

Interplay of experimental harvesting and climate-related disturbance on benthic assemblages of rocky seashores

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ABSTRACT: Assessing responses of assemblages to compounded perturbations is a crucial goal of research on ecological impacts of current and predicted environmental changes. We examined the interactive effects of changes in temporal variance of 'storm-like' mechanical disturbance and in harvesting intensity of mussels (*Mytilus galloprovincialis*) on sessile assemblages associated with mussel beds on rocky shores in north Portugal. Response variables were measures of temporal variance in the abundance of individual taxa and in the structure of assemblages. Events of disturbance regularly distributed over the period of the experiment determined a lower temporal heterogeneity in assemblage structure than events characterized by larger temporal variance, but only in the presence of an intact mussel bed. The opposite pattern was documented in plots where mussels were completely removed. Univariate results indicated taxon-specific responses, with macroalgae, such as *Corallina* spp. and *Porphyra linearis*, showing patterns analogous to the multivariate one and grazing invertebrates displaying an opposite trend. This is one of the first manipulative examples aimed at examining effects of temporal variability of climate-related disturbance on systems increasingly depleted by concomitant stressors. The main finding was that effects of temporal variability of climate-related events of mechanical disturbance are mediated by the presence of intact stands of a foundation species. This may contribute to understanding and predicting responses of populations and assemblages under scenarios of concomitant climatic and non-climatic changes.

KEY WORDS: Climate change · Foundation species · Multiple disturbances · *Mytilus galloprovincialis* · Human impact · Intertidal · Temporal variance

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INTRODUCTION

Disturbance is a major driver of patterns of distribution, abundance and diversity of natural assemblages (Pickett & White 1985, Fraterrigo & Rusak 2008). The rate and scale of anthropogenic disturbances, however, are often much larger than those of natural ones, providing a serious threat to the main-

tenance of biodiversity and of its basic processes (see Gosling et al. 2011 for a review). Under observed and predicted climate change (Helmuth et al. 2006, Rosenzweig et al. 2008), there is special interest in responses of populations and assemblages to extreme events (Smith 2011).

In spite of the number of available studies on ecological effects of climate-related disturbance, several

relevant issues still remain to be addressed. Most previous studies examined the effects of variations in mean intensity of environmental variables (Zavaleta et al. 2003, Stuart-Smith et al. 2010) or extreme events (Zimmerman et al. 2010). However, climate change also implies alterations in temporal patterns of meteorological events, including their timing, frequency and variance (Muller & Stone 2001, Gutschick & BassiriRad 2003). While the traditional approach for experimentally examining the effects of temporal variability of disturbance focused on manipulating the frequency of events (Collins 2000, McCabe & Gotelli 2000), the consideration that the temporal variation and the total intensity of disturbance applied over the period of the experiment can be confounded (Benedetti-Cecchi 2003) led to temporal variance of disturbance being taken into account (Bertocci et al. 2005, Benedetti-Cecchi et al. 2006, Vaselli et al. 2008, Molinos & Donohue 2011, Buckley & Kingsolver 2012). Few studies, however, specifically examined how variable regimes of disturbance can affect temporal fluctuations of assemblages (e.g. Collins 1992, 2000, Bertocci et al. 2005). In addition, in some cases, different traits of a single type of disturbance were manipulated simultaneously (McCabe & Gotelli 2000, Bertocci et al. 2005, Vaselli et al. 2008, Pincebourde et al. 2012), but little effort was put on experimentally examining the effects of variable regimes of disturbance combined with other concomitant perturbations that themselves alter local populations and assemblages. This is of overwhelming importance under real global change scenarios and current ecological theories on disturbance (Wernberg et al. 2012). Natural assemblages are normally exposed to multiple disturbances, potentially determining biological responses that are difficult to predict as being linked in complex ways to life traits of species (Bertness et al. 1999). Global decline of top predators (Heithaus et al. 2008) and foundation species (Bruno & Bertness 2001, Ellison et al. 2005), for instance, is likely to exacerbate the sensitivity of natural populations and assemblages to further disturbances whose patterns are modified by other factors. This would occur in all cases where natural populations depressed by anthropogenic factors (e.g. Connell et al. 2008, Lotze et al. 2011) are simultaneously exposed to climate change, including increases in frequency, variance and intensity of storms and other environmental extremes (Paine et al. 1998).

This study investigated the compounded effects of changes in temporal variability of climate-related disturbance (i.e. simulating the mechanical impact of

major storms) and of varying intensity of loss of a foundation species (i.e. subject to human harvesting), using the mussel beds dominating rocky intertidal habitats in north Portugal as a study system. Mussel beds host diverse algal and invertebrate assemblages (e.g. Chapman 2005) and may protect understorey organisms from physical disturbance, analogously to other foundation species such as canopy-forming macroalgae (Lilley & Schiel 2006, Bertocci et al. 2010). In fact, they can be removed or damaged by waves (McQuaid & Lindsay 2000) whose impact is likely positively related to the integrity of the mussel bed as isolated mussels are more vulnerable to lifting and dislodging by waves (Denny 1987, Romme et al. 1998). In addition, mussels are intensively harvested for different purposes at several locations (Lasiak 1991, Airoidi et al. 2005, Atkinson et al. 2010). As classic studies documented, however, the loss of mussel beds may also make space available for organisms, such as green and red macroalgae, that are less efficient in the competition for space (e.g. Paine 1974). No previous studies have specifically examined hypotheses on the compounded effects of temporal variance of disturbance events (we refer here to the variation of a predictor variable) and of different levels of experimental harvesting of a foundation species on the temporal variation of associated organisms (here, we refer to the variation of the dependent variable). Filling this gap is needed as temporal changes in patterns of distribution, abundance and diversity of species are related to changes in important properties of natural systems, including productivity, stability and risk of local extinctions (Lundberg et al. 2000, Inchausti & Halley 2003).

We hypothesized that an intact mussel bed could buffer the effects of physical disturbance, leading us to anticipate an interaction between experimental harvesting of mussels and the climate-related mechanical treatment. Specifically, we expected that temporally variable (i.e. regularly vs. irregularly distributed over time) events of mechanical disturbance would exert limited effects on associated assemblages in the presence of an intact mussel bed, with the exception of the particularly stressful case where consecutive events, aggregated in short periods of time, were themselves able to remove the mussel bed. At the other extreme, the complete removal of the mussel cover would allow the dominance of fast-growing organisms, such as turf-forming algae, in the absence of disturbance, while increasing the aggregation of disturbance events would reduce such effects due to the sensitivity of turfs to mechanical disturbance (Bulleri 2006), indirectly facilitating

more resistant species, such as encrusting algae and invertebrates (Lubchenco & Menge 1978). At intermediate levels of mussel removal, the responses of associated organisms would depend on the interactions among the available space, the ability of organisms to colonize and the temporal variability of concomitant mechanical disturbance. In fact, levels of removal of the mussel bed could be proportionally related to losses of associated organisms from experimental plots, but fast-growing species would rapidly colonize free patches. This would increase temporal fluctuations in patterns of abundance of these species, but such effects could be predicted to decrease with increasing variance of disturbance. Repeated events of disturbance clustered in time may drastically reduce the mean abundance of organisms for a relatively longer period than regularly distributed events, at the same time reducing their temporal fluctuations due to the mean-variance scaling relationship (Taylor 1961). These hypotheses were tested with an experimental design where the irregular treatment of disturbance was replicated through 2 random sequences (Vaselli et al. 2008) and where the same experiment was repeated at 2 different sites.

MATERIALS AND METHODS

Study site

The study was performed between February 2011 and July 2012 at 2 rocky sites (about 20 km of sandy coast apart), in north Portugal: Praia da Aguda (41° 2.71' N, 8° 39.20' W) and Praia do Marreco (41° 14.00' N, 8° 43.27' W). Each site is hundreds of meters long and occurs within an almost continuous sandy beach extending for nearly 200 km south of Aguda and 70 km north of Marreco. Both sites are characterized by the same south to north orientation and exposure of the coastline, gentle slope of typically granitic substratum and a semi-diurnal tidal regime with maximum range of spring tides of 3.5 to 4 m. Experimental plots were established at mid intertidal level, between 1 m and 2 m above chart datum. At this height, assemblages are dominated by mussels *Mytilus galloprovincialis* Lamarck, associated with diverse algal organisms. These include red algae such as *Chondrus crispus* Stackhouse and encrusting and articulated corallines (e.g. *Lithophilum incrustans* Philippi and *Corallina* spp., respectively). Other algae are noticeably more abundant during summer, such as the brown *Bifurcaria bifurcata* R. Ross and the green *Ulva* spp. The most com-

mon grazers are topshells and limpets in the genera *Gibbula* and *Patella*, respectively. Details on distributional and demographic patterns of mussels over a range of scales at the study region can be found in Bertocci et al. (2012). Both sites are affected by severe natural and anthropogenic disturbances, including the mechanical impact of waves during storms, aerial exposure at low tide and harvesting of organisms for commercial and recreational purposes.

Experimental design

The interactive effects of changing the harvesting intensity of mussels and the temporal variation of storm-related mechanical disturbance on animal and algal assemblages associated with the *Mytilus galloprovincialis* bed were examined through a manipulative experiment. A total of 39 plots (35 × 35 cm, 10s of cm to meters apart) were marked at the beginning of the experiment at each site, within the belt dominated (i.e. cover in each plot ≥ 90%) by *M. galloprovincialis*. Three plots were left unmanipulated as controls. Nine plots were randomly assigned to each of the 4 treatments of experimental removal of *M. galloprovincialis*, simulating increasing intensities of human harvesting: (1) mussels intact (0% removal: '0'), (2) 70% cover of mussels remaining (about 30% removal: '30'), (3) 40% cover of mussels remaining (about 60% removal: '60') and (4) mussels completely eliminated (100% removal: '100'). Removal was performed using a knife, with particular care taken to leave the surrounding organisms unaffected. Mussels were removed at random until the desired level of abundance, but with focus on the largest individuals (i.e. those most likely targeted by human harvesting) occurring in each plot. Each harvesting treatment was crossed, in 3 out of the 9 plots, with 3 treatments manipulating the temporal variation of mechanical disturbance, one (regular treatment) characterized by an homogenous temporal distribution of events over the experiment, the other 2 (irregular treatments) characterized by a heterogeneous temporal distribution of the same total number of events. In the first treatment, a total of 6 events of disturbance were performed every 3 mo over the period of the experiment, generating a variance of 0 for the time intervals between consecutive events. In the other 2 treatments, the same 6 events in total were arranged in 2 randomly chosen sequences where some events were aggregated over short periods of time, separated by prolonged periods without disturbance, both producing the same value of variance for

the time intervals between consecutive events. Replicating sequences within the same level of variance allowed us to separate the effects of temporal variation of disturbance from those of the particular sequence of events used to produce that desired level of variation (Vaselli et al. 2008). Climate-related mechanical disturbance was simulated by hand using a small weeding hoe and battering the plot in 2 orthogonal directions. The intensity of this disturbance was standardized to half of the number of hits able to remove, on average, all biomass of intertidal organisms from the substratum, as identified after a preliminary study (see also Bertocci et al. 2010). The chosen level of intensity, however, was considered as an ‘extreme’ event as it was potentially able to create patches of free substratum interspersed within intact assemblages, analogously to the effects of the mechanical impact of waves during severe storms and with patterns comparable to those observed in other intertidal systems (e.g. Benedetti-Cecchi & Cinelli 1994). Therefore, our study was designed to examine the effects of changes in the temporal regime of extreme disturbance events (combined with different intensities of harvesting) and not those of variations in the intensity of the mechanical disturbance itself.

Obviously, our mechanical disturbance was able to remove some mussels from experimental plots, including those assigned to the intact bed treatment, but such an effect was analogous to that of any natural disturbance occurring on assemblages subject to previous events. Thus, we assumed that this could not hinder our ability to test the model of interactions between mussel harvesting and mechanical disturbance in an unconfounded way.

Details on the design and on the choice of the total number of experimental disturbance events disturbance on the basis of the natural occurrence of storms at the study area are illustrated in Fig. 1 and Supplement 1 at www.int-res.com/articles/suppl/m495p131_supp.pdf, respectively.

Sampling and analysis of data

Organisms in each plot were sampled on each of the 9 dates selected at each site. Owing to the structure of the experiment, on each sampling date, the time elapsed since the previous disturbance event differed between levels of temporal variation or sequences of disturbance. In order to eliminate this potentially confounding factor, the 9 dates were selected in a way that the average time between a

disturbance event and the next sampling was the same for all treatments (Fig. 1). As a consequence, the treatment effects could only be examined on response variables integrated over the whole course of the study, but not on single sampling dates.

Organisms were sampled visually utilizing a 30 × 30 cm frame, divided into twenty-five 6 × 6 cm sub-quadrats. The abundance of sessile organisms was estimated by assigning to each taxon a score from 0 to 4 in each sub-quadrat, adding up the 25 estimates and expressing final values as percentage covers (Dethier et al. 1993). Mobile animals were quantified as number of individuals. Each taxon was identified to the finest level of taxonomic resolution achievable in the field, in some cases lumping different species into broader taxonomic or morphological categories.

Univariate and multivariate procedures were carried out to test for the effects of experimental treatments on the temporal variance of the abundance and number of individual taxa and of the structure of whole assemblages. Analyses were based on an asymmetrical design including a first partitioning of the total variability into a Control vs. Treatments contrast and the Among treatments variation. The latter was then partitioned into the main effects of harvesting intensity (4 levels), disturbance variability (3 levels, provided by the regular, i.e. low variability, treatment and the 2 irregular, i.e. high variability, sequences) and their interaction. The main effect of temporal variability and the interaction term were further partitioned into a Low vs. High variability contrast and the Among sequences variation and into an Intensity × Low vs. High variability term and an Intensity × Sequences term, respectively. Dependent variables were measures of temporal variance over the period of the experiment in the abundance of common organisms and of the total number of taxa (a proxy for species richness) and their analogues for multivariate data. Each response variable was ana-

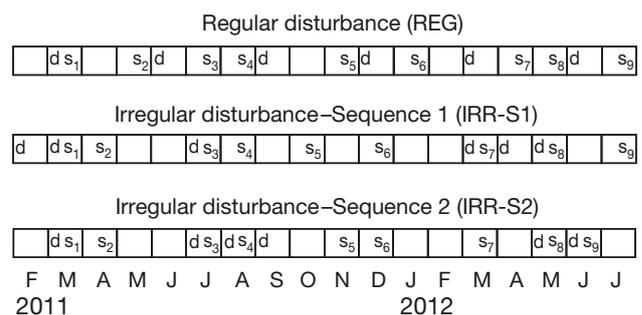


Fig. 1. Experimental and sampling design (d = disturbance event; s₁ to s₉ = sampling dates)

lyzed with analysis of variance (ANOVA). When relevant, Student-Newman-Keuls (SNK) tests were performed for post-hoc comparisons of means. Details of statistical methods are described in Supplement 2.

RESULTS

Structure of assemblages

A total of 37 (16 animal and 21 macroalgal) taxa associated with the *Mytilus galloprovincialis* bed were identified and used for multivariate analyses. At both sites, assemblages regularly disturbed over the period of the experiment showed lower temporal heterogeneity than those subjected to disturbance events irregularly distributed in the presence of an intact mussel bed, while an opposite pattern was documented in plots where the mussel bed was completely removed (Fig. 2). At intermediate levels of mussel harvesting, no differences occurred in the effects of disturbance variability on the temporal heterogeneity in the structure of assemblages (Fig. 2). In addition, only Marreco control plots hosted assemblages less temporally variable compared to those sampled in plots assigned to all other treatments (Fig. 2B). These patterns were supported by a significant interaction of Intensity \times Low vs. High variance at Aguda and by the significant Control vs. Treatments contrast at Marreco. At this second site, in spite of graphically evident differences and of the relatively large value of the *F*-test, the same interaction was not significant, likely due to the low power of the test. Temporal patterns of the structure of assemblages and results of statistical analyses are illustrated in detail in Figs. S1 & S2 in Supplement 3 and Table S2 in Supplement 5, respectively.

Total number of taxa and individual taxa

Although their total number was not affected by any experimental factor, individual taxa showed different responses to experimental treatments (Figs. 3 & 4). Interactive effects of harvesting intensity of mussels and disturbance variability were detected for topshells *Gibbula* spp., limpets *Patella* spp. and articulated coralline algae *Corallina* spp., at both sites and for the red alga *Porphyra linearis* at Marreco. The temporal variance in the abundance of *Gibbula* spp. was larger under regularly, compared to irregularly, distributed disturbance in the presence of a slightly reduced cover of mussels (treatment '30')

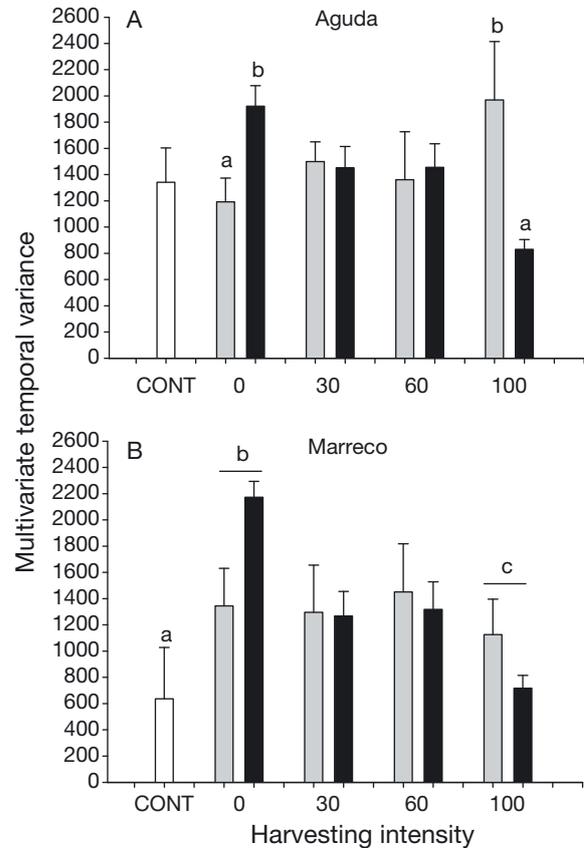


Fig. 2. Mean values (+1 SE) of multivariate temporal variance in unmanipulated controls (white, data averaged over 3 replicate plots) and in each combination of experimental harvesting intensity (0: intact mussel bed; 30 and 60: mussel bed reduced to 70% and 40% cover after removing about 30% and 60%, respectively; 100: mussel bed completely removed) and temporal variability of mechanical disturbance (grey: regular treatment, data averaged over 3 replicate plots; black: irregular treatment, data averaged over 3 replicate plots and 2 sequences) at (A) Aguda and (B) Marreco. Different lowercase letters above bars represent means that differed significantly (at $p < 0.05$, SNK test)

at both sites (Figs. 3B & 4B; SNK tests) or of an intact mussel bed (treatment '0') at Marreco (Fig. 4B; SNK test). Such a response was reversed in Aguda for plots where the mussel bed was completely removed (Fig. 3B; SNK test). At Aguda, besides a significant effect of the experimental sequence of irregularly distributed disturbance events (see Table S3 in Supplement 5), the temporal variance of *Patella* spp. was reduced under irregular, compared to regular, disturbance combined with the lowest experimental level of mussel harvesting ('30' treatment) (Fig. 3C; SNK test). At Marreco, a similar pattern was documented in plots where the mussel bed was left intact, while it was clearly reversed in plots where it was fully

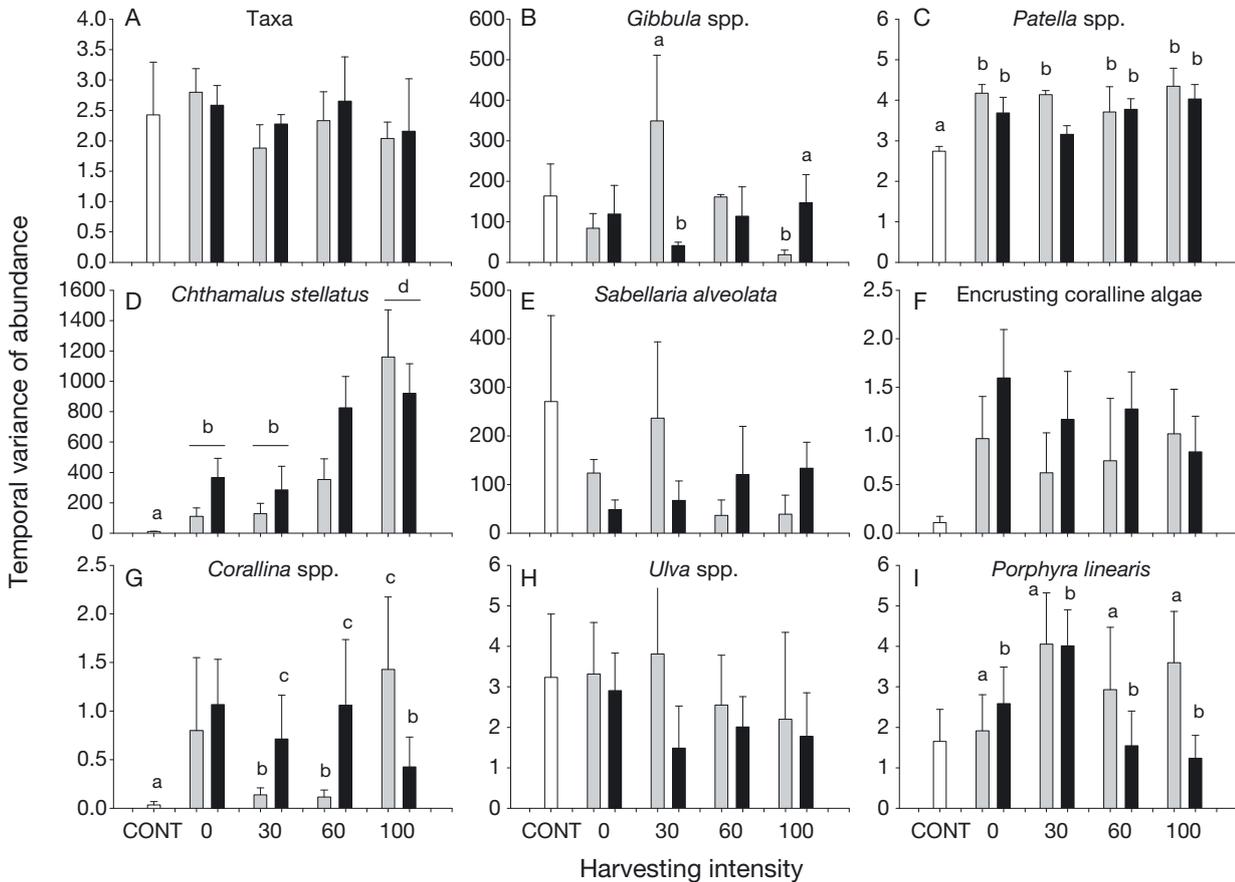


Fig. 3. Mean values (+1 SE) of univariate measures of temporal variance of abundance (A, B, D and E untransformed; C, F, G, H and I in logarithmic form) for the total number of taxa and the most abundant taxa sampled at Aguda. Abbreviations, symbols and sample sizes as in Fig. 2 (C and D: data averaged over sequences in spite of their significant effect for ease of reading and consistency)

removed (Fig. 4C; SNK tests). Temporal variance in the percentage cover of *Corallina* spp. was clearly reduced, at Aguda, under irregularly, compared to regularly, distributed disturbance events combined with both intermediate levels of mussel removal, while the opposite response occurred in plots where mussels were completely removed (Fig. 3G; SNK test). Analogous significant responses were not documented at Marreco. There, however, unharvested plots were still characterized by lower temporal variance of *Corallina* spp. when the regular treatment was compared with the irregular ones, while plots entirely free of mussels showed an opposite pattern (Fig. 4G; SNK test). The temporal variance of *P. linearis* at Marreco was affected by the interaction of harvesting intensity with the particular experimental sequence of events, rather than with the temporal variability of the disturbance itself (Fig. 4I and Table S4 in Supplement 5). Smaller fluctuations of this variable over the period of the experiment,

in particular, occurred under disturbance events applied according to Sequence 1 in plots where mussels were completely eliminated compared to all plots where mussels were only partially removed (treatments '30' and '60', with the treatment having an intact mussel bed inconsistently ranked: SNK test). Disturbance events applied according to Sequence 2, instead, determined lower variance of *P. linearis* in extremely (treatment '100') and highly (treatment '60') harvested compared to not harvested plots (with treatment '30' inconsistently ranked: SNK test). An effect of disturbance variability on *P. linearis*, independent of harvesting intensity of mussels, was detected at Aguda, with the regular treatment determining lower temporal variance of this variable compared to the irregular one (Fig. 3I; SNK test). The barnacle *Chthamalus stellatus* Poli showed, consistently between sites, a pattern of increasing temporal variance with increasing harvesting intensity (Figs. 3D & 4D), although SNK tests could only detect signifi-

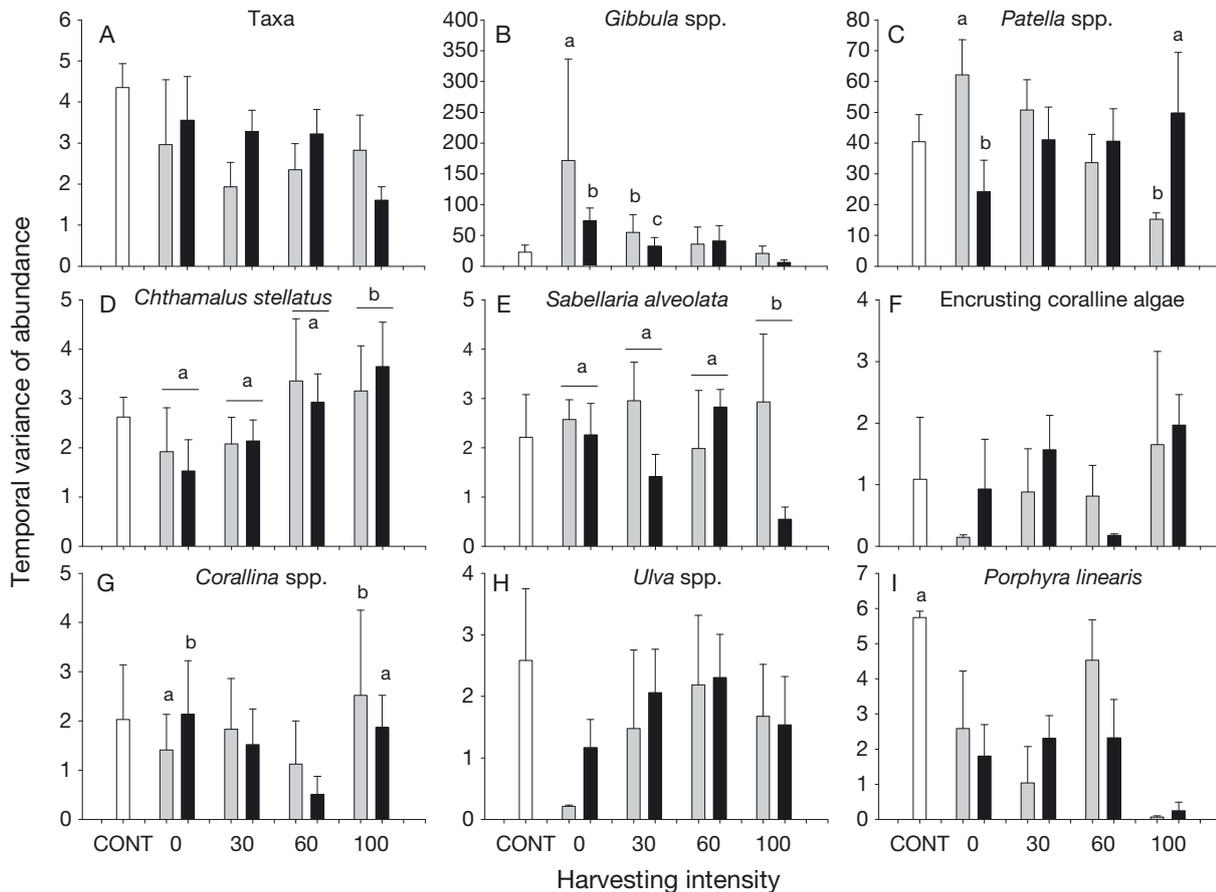


Fig. 4. Mean values (+1 SE) of univariate measures of temporal variance of abundance (A, B, and C untransformed; D, E, F, G, H and I in logarithmic form) for the total number of taxa and the most abundant taxa sampled at Marreco. Abbreviations, symbols and sample sizes as in Fig. 2 (H: data averaged over sequences in spite of their significant effect for ease of reading and consistency)

cant differences between the complete removal treatment vs. not or mildly harvested treatments ('0' and '30', respectively) and between the '60' vs. the '0' treatment at Aguda, and between the complete removal treatment vs. other treatments at Marreco. Only at Aguda was the temporal variance of *C. stellatus* reduced in unmanipulated plots compared to all other treatments and was affected by the sequence of disturbance events (Fig. 3D and Table S3 in Supplement 5). No significant responses to experimental treatments were provided by the honeycomb worm *Sabellaria alveolata* L., encrusting coralline algae and the green alga *Ulva* spp. at Aguda (Fig. 3E,F,H and Table S3 in Supplement 5). Nevertheless, a trend towards larger temporal variance of *S. alveolata* subject to regular, compared to irregular, disturbance combined with no or mild mussel harvesting was evident, while an opposite trend was observed in plots more intensively harvested (Fig. 3E). The temporal variance of encrusting corallines, instead, tended to

be reduced in unmanipulated plots compared to all other treatments (Fig. 3F). A significant main effect of harvesting intensity on the temporal variance of *S. alveolata* was detected at Marreco, where this variable was reduced in completely compared to less or no harvested plots (Fig. 4E, Table S4 in Supplement 5 and SNK test). Finally, a main effect of disturbance variability was detected for *Ulva* spp. at Marreco, but this was driven by a response of this taxon to the particular irregular sequence of events rather than to variation of the level of temporal variability itself (Fig. 4H and Table S4 in Supplement 5). Univariate temporal patterns are illustrated in Fig. S3 in Supplement 4.

DISCUSSION

Our proposed model involving a buffering effect of an intact mussel bed on physical disturbance led us

to predict an interaction between experimental mussel harvesting and climate-related mechanical disturbance. This was generally supported by multivariate findings, indicating that disturbance events regularly distributed over the period of the experiment determined lower temporal heterogeneity in the structure of assemblages than events characterized by larger temporal variance, but only in the presence of an intact mussel bed. The opposite pattern was documented in plots where the mussel bed was completely removed. These results were in most cases consistent across sites. As expected, an intact mussel bed, analogously to other habitat-forming organisms (e.g. Bertocci et al. 2010, Maggi et al. 2012), could mitigate the effects of regularly distributed disturbance events, thus maintaining the structure of associated assemblages relatively stable over the experiment. The application of several disturbance events clustered in shorter periods of time could overwhelm such buffering ability, creating patches of available resources, mainly space, that allowed the colonization by organisms otherwise excluded as inferior competitors per se. This could logically explain the larger temporal heterogeneity in the structure of assemblages when subjected to the irregular disturbance treatment, in general in agreement with previous findings on freshwater benthic assemblages under constant vs. temporally variable sediment disturbance (Molinos & Donohue 2011). Such a mechanism has also been documented in terrestrial systems through a progressive reduction of the ability of organisms to resist or recover from increasingly stressful disturbance, leading to a destabilization of assemblages and to an increased variability of the system (Collins 2000, Fraterrigo & Rusak 2008). In contrast, in plots where mussels were completely removed, irregularly distributed disturbance events reduced the temporal heterogeneity of assemblages compared to regularly distributed ones, analogously to findings of Burgmer & Hillebrand (2011) on phytoplankton assemblages exposed to increasing temperature variance in a microcosm experiment. This result is consistent with the expected effects of increasing disturbance intensity, defined as the physical force of the event per unit of area and time (Pickett & White 1985). Intense disturbances can reduce the variability of assemblages by eliminating most organisms and thus homogenizing patches, while weaker disturbances can maintain a more heterogeneous mosaic of available resources and local organisms, thus enhancing the spatial and temporal patchiness of the system (e.g. Collins et al. 2001, Bertocci et al. 2005). Although the total intensity of

applied disturbance was kept constant among all our experimental treatments, a similar mechanism was hypothesized also in the present study. In fact, disturbance events clustered in time could drastically reduce the abundance of organisms for a longer period than regularly distributed events, thus reducing their temporal fluctuations due to the scaling relationship between the mean and the variance (Taylor 1961). The homogenization of damaged patches and their prolonged maintenance under the relatively more severe treatment might explain the reduced heterogeneity of assemblages subjected to irregular disturbance in the absence of mussels (see also Frascchetti et al. 2001). In fact, the mean cover of bare rock (b.r.) over the whole period of the experiment was much lower for the regular treatment than for the irregular ones at both sites (Aguda: $b.r._{Reg} = 33.7\%$, $b.r._{Irr} = 60.1\%$; Marreco: $b.r._{Reg} = 44.1\%$, $b.r._{Irr} = 71.2\%$).

Univariate responses analogous to the multivariate one were displayed by *Corallina* spp., at both sites, and by *Porphyra linearis*, particularly at Aguda. Opposite effects of temporal variability of disturbance were exerted on *Corallina* spp. depending on the presence of an intact or fully removed mussel bed, conditions where this taxon tended to maintain relatively lower and larger abundance, respectively. Such patterns are consistent with previous findings indicating that algal turfs often tend to become dominant after the loss of a foundation species, such as canopy-forming macroalgae (e.g. Benedetti-Cecchi et al. 2001, Lilley & Schiel 2006, Eriksson et al. 2007), likely due to the greater competitive abilities of turfs under the new harsher conditions (reviewed by Airoidi et al. 2008). A combination of reduced competition and large mechanical resistance can also facilitate articulated coralline algae to become dominant at sites characterized by intense disturbance, including wave exposure (Bulleri & Airoidi 2005). In the present case, the abundance of *Corallina* spp. within an intact mussel bed was particularly low and tended to remain relatively steady under regularly distributed disturbance events which could likely be buffered by the mussel bed. As expected, the irregular treatment, where the occurrence of disturbance events were clustered in relatively shorter periods of time, could lead to more resource availability, i.e. mostly space, for coralline algae within the mussels. As a consequence, *Corallina* spp. could increase slightly in abundance and their temporal heterogeneity over the period of the experiment could increase relative to regular treatment plots. Irregular disturbance events applied to plots where mussels

were completely removed were consistently associated with a larger observed cover of *Corallina* spp. The maintenance of steady values over the course of the experiment resulted in lower temporal heterogeneity of this taxon under irregular, compared to regular, treatments after the removal of the mussel bed. An opposite response to the removal of mussels could explain *P. linearis* results. Although not exclusively associated with mussels as has been observed elsewhere (e.g. Crowe et al. 2011), we found this alga clearly more abundant within the mussel bed than in plots where mussels had been removed. It was not surprising that the complete removal of a relevant component of the habitat, besides a drastic reduction of *P. linearis*, also determined, through the mean/variance relationship (Taylor 1961), a reduction of its temporal heterogeneity in all treatments, compared to the control, at Marreco and under the irregular vs. regular treatment at Aguda. Consistently, at both sites, also where mussels were heavily, although not completely, removed (i.e. 60% treatment), the more stressful irregular treatment could reduce the temporal heterogeneity of *P. linearis* relative to the regular one.

Grazers of the genus *Gibbula* and *Patella* showed responses to experimental treatments substantially reversing those of turf-forming algae. The temporal heterogeneity of both taxa was reduced by irregularly, compared to regularly, distributed disturbance events applied to an intact mussel bed, while the opposite pattern was observed in plots where mussels were completely removed. However, mussel-intact plots tended to be associated with a larger abundance of *Gibbula* spp. and lower abundance of *Patella* spp. compared to mussel-depleted plots, suggesting possible different mechanisms for comparable effects. For topshells, we could hypothesize that a fully or almost intact mussel bed could provide a favorable habitat in terms of protection from desiccation, waves and predators, analogously to previous findings documenting strong reductions of whelks after the removal of a canopy-forming macroalga (Underwood 1998). Under these conditions, the abundance of such animals could be maintained relatively high, while their temporal heterogeneity could be mostly driven by temporal patterns of relevant abiotic and biological factors (e.g. Broitman et al. 2008). Intense disturbance events could then reduce, directly or indirectly, the abundance of topshells, logically determining lower fluctuations of this response variable over the period of the experiment observed under the irregular vs. regular disturbance treatment. Limpets, instead, could be more resistant than top-

shells to disturbance, including desiccation and mechanical impacts, while they could be excluded from substrates monopolized by sessile organisms (Underwood & Jernakoff 1981). Thus, they tend to increase in abundance once free patches were made available by relatively intense disturbances (e.g. Bertocci et al. 2005). In the present system, although more evidently at Marreco, the larger and more persistent availability of free space determined by the irregular treatment could have also made limpets more homogeneously distributed over the period of the experiment within the mussel bed. Once mussels were completely removed, temporal patterns of limpets could have remained relatively stable due to the increased abundance and homogenous distribution of these animals driven by their resistance/recovery abilities, and enhanced in variability by the irregular treatment through its harsher effect on such processes. Increases in grazing intensity after the removal of habitat-forming species have been previously documented (Jenkins et al. 2004).

Independent effects of harvesting intensity and of the sequence of disturbance were documented for barnacles *Chthamalus stellatus*. Increased temporal variance of *C. stellatus* with increasing intensity of mussel harvesting could be a function of increased amounts of available space after mussels and possibly associated algal turfs were eliminated (e.g. Bertness et al. 2001). Not mutually exclusive direct and indirect mechanisms could explain the effect of the particular sequence of disturbance events at Aguda. First, *C. stellatus* showed its largest peak in abundance in July 2011, likely falling within the period of greatest recruitment of this species, as documented for nearby locations (O'Riordan et al. 2004). Second, potential better competitors for space were reduced during the same period, likely leaving room for colonizing barnacles. It could be hypothesized that a disturbance occurring in the same period could affect recruits and abundance patterns of barnacles independent of its irregular vs. regular trait, potentially determining significant effects of the sequence of disturbance alone. In the present experiment, the IRR-S2, but not the IRR-S1, treatment involved a disturbance event in August 2011, i.e. still within peak recruitment of *C. stellatus*, and this might have driven the significant effect of experimental treatments characterized by the same overall variance, but different temporal arrangements of events. The same results were not obtained at Marreco, leading us to reject our hypothesis of consistent responses of some individual taxa over 2 sites kilometers apart and characterized by a number of comparable abiotic

factors that were controlled in the experimental design. Variability in the patterns of colonization of sessile organisms was also documented in other systems over similar scales and was attributed, for instance, to variation in availability of larvae (Raimondi 1990).

In spite of even large fluctuations in the abundance of individual taxa, in a system such as the present one, where most organisms are able to effectively resist or recover from disturbance, the overall number of taxa over the examined temporal scale remained relatively stable, as the variability of assemblages was due to large changes in relative abundances rather than in the identity of taxa. However, this contrasts with empirical and theoretical evidence that environmental variability might increase richness by reducing competition and promoting the coexistence of species with different life-traits (Chesson & Huntly 1997), or decrease it through increased risk of extinction for most species (Vucetich et al. 2000). Here, most organisms could persist over the period of the experiment (or they could rapidly re-colonize after temporary extinctions), suggesting caution in assuming general relationships between disturbance traits and richness of assemblages (see also Inchausti & Halley 2003).

The present findings could be applied to other systems characterized by organisms able to resist or recover quickly after disturbance events, particularly when these occur to populations and assemblages already maintained in altered states. This could be the case for populations collapsed due to overfishing, chronic pollution or climate-related factors, including changes in the regime of storms (e.g. Paine et al. 1998). In addition, our results are relevant to understanding responses of organisms to environmental variations. Climatic models forecast an increase in the occurrence of extreme events (e.g. Smith 2011), with changes in temporal patterning so that they would cluster in short periods of time, interspersed within calm periods (D'Odorico & Bhattachan 2012 and references therein). Different effects of multiple traits of single disturbances have been previously documented, but it is obvious that any disturbance occurs simultaneously and interacts with other natural or human perturbations drastically threatening biodiversity. This complicates predictions arising from the evaluation of each disturbance separately (Paine et al. 1998). We provided one of the first manipulative examples of opposite responses of assemblages associated with intact vs. depleted foundation species to changes in environmental variance. Although climate events occur on scales larger

than the present ones, this study can contribute to predicting responses of assemblages under scenarios of combined climate and non-climate processes (Rosenzweig et al. 2008).

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