  
427 combination of different life traits among turf algae, and are not influenced by variable mechanical  
428 disturbances. Heterogeneity in life traits, however, determined a hierarchy in abilities of space  
429 occupancy, with *Dictyopteris* and filamentous algae reaching larger covers than other sheet-like  
430 algae and *E. elongata*. Filamentous algae includes numerous species, characterized by temporally  
431 different reproductive events, which result in overall frequent reproductive outputs. This feature, in  
432 addition to a high maximum specific growth rate and rapid nutrient uptake, arguably determined a  
433 good competitive ability on the short term, especially in presence of open space (Rindi and Cinelli  
434 2000; O'Brien and Scheibling 2018). Differently, the increase in cover of *Dictyopteris* after the

435 removal of *Cystoseira* should be mostly ascribed to a vegetative growth starting from December up  
436 to July (Feldmann 1937). It is worth noting, however, that frequent growth of new thalli during the  
437 experiment (including under removal of *Dictyopteris* itself; auth. pers. obs.) suggests that this alga  
438 could be fertile and reproduce not only during summer months (differently to what reported by  
439 Feldmann 1937). Overall, these traits resulted in larger competitive ability of filamentous algae  
440 and *Dictyopteris* in comparison to *Dictyota* spp. and *E. elongata*, which are generally fertile in a  
441 temporarily limited period during the year (in May/June and September, respectively; Feldmann  
442 1937, 1939) and are characterized by a lower mass-specific productivity than filamentous algae  
443 (especially *E. elongata*) (Littler and Littler 1984; Steneck and Dethier 1994). Nevertheless, on a  
444 longer time scale *Dictyopteris* was able to outcompete the rest of turf, probably due to larger size of  
445 adult thalli. This morphological trait likely acted as a positive, density-dependent feedback in  
446 reinforcing competitive abilities of the alga. Inside these rockpools, in fact, *Dictyopteris* is  
447 characterized by a relatively simple architecture, with a small holdfast and a sheet-like thallus with  
448 a midrib and a few dichotomies. An increase in cover can thus be considered as positively  
449 correlated with density of individuals. Once it was established and fully grown, thalli outcompeted  
450 other primary producers by intercepting more light, as the coverage (and likely density) of  
451 *Dictyopteris* increased, as confirmed by PAR values. It is possible that the production of chemical  
452 defenses also favored this species in presence of mesograzers, to the detriment of more palatable  
453 ephemeral algae within the turf (Schnitzler et al. 2001).

454 Shifts from canopy- to turf-dominated assemblages usually determine a net decrease in the  
455 ecological, aesthetic and economic value of the habitat, because of changes in species composition,  
456 diversity and biomass of organisms (Benedetti-Cecchi et al. 2001, Benedetti-Cecchi et al. 2015,  
457 Wernberg et al. 2016). Our study confirmed a change in the structure of assemblages when  
458 *Cystoseira* was removed, but revealed further differences when plots dominated by *Dictyopteris*  
459 were compared to those more evenly colonized by numerous turf species (i.e. in removal plots at the  
460 end of experimental manipulations). This included an impoverishment in diversity of assemblages

461 where the replacement of *Cystoseira* by *Dictyopteris* took place in areas as large as our rockpools  
462 (see differences in diversity in No boulders rockpools). Differences between *Cystoseira*- and  
463 *Dictyopteris*-dominated assemblages were likely related to algal morphologies, which implied  
464 differences in availability of light or space (both in terms of total area and spatial arrangement  
465 (Chemello and Milazzo 2002). Firstly, the sheet-like thalli of *Dictyopteris* do not provide as much  
466 primary space or complex secondary substratum as those supplied by the canopy of *Cystoseira*.  
467 Secondly, morphological differences between the two brown seaweeds have implications for light  
468 availability. Contrary to *Dictyopteris*, *Cystoseira* did not show a significant relationship between  
469 PAR reduction and cover; this suggests a patchiness in light distribution under the canopy, likely  
470 due to fronds' morphology as well as wave action, as observed on kelps (Gerard 1984; Wing et al.  
471 1993). On the contrary, where *Dictyopteris* was fully grown and at high abundance, we observed a  
472 significant PAR reduction, indicating that this species was blocking the penetration of light to the  
473 substrate, influencing the presence of other species (i.e. inhibiting most macroalgae, but favoring  
474 species such as the invasive alga *C. cylindracea* or serpulids).

475 Under removal conditions, *Cystoseira* was almost absent, while *Dictyopteris* started re-colonizing  
476 plots but only at relatively low abundance and small size, so that numerous turf species could rely  
477 on larger availability of light for growth. Only under these conditions, benthic organisms were  
478 susceptible to an increase in intensity of events of disturbance. While a protection by *Cystoseira* of  
479 associated assemblages against physical disturbance may be expected (Bertocci et al. 2010), the  
480 possible role of *Dictyopteris* in buffering effects of mechanical stressors deserves further  
481 investigation. Importantly, these results highlight how changes in feedback mechanisms  
482 maintaining degraded states may influence the ability of the system to withstand an extreme abiotic  
483 stress (Maxwell et al. 2016).

484 Understanding how the progressive fragmentation of canopies alter the structure, functioning and  
485 resistance of macroalgal forests is of key importance for *Cystoseira* species, currently under threat

486 in the Mediterranean Sea. Studies on restoration of *Cystoseira* beds highlighted the importance of  
487 reversing human-derived conditions that could induce further loss or prevent recruitment of this  
488 species (Perkol-Finkel and Airoidi 2010). As a possible solution, a few studies have proposed that  
489 an active translocation of recruits could be an efficient approach for restoring highly isolated stands,  
490 due to the low dispersal capacity of propagules (Perkol-Finkel et al. 2012) (Gianni et al. 2013). Our  
491 results warns about the presence, within the turf, of species characterized by distinctive competing  
492 life traits, and potentially able to dominate assemblages through positive density-dependent  
493 feedback mechanisms. Furthermore, the consequent modification of the multivariate structure of  
494 assemblages might influence the resilience or resistance of the new degraded system to climatic  
495 extremes. Our results are in accordance with the idea that alternative states to canopy beds  
496 incorporate positive feedbacks and are internally reinforced states (Suding et al. 2004). This  
497 approach recognizes that the dynamics of the degraded states are usually different from those of the  
498 pristine habitats, due to species effects (either native or exotic), trophic interactions, connectivity  
499 and long-term climatic changes (Suding et al. 2004). Therefore, restoration efforts might focus not  
500 only on the removal of factors/processes that can lead to the original collapse, but on the  
501 management of complex interactions, as for instance those between life-traits of new coexisting  
502 species (including invasive ones and herbivores) and predicted changes in climatic extremes.  
503 Deepening our understanding on all these factors will provide the necessary knowledge to avoid  
504 approaching critical states, where slight perturbations might trigger abrupt shifts in the ecosystem  
505 state (Benedetti-Cecchi et al. 2015; Rindi et al. 2017), as well as to optimize restoration activities on  
506 Mediterranean macroalgal forests (Perkol-Finkel et al. 2012; Gianni et al. 2013).

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#### 509 **Conflicts of interest**



510 The authors declare no conflict of interest.

## 511 **Author's contributions**

512 EM and LBC conceived the ideas and designed the experiment; EM and EP collected the data; EM  
513 performed statistical analysis; EM wrote the first draft of the manuscript. All authors contributed on  
514 subsequent drafts and gave final approval for publication.

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