

1 Running head: multiple perturbations on rocky shores

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3 COMPOUNDED PERTURBATIONS IN COASTAL AREAS: CONTRASTING  
4 RESPONSES TO NUTRIENT ENRICHMENT AND THE REGIME OF STORM-RELATED  
5 DISTURBANCE DEPEND ON LIFE-HISTORY TRAITS

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27 **Summary**

28 **1.** Natural systems are exposed to compounded perturbations, whose changes in temporal  
29 variance can be as important as those in mean intensity for shaping the structure of  
30 assemblages. Specifically, climate-related physical disturbances and nutrient inputs due to  
31 natural and/or anthropogenic activities occur concomitantly, but experimental tests of the  
32 simultaneous effects of changes in the regime of more than one perturbation are generally  
33 lacking. Filling this gap is key to understand ecological responses of natural assemblages to  
34 climate-related change in the intensity and temporal patterning of physical disturbance  
35 combined with other global stressors.

36 **2.** Responses to factorial manipulations of nutrient enrichment, mean intensity and temporal  
37 variability of storm-like mechanical disturbance were examined, using benthic assemblages of  
38 tide-pools as model system.

39 **3.** Response variables were mean abundance values and temporal variances of taxa with  
40 different life-traits. Consistent negative effects of disturbance intensity were observed for the  
41 mean cover of long-living taxa (algal canopies and the polychaete *Sabellaria alveolata*), whose  
42 temporal fluctuations were also reduced by more severe mechanical stress. More resilient taxa  
43 (ephemeral algae, mostly green of the genus *Ulva*) increased under enriched conditions,  
44 particularly when low intensity events were irregularly applied over time. Opposite effects of  
45 disturbance intensity depending on nutrient availability occurred on filamentous algae (e.g. red  
46 of the genus *Ceramium*). This was probably due to the fact that, although nutrient enrichment  
47 stimulated the abundance of both algal groups, when this condition was combined with  
48 relatively mild physical disturbance the competitively superior ephemeral green algae tended to  
49 become dominant over filamentous red algae. The same did not occur under high intensity of  
50 disturbance since it likely damaged large, foliose fronds of *Ulva*-like forms more than small,  
51 filamentous fronds of *Ceramium*-like forms. Grazers were positively affected by nutrients,  
52 likely responding indirectly to more food available.

53 4. A direct relationship between the mean abundance of most organisms and their temporal  
54 fluctuations was documented. However, all organisms persisted throughout the study, even  
55 under experimental conditions associated to the largest temporal variation of their abundance,  
56 likely due to their ability to resist to/quickly recover from, the applied perturbations. Therefore,  
57 in systems with great recovery abilities of dominant organisms (e.g. rocky intertidal,  
58 grasslands), effects of traits of the regime of disturbance and nutrient enrichment may modulate  
59 the fluctuations of populations not through the elimination and substitution of species, but  
60 through changes in relative abundances of the same species. This contrasts with the theory that  
61 temporal variation in abundance would be directly related to the risk of local extinction.  
62 Present findings enable more accurate predictions of the consequences of climatic and non-  
63 climatic scenarios on the biodiversity of marine and terrestrial systems sharing analogous  
64 functional traits of organisms. Future more intense physical disturbances are expected to exert  
65 negative effects on slow growing/recovering species (e.g. habitat-formers) irrespectively of the  
66 temporal patterning of the same disturbances and nutrient inputs. On the contrary, more  
67 resistant species (e.g. encrusting algae on rocky shores or below-ground vegetation in  
68 grasslands) are expected to benefit from intense physical disturbance. Species whose  
69 abundance is more directly related to the availability of nutrients (e.g. filamentous and  
70 ephemeral algae or herbs) are expected to generally increase under enriched conditions, but  
71 their ability to eventually become dominant would depend on their ability to grow fast and  
72 attain cover large enough to overwhelm any possible control of concomitant disturbance  
73 intensity on their abundance. If, such as in the present examined system, virtually all organisms  
74 can persist, over the temporal scale of the experiment, under any combination of physical  
75 disturbance and nutrient availability, the resulting overall diversity is not predicted to change  
76 drastically. Nevertheless, low intensity events evenly distributed and high intensity events  
77 irregularly distributed appear as the conditions supporting the highest richness of taxa,  
78 independently of the availability of nutrients.

79

80 **Key-words:** climate change, eutrophication, mean intensity, rocky intertidal, storminess,  
81 temporal variance

82

### 83 **Introduction**

84 Human disturbances are critical drivers of changes on spatial and temporal patterns of  
85 distribution, abundance and diversity of populations and assemblages in both terrestrial (Ellis  
86 *et al.* 2010; Tognetti & Chaneton 2015) and marine (Halpern *et al.* 2008; Doney *et al.* 2012)  
87 systems. Anthropogenic transformations of the environment, occurring at faster rates than most  
88 natural disturbances, threaten the ability of natural systems to maintain their basic processes,  
89 making the understanding of the consequences of such changes a main focus of ecology  
90 (Thomas *et al.* 2004; Ruokolainen *et al.* 2009) and society (Lubchenco 1998; Costanza *et al.*  
91 2014).

92 A key challenge in the study of disturbance is its variability in a range of attributes,  
93 including the intensity, timing and extent of individual events (Sousa 1984; Pickett & White  
94 1985) and the temporal and spatial patterns changing in frequency (Collins 2000; McCabe &  
95 Gotelli 2000), variance (Bertocci *et al.* 2005; Benedetti-Cecchi *et al.* 2006; Pausas, Lloret &  
96 Vilá 2006; Buckley & Kingsolver 2011; García-Molinos & Donohue 2010, 2011) and  
97 correlation (Banitz *et al.* 2008; Tamburello *et al.* 2014). Despite this complexity, a number of  
98 past studies have focused on a single trait of disturbance, such as its mean intensity or spatial  
99 extent as drivers of biological invasions (Belote *et al.* 2008; Clark & Johnston 2011), or have  
100 assumed steady levels of stress along gradients through time, such as experimental tests of the  
101 influence of increasingly harsher environmental conditions on negative vs. positive biological  
102 interactions (Brooker *et al.* 2008). Following the recognition of confounding issues inherent in  
103 the traditional approach of manipulating temporal variability in terms of frequency of events  
104 and the implementation of a framework suitable to separate the effects of variability *per se*

105 from those of the overall intensity of disturbance (Benedetti-Cecchi 2003), several studies have  
106 involved crossed levels of intensity and temporal variance of disturbance. Manipulative  
107 (Bertocci *et al.* 2005; Benedetti-Cecchi *et al.* 2006; García-Molinos & Donohue 2010; Miller,  
108 Roxburgh & Shea 2011) and simulation (Bulleri *et al.* 2014) studies provided evidence that  
109 changes in the temporal variance of disturbance can be as important as those of the mean  
110 intensity for shaping the structure of exposed assemblages. Such findings are crucial to  
111 understand and predict responses of populations and assemblages under climate change  
112 characterized by alterations of the mean intensity and temporal variability of meteorological  
113 variables (Easterling *et al.* 2000, Maestre, Salguero-Gómez & Quero 2012).

114 In addition, natural systems are exposed to compounded perturbations interacting with  
115 each other in complex ways (Paine, Tegner & Johnson 1998; Clark & Johnston 2005; Martone  
116 & Wasson 2008; Pincebourde *et al.* 2012). Climate-related events, in particular, occur in  
117 complex combinations (Darling & Côté 2008), but have been examined simultaneously only in  
118 relatively few cases (e.g. Martin & Gattuso 2009; Russell *et al.* 2009; Connell & Russell 2010).

119 Multiple anthropogenic stressors may alter the structure of communities by causing the  
120 elimination/decline of some species and the appearance/increase in abundance of others able to  
121 take advantage of new resources made available (Grime 1998; Zavaleta *et al.* 2009).

122 Examining how and under which circumstances such shifts occur is needed in both terrestrial  
123 and marine habitats. Specifically, human-dominated landscapes are increasingly reduced to  
124 patches of native vegetation embedded in larger areas converted to agriculture and pasture  
125 (Ellis *et al.* 2010). Human disturbances, such as burning for ultimate agriculture purposes and  
126 grazing by cattle (e.g. Laterra *et al.* 2003; Westerling *et al.* 2006), can directly affect dominant  
127 plant species (Mazía *et al.* 2010) and indirectly modify the availability of resources, including  
128 soil nutrients (Gross, Mittelbach & Reynolds 2005; Besaw *et al.* 2011). Analogously, marine  
129 coastal systems are exposed to the impact of waves during storms and to increases of nutrient  
130 inputs due to terrestrial runoff associated with the overuse of land and deforestation (Ambasht

131 & Ambasht 2003). Nutrient inputs into coastal systems are a global phenomenon which has  
132 increased in the last decades, with direct positive effects on primary producers (Nielsen 2001)  
133 and indirect interactions with biological processes, including grazing (Worm, Lotze & Sommer  
134 2000; Hillebrand 2003). Climate change-related physical disturbance and nutrient  
135 inputs/availability are strictly interlinked through increasing erosion and runoff due to the  
136 anthropogenic alteration of the hydrological cycle (French 1997). In fact, changes in the  
137 intensity and in spatial and temporal patterns of precipitation, usually associated with storms,  
138 are positively related to the delivery to coastal waters of nutrient-rich water from inland  
139 agricultural fields, industrial plants and urban areas (e.g. McClelland & Valiela 1998; Cloern  
140 2001; DeBruyn & Rasmussen 2002).

141 It is widely recognized that disturbance can critically shape community structure through  
142 positive and negative mechanisms critically depending on life-traits of exposed organisms (e.g.  
143 Huston 1994). Dominant organisms can be removed proportionally to the intensity of  
144 disturbance (e.g. Benedetti-Cecchi 2000), consequently releasing resources usable by other  
145 species (Shumway & Bertness 1994; Bertocci *et al.* 2005). As indicated by a number of  
146 classical studies, the response of individual taxa to possibly analogous disturbances is driven  
147 by their ability to cope with the balance between increased mortality/emigration and the  
148 availability of opportunities for colonization/immigration determined by the release of new  
149 resources (Connell 1978; Huston 1979, 1984; Sousa 1979, 1984; Pickett & White 1985;  
150 Connell, Hughes & Wallace 1997). For example, the timing of disturbance relative to that of  
151 reproduction and recruitment of organisms is key to modulate their actual ability to colonize  
152 disturbed habitats (Dayton *et al.* 1984; Breitburg 1985), while disturbed patches differing in  
153 size and isolation can be re-occupied by species with different dispersal and competitive  
154 abilities (Keough 1984; Shumway & Bertness 1994). On the other hand, nutrients can increase  
155 algal productivity, especially under reduced grazing pressure, but the abundance of herbivores

156 can be decoupled from that of resources depending on their preferences for more palatable  
157 food, such as non-calcified algae in tide pools (Nielsen 2001).

158       However, several previous experimental and observational studies aimed at examining  
159 general responses of populations and assemblages to disturbance have overlooked the effects of  
160 productivity (e.g. Mackey & Currie 2001), while taking them into account is required to assess  
161 general disturbance/species diversity relationships (Huston 2014). Simultaneous manipulations  
162 of multiple traits (mean intensity and temporal variance) of mechanical disturbance and the  
163 availability of nutrients are needed to test for their interactions under realistic scenarios of  
164 compounded environmental stressors (but see Bertocci *et al.* 2015).

165       The present study used benthic assemblages of algae and invertebrates from tide-pools as  
166 model system to contribute to fill this gap. Assemblages from rocky intertidal habitats were  
167 considered a convenient study system as they are exposed to variable physical conditions that  
168 can affect their structure or even become detrimental to their life (Bertness & Leonard 1997).  
169 Specifically, increasing intensity and temporal variability of storms and precipitation may  
170 enhance physical disturbance (Underwood 1998) and nutrient inputs (Díez *et al.* 1999), which,,  
171 possibly modulated by biological interactions (Dayton 1971; Levin & Paine 1974; Williams,  
172 Bracken & Jones 2013), may exert quantifiable effects on such assemblages.

173       Levels of intensity and temporal variability, intended as changes in the variance of events  
174 with the same overall frequency, of storm-like mechanical disturbance and nutrient enrichment  
175 were manipulated in a multi-factorial design, examining mean values and temporal fluctuations  
176 of abundance of individual taxa and of the richness of taxa as response variables. It was  
177 hypothesized that the combination of large variance and severe intensity of disturbance could  
178 determine markedly different responses depending on life-traits of organisms (Fig. 1). In fact,  
179 large temporal variance implies that several events occur over short intervals, alternating with  
180 prolonged periods lacking disturbance (Benedetti-Cecchi 2003). Therefore, populations of  
181 relatively long-living species characterized by episodic recruitment and/or low dispersal (Caley

182 *et al.* 1996), such as habitat-forming macroalgae and invertebrates, would be exposed to more  
183 extreme physical conditions under disturbance events occurring with large, compared to small,  
184 temporal variance. On the contrary, ephemeral species might take advantage of the same  
185 condition as a consequence of the released resources (Dayton 1971). Such effects were  
186 expected to be related to the mean intensity of disturbance as it was reasonable to assume that  
187 effects characterized by the same temporal variance were exacerbated by higher, compared to  
188 lower, intensity. Specifically, a series of intense disturbances operating at short intervals was  
189 predicted to reduce the mean value and, thus, to dampen the temporal fluctuations of  
190 abundance of less resilient taxa over the experimental period (Taylor 1961). Taxa with quick  
191 recovery ability, instead, even if temporarily reduced by intense disturbance, would have re-  
192 established large densities in short times, which, combined with the effect of the concomitant  
193 reduction of potential competitors, would have determined larger mean values and larger  
194 fluctuations in abundance under high intensity and large variance compared to low intensity  
195 and small variance of disturbance. Effects of intensity and temporal variability of disturbance,  
196 however, were hypothesized to depend on the increased availability of nutrients, which can  
197 determine an increase in the abundance of ephemeral, fast-growing macroalgae, often followed  
198 by a decline of perennial, slow-growing species (Valiela *et al.* 1997; Raffaelli, Raven & Poole  
199 1998). If this was true for the studied system, increased concentration of nutrients could have  
200 maintained temporally consistent larger abundances of fast-growing (e.g. ephemeral algae) and  
201 fast-colonizing (e.g. grazing gastropods) and lower abundances of less resilient (e.g. algal  
202 canopies and habitat-forming polychaetes) organisms, counteracting any effect of concomitant  
203 disturbance events compared to the natural nutrients conditions. Such issues applied also to the  
204 richness of taxa (Fig. 2), as the effects of “extreme” combinations of intensity and variability of  
205 disturbance could be expected to reverse between low- and high-nutrient conditions (reviewed  
206 by Huston 2014). Low growth rates associated with low productivity could support high levels  
207 of richness of taxa only under mild disturbances causing low levels of mortality, as very severe



208 disturbances would drive populations to extinction. On the contrary, when growth rates  
209 associated with high productivity are high, high levels of richness could be determined by  
210 severe disturbance causing high levels of mortality required to prevent competitive exclusion.  
211 Although this study focused on a single location and particular aspects of environmental  
212 change, it addressed the general issue of how climate-related disturbance, changing in mean  
213 intensity and temporal variance and combined with other globally relevant anthropogenic  
214 stressors, drives patterns of biodiversity in rocky shores and possibly other systems  
215 characterized by analogous functions and life-traits of dominant organisms.

216

## 217 **Materials and methods**

### 218 STUDY SITE AND EXPERIMENTAL DESIGN

219 The study was carried out between February 2012 and September 2013 in the mid-shore  
220 (0.5 m to 1 m above Chart Datum) tide-pool habitat located along 1 km of rocky coast in  
221 northern Portugal (between 41°42'01''N and 41°42'16''N). This system and hosted benthic  
222 assemblages are described in detail elsewhere (Bertocci *et al.* 2012, 2015). Briefly,  
223 conspicuous elements of assemblages are canopy-forming macroalgae, including the kelp  
224 *Laminaria ochroleuca* Bachelot de la Pylaie and the smaller red *Mastocarpus stellatus*  
225 (Stackhouse) Guiry, *Chondrus crispus* Stackhouse and *Gigartina pistillata* (S. G. Gmelin)  
226 Stackhouse (Bertocci *et al.* 2010), encrusting Corallinales (mostly *Lithophyllum* spp.), red  
227 filamentous (e.g. *Ceramium* spp. and *Polysiphonia* spp.) and ephemeral green algae (*Ulva*  
228 spp.). Sessile invertebrates are mostly represented by the reef-forming polychaete *Sabellaria*  
229 *alveolata* (L.), and grazers by top-shells (*Gibbula* spp.), limpets (*Patella* spp.) and sea urchins  
230 (*Paracentrotus lividus* Lamarck).

231 At the beginning of the study, three pools were left unmanipulated as control and three  
232 were randomly assigned to each combination of the following treatments: intensity (low vs.  
233 high), temporal variability (small vs. large, represented by regular or irregular distribution of

234 events, respectively) and sequence (two temporal patterns, replicated only within the large,  
235 irregular level of variability) of mechanical disturbance, and nutrient availability (natural vs.  
236 enriched). Three 35 x 35 cm plots were marked in each pool (Fig. 3 A). Experimental  
237 disturbance, simulating the mechanical impact of waves during severe storms (Bertocci *et al.*  
238 2005), was performed by battering the substratum of each plot with a rubber-covered chisel  
239 mounted on a battery hammer. The area of each plot was disturbed once or twice in a row to  
240 produce, respectively, the low (LI) and the high (HI) level of intensity. The temporal variability  
241 was manipulated (see Fig. 3 B) by performing a total of five events of disturbance distributed  
242 regularly at four-months intervals (small level: Reg) or irregularly (large level: Irr) according  
243 to clustered events interspersed within longer periods lacking disturbance (Benedetti-Cecchi  
244 2003; Bertocci *et al.* 2005). Two random sequences (S1 and S2) of events characterized by the  
245 same value of variance of the intervals of time between consecutive disturbances were  
246 replicated within the Irr level to separate the actual effects of temporal variability from those of  
247 the particular pattern of events used to produce the intended level of variability. Nutrient  
248 enrichment was produced by deploying 200 g of slow-release fertilizer pellets (Osmocote®  
249 Exact® Standard, NPK: 15-3.9-9.1 + 1.5 Mg) in each of two PVC dispensers applied in each  
250 pool assigned to this treatment. Pellets were replaced every two months. Full details on  
251 experimental procedures and design, data on the effectiveness of the enrichment treatment and  
252 information on the links between manipulated and natural events of disturbance are reported in  
253 Bertocci *et al.* (2015).

254

## 255 SAMPLING AND STATISTICAL ANALYSES

256 The percentage cover of sessile organisms and the number of individuals of mobile  
257 animals were visually (Dethier *et al.* 1993) estimated, in the three plots of each pool, at each of  
258 ten times established over the duration of the experiment, as illustrated in Fig. 3.

259 The mean value and the temporal variance of the abundance of conspicuous taxa and of  
260 the richness of taxa were analysed with ANOVA, for which the three plots in each pool were  
261 averaged and the three pools assigned to each experimental condition provided the replicates.  
262 The analysis was based on an asymmetrical design involving the partitioning of the total  
263 variability into the 'Control vs. Treatments' contrast and the 'Among treatments' variation.  
264 The latter was also partitioned into the main effect of each factor and their interactions, with  
265 the 'Temporal variability' of disturbance further partitioned into a 'Reg vs. Irr' and a 'Between  
266 sequences' contrast. The assumption of homogeneity of variances was assessed with Cochran's  
267 test and data were log-transformed if necessary. The details of analyses are reported in  
268 Supplementary information (SI 1) and Bertocci *et al.* (2015). When relevant, Student-Newman-  
269 Keuls (SNK) tests were used for post-hoc comparisons of means.

270

## 271 **Results**

272 A total of 57 taxa (39 macroalgae and 18 invertebrates: see Supplementary information SI  
273 2) were identified over the experiment and provided the examined total richness of taxa or  
274 were collapsed, as relevant, into four morpho-functional algal groups (canopy-forming,  
275 filamentous, ephemeral green, encrusting) and the grazers. Single taxa showed idiosyncratic  
276 responses to the treatments (detailed analyses reported in SI 1).

277 The mean and the temporal variance in the abundance of habitat-formers, i.e. canopy-  
278 forming macroalgae (Fig. 4 A and 5 A) and the polychaete *S. alveolata* (Fig. 4 B and 5 B),  
279 were significantly larger in the low than in the high intensity treatment, independently of other  
280 experimental conditions.

281 The intensity of disturbance also affected the mean abundance and the temporal variance  
282 of filamentous algae, but in opposite directions depending on the availability of nutrients.  
283 Under the natural condition, both response variables attained larger values in the low  
284 compared to the high intensity treatment, while this pattern reversed in the enriched condition

285 (Fig. 4 C and 5 C1). In addition, when disturbance events were applied at regular intervals, the  
286 natural condition maintained the temporal variance in abundance of this algal group larger  
287 compared to the enriched condition, while the opposite effect of nutrients occurred in the  
288 irregular treatment (Fig. 5 C2).

289 The mean percentage cover of ephemeral green algae was significantly lower in control  
290 than, on average, all other pools (Fig. 4 D). In treated pools, however, these algae were affected  
291 by the interaction between nutrients, the intensity and the sequence of irregularly distributed  
292 disturbance events. Low intensity events applied according to sequence 2 (S2) under the  
293 natural condition determined larger mean and larger temporal variance of cover compared to  
294 the other combinations of intensities and sequences (Fig. 4 D and 5 D). Under the enriched  
295 condition, the mean abundance of ephemeral green algae was larger in the low than in the high  
296 intensity treatment independently of the sequence of disturbance (Fig. 3 D), while the temporal  
297 variance was larger for low intensity events applied according to sequence 1 (S1) than in all  
298 other experimental combinations (Fig. 5 D).

299 The mean abundance of encrusting corallines was larger in the high than the low intensity  
300 treatment independently of all other treatments (Fig. 4 E1) and in the enriched than in the  
301 natural condition, but only when disturbance events were established according to S1 (Fig. 4  
302 E2). The temporal variance in the percentage cover of this group was significantly reduced in  
303 control than, on average, treated pools. Moreover, this response variable was increased by low,  
304 compared to high, intensity events applied according to the regular and the S1 pattern, while  
305 the opposite effect of intensity was shown under S2 (Fig. 5 E).

306 Grazers were consistently more abundant in enriched than in natural pools (Fig. 4 F).  
307 Nutrients had a positive effect also on their temporal variance, but only combined with  
308 regularly distributed disturbances, as no significant effects of nutrients were found under  
309 irregular events (Fig. 5 F).

310 Regularly distributed disturbances were associated with a larger richness of taxa when  
311 applied at low compared to high intensity, while the opposite effect of intensity was observed  
312 under irregular events (Fig. 4 G). Low intensity of regularly distributed events also increased,  
313 compared to high intensity, the temporal variance of richness, while disturbance intensity did  
314 not exert significant effects on this variable when events were applied irregularly (Fig. 5 G).  
315 Variations in the abundance of each taxon and in the total richness over the period of the  
316 experiment are illustrated in Supplementary information (SI 3).

317

### 318 **Discussion**

319 Present findings supported the proposed hypotheses only in terms of some aspects related  
320 to the general direction of responses to the manipulated factors, but not in terms of the  
321 interactions among them. Specifically, the mean abundance of the most structured species  
322 (canopy-forming algae and *S. alveolata*) was inversely related to the intensity of disturbance,  
323 but this response was not modulated by the other treatments. It has been demonstrated that  
324 even algae well adapted to very exposed areas can be removed by extreme storms due to the  
325 wave force itself and to the impact of rolling rocks (Shanks & Wright 1986; Denny *et al.*  
326 1989). These mechanisms are most likely to occur for arborescent species, such as the present  
327 canopy-former *C. crispus* and kelps, for which extensive dislodgement has been observed due  
328 to winter storms (Seymour *et al.* 1989; Dudgeon & Johnson 1992). In fact, extreme waves can  
329 exert self-reinforcing negative effects on algal beds once they open patches within an originally  
330 aggregated canopy, thus exposing the remaining individuals to increased hydrodynamic forces  
331 (Boller & Carrington 2006). Analogously, *S. alveolata* reefs are extremely sensitive to natural  
332 (storms) and human (trampling) mechanical disturbance which can critically damage the adult  
333 bio-constructions and reduce the density of recruits (Dubois *et al.* 2006). In general, such  
334 mechanisms are classically known to contribute to make wave-generated disturbance a key  
335 driver of the structure of intertidal assemblages on rocky shores (Dayton 1971) and may also

336 explain the overwhelming effect, not initially hypothesized, of intensity of disturbance  
337 compared to those of temporal variability and nutrient enrichment on slow-growing habitat-  
338 formers. Moreover, this effect was likely exacerbated by the slower recovery ability of such  
339 organisms compared to potential competitors. It was documented, in particular, that limited  
340 damage of *S. alveolata* reefs can be repaired in some weeks through the tube-building activity  
341 (e.g. Plicanti *et al.* 2016), but the recovery of severely disturbed reefs critically depends on  
342 other processes, such as larval supply, occurring at much larger time scales (Ayata *et al.* 2009).  
343 Large variations in recruitment of *S. alveolata* were documented over periods up to years  
344 (Gruet 1986), a time scale which is clearly larger than the longest time for recovery available to  
345 this species to recolonize after disturbance in the present experiment. Analogously, there is  
346 evidence that even considerably damaged beds of canopy-forming algae may recover in some  
347 months, but large patches where the canopy was completely removed by very intense  
348 disturbance take much longer (Underwood 1998; Speidel, Harley & Wohnam 2001). In this  
349 context, but in the opposite direction, the main positive response of encrusting coralline algae  
350 to disturbance intensity is consistent with their described poor competitive abilities and great  
351 resistance to physical stress (Breitburg 1984). In fact, unlike algal canopies, even intense  
352 mechanical disturbances are unlikely to completely eliminate these forms, which can then  
353 quickly re-grow from the crust. Such traits typically make them dominant in physically and/or  
354 biologically harsh habitats where potential competitors are eliminated (Steneck 1986; Bertocci  
355 *et al.* 2005; McCoy & Kamenos 2015). According to such interactions, however, the observed  
356 increase, though modulated by the sequence of disturbance events, in the abundance of this  
357 algal group in enriched pools, where several erect algae were also more abundant, could be  
358 puzzling based on the present original hypotheses. The productivity of encrusting corallines,  
359 however, can be directly enhanced by nutrient enrichment (Smith, Smith & Hunter 2001),  
360 while the ability to tolerate overgrowth for relatively long periods (Underwood 2006) may  
361 allow these algae to take advantage of the ameliorated environment provided by the upper algal

362 layer (Figueiredo, Kain & Norton 2000). The dependence of the effect of nutrients on the  
363 sequence of disturbances is more difficult to interpret, but likely involved direct and indirect  
364 causes. For instance, encrusting corallines can quickly recover in disturbed patches through  
365 vegetative growth (Steneck 1986) and field measurements from the same geographic area have  
366 indicated no growth of several species during winter (October to March) and maximum growth  
367 rates during summer (June-July) (Adey & McKibbin 1970). In summer, present irregular,  
368 sequence 1 treatment included more (two versus one) events of disturbance than sequence 2  
369 treatment and this may have implied temporary more stressful conditions for potential  
370 competitors, concomitantly to nutrient and life-cycle conditions determining the peak of  
371 growth of encrusting corallines.

372       Increasing availability of nutrients is known to directly stimulate the abundance and  
373 growth of ephemeral and epiphytic macroalgae in coastal habitats (Valiela *et al.* 1997;  
374 Masterson *et al.* 2008), which is, as in general originally hypothesized, consistent with the  
375 general increase in abundance of red filamentous and ephemeral green algae in present  
376 enriched pools. More interesting and somehow unexpected were the interactive effects, as the  
377 high intensity treatment combined with the natural nutrient condition reduced, compared to the  
378 low intensity treatment, the cover of the first group, while the effect of intensity reversed under  
379 the enriched condition. These findings can be interpreted by first noting that red filamentous  
380 species of the genus *Ceramium* can become nutrient-limited in very oligotrophic waters  
381 (Pedersen, Borum & Leck Fotel 2010). Even without reaching such an extreme, this makes  
382 logically explainable that the high experimental intensity of disturbance reduced the cover of  
383 this algal group when combined with the natural condition, where growth was likely lower than  
384 in the enriched treatment. On the contrary, nutrient enrichment could have determined faster  
385 growth rates of filamentous algae, consequently buffering the negative effect of severe  
386 disturbance. Eventually, this effect might have reversed to positive through the reduction of  
387 algal canopies, as generally observed here and invoked as a main mechanism for the

388 replacement of perennial macroalgae by ephemeral forms (e.g. Valiela *et al.* 1997). The same  
389 pattern of responses, however, was not shown by ephemeral green algae, whose abundance was  
390 generally increased by the low intensity treatment in enriched pools, but only when  
391 disturbances were established according to one irregular sequence (S1). As documented here  
392 too, ephemeral green algae of the genus *Ulva* can become dominant under enriched conditions  
393 (Raffaelli *et al.* 1998), which, in principle, could have prevented any possible control of  
394 intensity of disturbance on their abundance (Masterson *et al.* 2008). The fact that this did not  
395 happen, adding to the overall high intensity-associated reduction of potential space-occupying  
396 competitors, suggests that direct effects of disturbance on these algae might occur even under  
397 high productivity. Analogous evidence was previously provided for biological disturbances,  
398 such as grazing (e.g. Paine 2002), rather than for physical factors. Under the natural condition,  
399 instead, the specific sequence of events became more relevant to modulate the effect of  
400 disturbance intensity. The specific mechanisms of such response still need to be elucidated, but  
401 they might involve interactions between the timing of experimental disturbance and factors  
402 responsible for the natural temporal variation of abundance of ephemeral green algae (see  
403 control trajectories in SI 2). For example, competition for space could have contributed to the  
404 general inverse response of filamentous red algae and ephemeral green algae to the intensity of  
405 disturbance combined with nutrient enrichment. In such a context, laboratory experiments have  
406 indicated that, under eutrophic conditions, the maximum growth rate of *Ulva* spp. can be more  
407 than double than that of filamentous red algae of the genus *Ceramium* (Pedersen & Borum  
408 1997). Both genera were among the most representative of the filamentous red and the  
409 ephemeral green algal group here examined. So, it can be hypothesized that, although both  
410 groups increased in abundance due to nutrient enrichment, competitively superior ephemeral  
411 green algae tended to become dominant over filamentous red algae, but that this outcome could  
412 be, at least in part, buffered by high intensity of physical disturbance which was likely to  
413 damage the large, foliose fronds of *Ulva*-like forms more than the small, filamentous fronds of



414 *Ceramium*-like forms. The lack of clear inverse patterns of abundance of the two algal groups  
415 during the course of the experiment did not provide full support to this mechanism, but it is  
416 worth noting that the largest peaks of cover of filamentous red algae were measured at the last  
417 time of sampling, concomitantly with some of the smallest recorded cover values of ephemeral  
418 green algae. Moreover, the overall consistent patterns of abundance of palatable algae, such as  
419 filamentous and ephemeral species, and grazers in response to nutrients suggest that  
420 increases/decreases in the availability of food could support analogous variations in the number  
421 of herbivores without implying a strong feedback-control by grazing even where grazers were  
422 more abundant. The stimulation of macroalgal blooms by enhanced nutrient supply, in spite of  
423 the top-down control by herbivores, has been documented in other tide-pool systems  
424 (Masterson *et al.* 2008).

425 In terms of overall diversity, regularly and irregularly distributed events determined a  
426 switch from a negative to a positive effect of high intensity of disturbance on the richness of  
427 taxa. It seems, therefore, that low intensity events evenly distributed and high intensity events  
428 irregularly distributed were the conditions able to support the highest richness of taxa over the  
429 time scale of the experiment, irrespectively of the availability of nutrients. The independence  
430 of effects of intensity and variance of disturbance from nutrient availability led to reject, in  
431 general, the proposed hypotheses regarding richness. The hypothesized direct or indirect  
432 relationship between disturbance severity and species richness under, respectively natural  
433 nutrients or enriched conditions was clearly not supported by present data. Discussing in detail  
434 the possible mechanisms for this unexpected outcome is beyond the scope of this study, as they  
435 likely involved complex interactions that could not be unequivocally tested by the present  
436 experiment. In fact, a recent review regarding general theories on links between traits of  
437 disturbance, productivity and species diversity has explicitly illustrated a number of logic and  
438 logistic difficulties in unambiguously testing for the effects of all factors and processes  
439 responsible for patterns of coexistence or competitive exclusion of species over proper spatial

440 and temporal scales (Huston 2014). For example, it was traditionally postulated that  
441 mechanisms responsible for species coexistence, hence for high species diversity, are effective  
442 only where competitive exclusion is prevented either by mortality-driven disturbance (Connell  
443 1978; Huston 1979), or by low productivity eventually reducing growth rates, and/or by the  
444 combination of both (Huston 1979). Anyway, long-term coexistence of species is unlikely to  
445 occur in systems exposed to periodic disturbances and where most species have similar  
446 resource requirements (e.g. Huston 2014). It is interesting, however, that a negative effect of  
447 high intensity, buffered by high temporal variance, of disturbance (aerial exposure) on the  
448 richness of benthic assemblages was reported in another rocky intertidal system (Benedetti-  
449 Cecchi *et al.* 2006) as a consequence of the replacement of less diversified (encrusting  
450 coralline algae) by more heterogeneous (filamentous algae) groups under such conditions.  
451 Given the present results, the same mechanism was unlikely here, while it can be hypothesized  
452 that the combination of intensity and temporal variability of disturbance exerted significant  
453 effects on the total richness by affecting several taxa that were numerically very rare in the  
454 collected samples and not included, for their characteristics, in the groups analyzed  
455 individually.

456 In a broader context, it is worth noting that, in spite of recent advances (e.g. Bertocci *et*  
457 *al.* 2005; Benedetti-Cecchi *et al.* 2006; García-Molinos & Donohue 2011; Bulleri *et al.* 2014),  
458 current knowledge on ecological effects of environmental change is still based on studies  
459 focusing on constant mean levels of relevant variables (Cardinale *et al.* 2002; Hutchings, John  
460 & Wijesinghe 2003) or on changes in the mean intensity (Mackey & Currie 2001) or the  
461 frequency (Collins 2000; McCabe & Gotelli 2000) of disturbance. Present findings, instead,  
462 suggest that examining the circumstances, the scales and in which direction the temporal  
463 variance and the mean of disturbance interact is relevant to increase the accuracy of the  
464 understanding and predictions of the influences of anthropogenic changes on natural diversity.  
465 This is of great importance since changes in disturbance regimes are already apparent and are

466 expected to continue in the future. For example, the temporal patterning and severity of fires in  
467 the USA are changing in association with climate warming (Westerling *et al.* 2006); insect  
468 outbreaks in forests are occurring over greater extents and involving new sets of species (Raffa  
469 *et al.* 2008); data showing trends towards the aggregation of extreme storms in short periods  
470 separated by prolonged periods of calm are available for tropical areas (Muller & Stone 2001;  
471 Wolff *et al.* 2016); further increases of both the mean intensity and the temporal variance of  
472 meteorological events are predicted by climate models (Michener *et al.* 1997; Easterling *et al.*  
473 2000; Trapp *et al.* 2007); changes in the temporal variance of environmental stress are  
474 expected to be as important as those in the mean intensity to modulate shifts between  
475 competitive and facilitative interactions (Bulleri *et al.* 2014).

476       In most cases, differences in temporal variance of abundances tracked those in the mean,  
477 with relatively smaller fluctuations occurring in treatments where organisms were, on average,  
478 less abundant over the experimental period. This is, in general, interpretable as a consequence  
479 of the scaling relationship between the mean and the variance, according to which persistent  
480 low mean abundance values would not allow large fluctuations (variances) around them  
481 (Taylor 1961). But what might be the ecological consequences of that? There is evidence that  
482 temporal variation in abundance may be directly related to the risk of local extinction of  
483 species (Lande 1993; Vucetich *et al.* 2000; Inchausti & Halley 2003). Analogously to a  
484 previous experiment in a Mediterranean rocky system (Bertocci *et al.* 2005), the analysed  
485 organisms did not support this hypothesis as, in spite of temporary even drastic drops in their  
486 abundances, all persisted throughout the experiment, likely due to their overall ability to resist  
487 to, or quickly recover from, the applied perturbations. It could be predicted that in systems with  
488 analogous recovery abilities of dominant organisms, the separated or interactive effects of traits  
489 of the regime of disturbance and nutrient enrichment could affect temporal fluctuations of  
490 exposed populations not through the elimination and substitution of species, but through  
491 changes in relative abundances.

492           The last point is linked to the question of whether present findings may be generalized to  
493 other systems, such as grasslands (Hooper *et al.* 2005), which share high resilience to  
494 disturbance and similar “response traits” of organisms with rocky intertidal ones. In fact,  
495 disturbances, such as grazing and fires, normally affect the aboveground vegetation, while the  
496 belowground vegetation can recover quickly (McNaughton 1985; Cooper, Huffaker & LoFaro  
497 1999; Lateral *et al.* 2003). Moreover, mowing and fire can suppress dominant tussock grasses  
498 and facilitate, particularly under increased nutrients, short-lived forbs (Mazía *et al.* 2010;  
499 Tognetti & Chaneton 2015). Based on present findings, preponderant effects of physical  
500 disturbance intensity, determining a reduction in both the mean abundance and temporal  
501 fluctuations of long-living plants, can be hypothesized in grasslands. On the contrary, large  
502 increases of ephemeral forbs could be predicted under nutrient enrichment, especially when  
503 concomitant with relatively mild events of physical disturbance occurring according irregularly  
504 over time. The different ability of species characterized by contrasting life-history traits,  
505 however, could drastically shape the final outcome of such mechanisms depending on the  
506 tension between the direct response to disturbance and nutrients and the indirect modulation of  
507 biological interactions, such as competitive and/or consumer-prey relationships. Analogously,  
508 in coral reefs, branched species, such as *Acropora* spp. and *Pocillopora* spp., are more likely to  
509 be killed by physical disturbance compared to massive species, such as *Platygyra* spp. and  
510 *Porites* spp., but they are also characterized by faster growth and consequent higher recovery  
511 ability after disturbance (Marshall & Baird 2000; Loya *et al.* 2001; Baird & Marshall 2002;  
512 McClanahan *et al.* 2004). Storm-related damage and recovery of coral reefs, however, are  
513 highly variable depending on complex interactions between storm characteristics, reef  
514 topography and size and biological traits of organisms (reviewed by Harmelin-Vivien 1994).  
515 Making predictions, based on present findings, on responses of coral reefs to analogous  
516 changes in environmental conditions is probably even more complicated. For instance, nutrient  
517 enrichment is widely considered responsible for observed declines of coral reefs (e.g. Fabricius

518 2005), but their underlying mechanisms are subject to strong and controversial debate (Szmant  
519 2002; Bell *et al.* 2007). In general, it can be hypothesized that, differently than in rocky  
520 intertidal habitats and grasslands, nutrients, either as a single stressor or combined with  
521 mechanical disturbance, affect corals not directly, but through their effects on phytoplankton  
522 and epiphyte loads. These may ultimately modulate the tolerance of corals to physical stress in  
523 complex ways (e.g. D'Angelo & Wiedenmann 2014). Overall, however, there is evidence that  
524 such complex interactions may result in healthy and diverse coral reefs within ranges of  
525 nutrient concentration and other pressures even broader than expected (D'Angelo &  
526 Wiedenmann 2014), which is, at least in part, consistent with the persistence of most species  
527 over the course of the present experiment in spite of temporarily 'extreme' conditions.  
528 Experiments analogous to the present one are needed to test whether responses similar to those  
529 of rocky intertidal systems would occur in grassland and coral reef systems. Nevertheless, to  
530 our knowledge, this experiment provided the first manipulative test of the effects of changes in  
531 the regime (mean intensity and temporal variance) of climate-related disturbance crossed with  
532 levels of a concomitant, globally relevant, stressor. As such, it can provide an advancement and  
533 more realistic contribution to understand and predict the ecological implications of variations  
534 of compounded perturbations occurring at the global scale as a direct and indirect consequence  
535 of anthropogenic activities.

536

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546

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## LEGEND TO FIGURES

Fig. 1. Schematic representation of how intensity and variance of mechanical disturbance and nutrient enrichment can affect patterns of abundance and temporal fluctuations of algal species with different life-traits. Under natural nutrient concentration (- NUTRIENTS), mechanical disturbance events characterized by increasing intensity and variance would be particularly detrimental to long-living/low dispersing species, while they could facilitate ephemeral/high dispersing species by releasing resources. During the course of the experiment, the abundance and temporal fluctuations of the first and the second group are expected to be, respectively, reduced and increased compared to conditions of low intensity and low variance of disturbance. Increased nutrient concentration ('+ NUTRIENTS') would primarily support higher abundance of ephemeral/fast-growing algae, possibly followed by a decline of perennial/slow-growing species. As a result, the enriched condition is expected to maintain temporally consistent larger abundances of fast-growing/fast-colonizing and lower abundances of less resilient organisms, buffering the effects of concomitant mechanical disturbance events compared to the natural nutrients condition.

Fig. 2. Conceptual model showing how intensity and variance of physical disturbance and nutrient enrichment can affect species richness. Under low productivity (natural nutrients: dashed line) and consequent low growth rates, large species richness would be supported only under mild (low intensity and low variance) disturbance, since very severe disturbance (high intensity and large variance) would drive most species to local extinction. Under high productivity (enriched: solid line) and consequent high growth rates, large species richness is expected under severe disturbance able to produce relatively high levels of mortality required to prevent competitive exclusion by few species that would otherwise become dominant.

Fig. 3. Experimental design. A) Schematic representation of the entire design, including two levels of nutrients (enriched and natural), two levels of both intensity (low and high) and temporal variability of mechanical disturbance (regular and irregular), two sequences (S1 and

S2) of events within the irregular treatment, three pools allocated to each combination of such manipulations, and three control (unmanipulated) pools. B) Representation of the distribution of mechanical disturbance events (D) over the course of the experiment, for each level of temporal variability. T1 to T10 are the times of sampling, established provided that the average time elapsed since the previous event of disturbance was the same between all levels of temporal variability and sequences of disturbance (Bertocci et al. 2005). The variance of the intervals of time (in months) between successive disturbances is 0 for the regular and 21 for each irregular treatment.

Fig. 4. Mean (+ SE) abundance over the experimental period of individual taxa and richness of taxa, illustrating significant differences among treatments (SI 1, Table 1). C, LI, HI = unmanipulated control (white), low (light grey), high (dark grey) intensity of disturbance, respectively; Reg, Irr = regular, irregular (two sequences: S1 and S2) pattern of disturbance, respectively; N, E = natural (dotted), enriched (dashed) condition, respectively. Relevant significant tests are reported below each panel. Different letters above bars represent treatments differing significantly at  $p < 0.05$  (SNK tests).

Fig. 5. Univariate measures of temporal variance of abundance (in logarithmic form) of individual taxa and of the richness of taxa calculated over the period of the experiment, illustrating significant differences among treatments (SI 1, Table 2). Symbols and abbreviations as in Fig. 4.

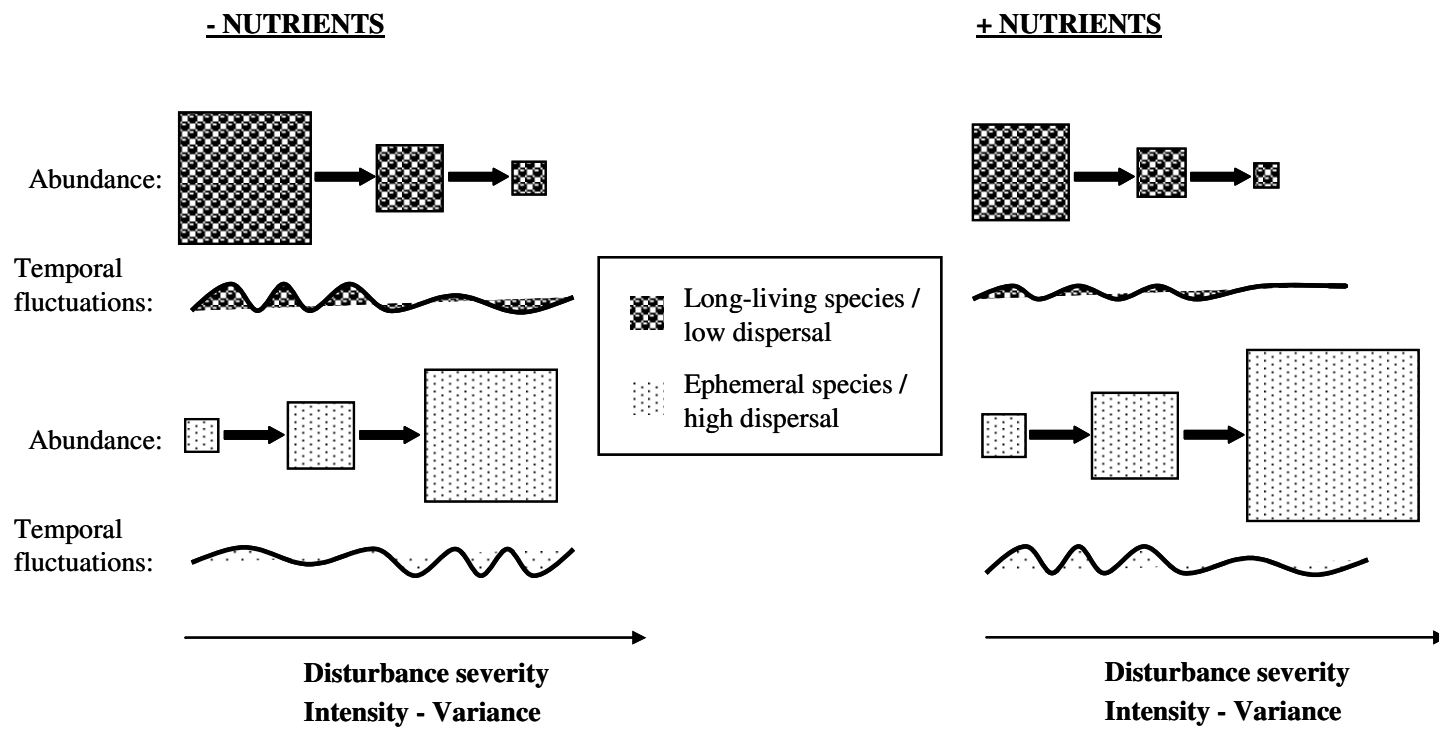


Fig. 1 Bertocci et al.

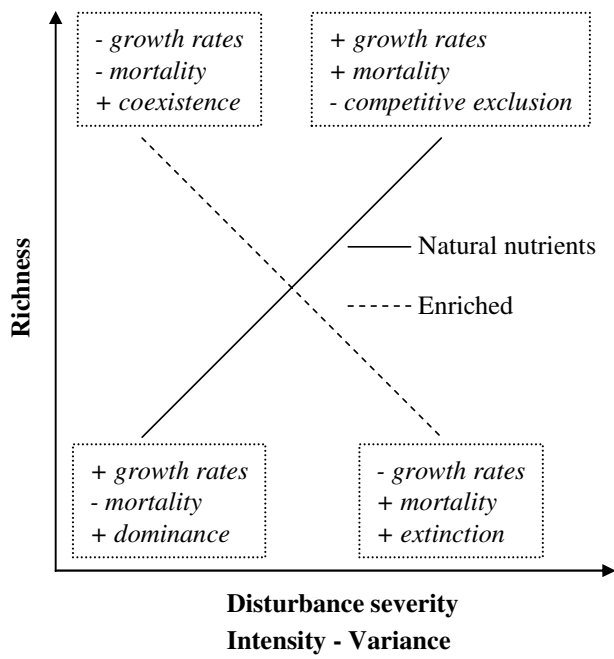
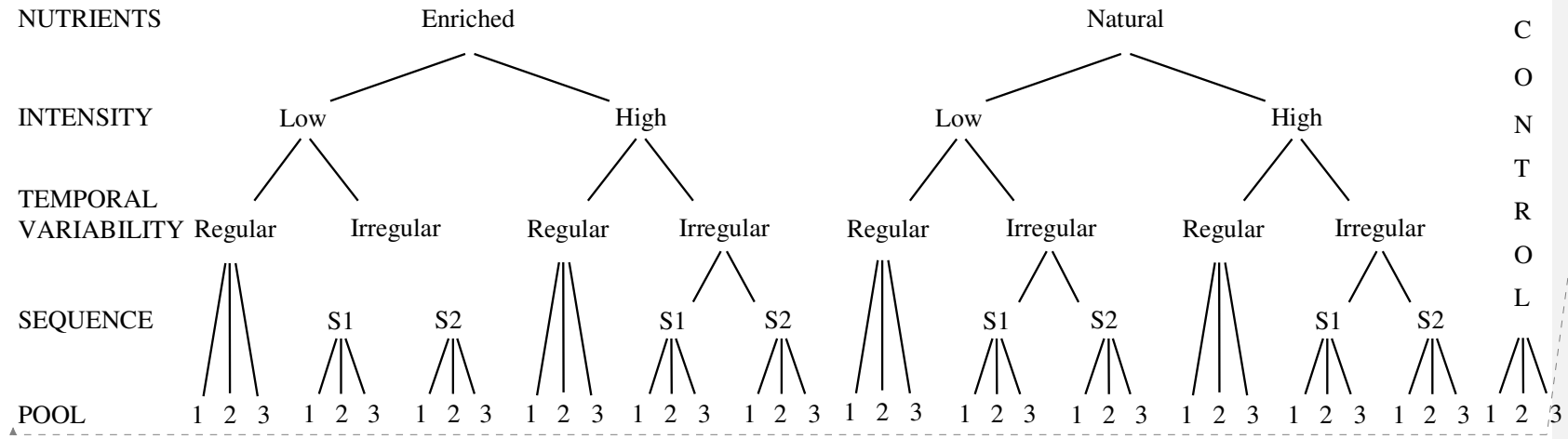


Fig. 2 Bertocci et al.

A)



Codice campo modificato

B)

REGULAR TREATMENT

	<b>D</b>				<b>D</b>				<b>D</b>				<b>D</b>				<b>D</b>			
--	----------	--	--	--	----------	--	--	--	----------	--	--	--	----------	--	--	--	----------	--	--	--

IRREGULAR TREATMENT (Sequence S1)

		<b>D</b>		<b>D</b>					<b>D</b>						<b>D</b>	<b>D</b>				
--	--	----------	--	----------	--	--	--	--	----------	--	--	--	--	--	----------	----------	--	--	--	--

IRREGULAR TREATMENT (Sequence S2)

		<b>D</b>	<b>D</b>		<b>D</b>						<b>D</b>					<b>D</b>			
Feb 2012	Mar	Apr	T1 May	T2 Jun	T3 Jul	Aug	T4 Sep	T5 Oct	T6 Nov	Dec	Jan 2013	T7 Feb	Mar	Apr	May	T8 Jun	T9 Jul	Aug	T10 Sep

Fig. 3 Bertocci et al.



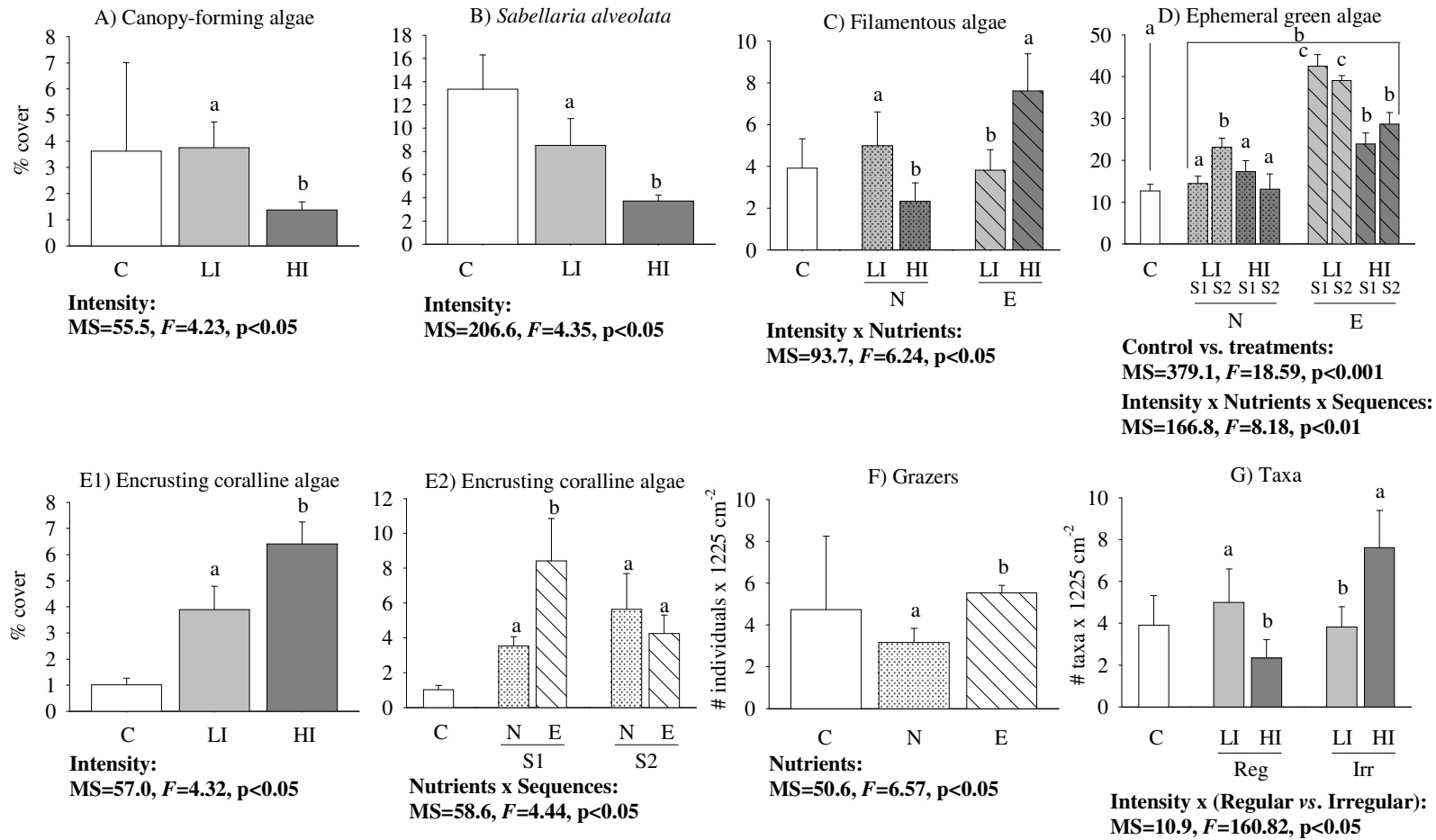


Fig. 4 Bertocci et al.

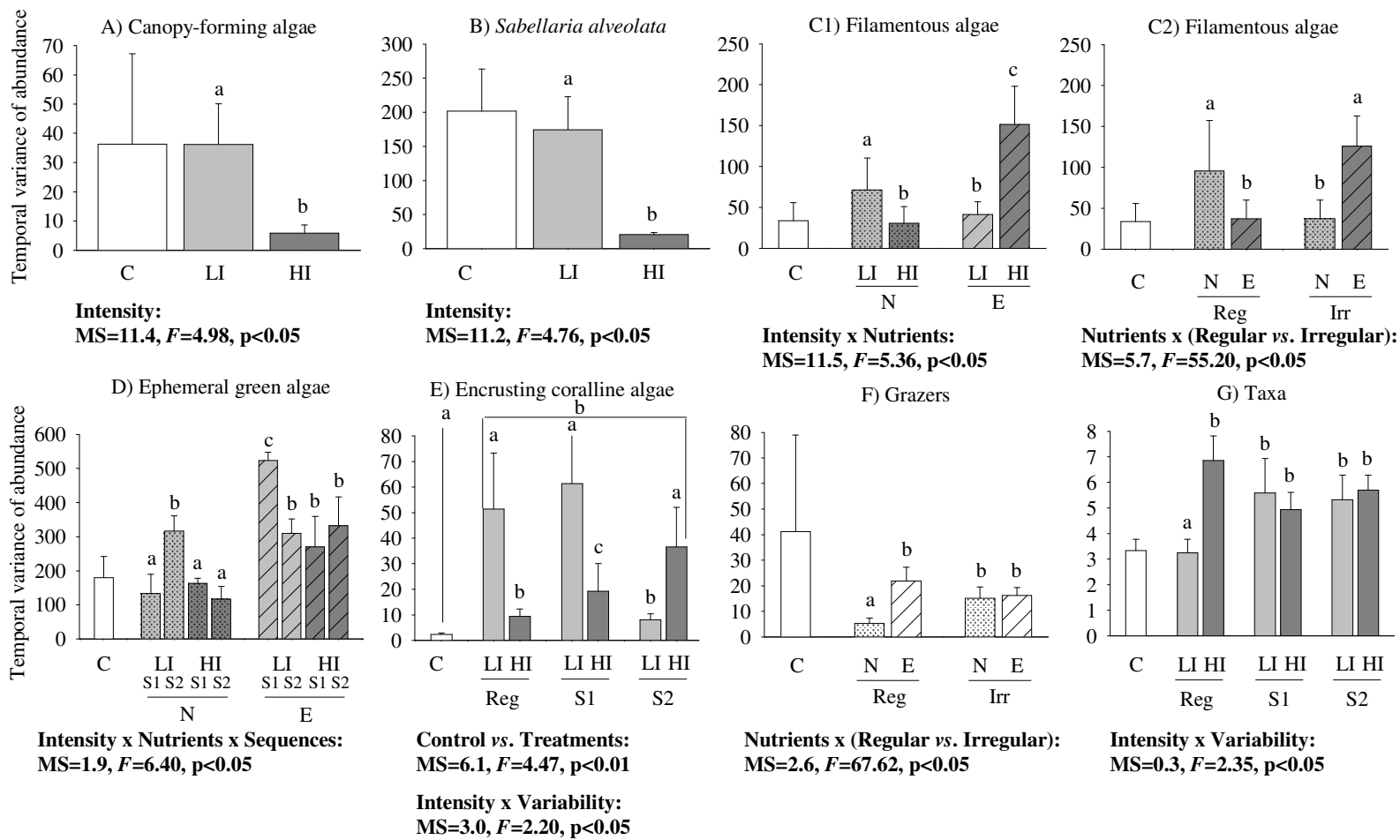


Fig. 5 Bertocci et al.