



Competitive ability of macroalgal canopies overwhelms the effects of variable regimes of disturbance

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ABSTRACT: Predicting the response of natural systems to climate change is key for maintaining their functioning and the services they deliver to humans. Along with variations in the mean intensity of environmental and meteorological events, climate change is expected to generate a substantial increase in their temporal variance, the ecological impact of which has been largely overlooked. In the marine environment, these changes may result in altered natural regimes of disturbance that, interacting with the current decline of species playing key ecological roles, could influence the structure of natural communities. The aim of this study was to experimentally investigate the compounded effects of changes in the mean intensity and temporal variance of storms and loss of canopy-forming macroalgae on the abundance and diversity of benthic assemblages in temperate rockpools. Our results showed that competitive effects of *Cystoseira* spp. on the cover and diversity of assemblages were more important than changes in intensity or temporal variance of events of disturbance per se. As a consequence, predicted changes in the regime of disturbance due to storms do not have the potential to counteract community shifts towards the dominance by algal turfs, once *Cystoseira* spp. are lost.

KEY WORDS: Canopy-forming species · Climate change · Disturbance · Rocky shore · Temporal variance

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INTRODUCTION

There is mounting evidence suggesting that the structure and functioning of natural systems and, hence, their ability to deliver goods and services to humans, could be altered by global climate change (Rosenzweig et al. 2008, Füssel 2009). Predicting the response of natural systems to alternative climate scenarios has, thus, become a central issue in ecology (Parmesan & Yohe 2003).

The majority of studies investigating the effects of climate change on natural systems has focused on variations in the mean intensity of physical variables, such as temperature and CO₂ (Grime et al. 2000, Zavaleta et al. 2003, Stuart-Smith et al. 2010),

or extreme meteorological events, including drought, floods and hurricanes (Easterling et al. 2000, Perez-Ramos et al. 2010, Zimmerman et al. 2010, Wethey et al. 2011). However, along with alterations to the mean intensity of environmental variables and meteorological events, global climate change is also associated with a substantial increase in their temporal variability (Easterling et al. 2000, Gutschick & BassiriRad 2003). Both correlative (e.g. Dayton et al. 1999, Johnson et al. 2011, Schiel 2011) and manipulative studies (Collins 2000, McCabe & Gotelli 2000) have investigated the role of changes in frequency of disturbance in terrestrial and aquatic systems. In particular, Dayton et al. (1999) investigated the role of both intensity and frequency of disturbance in

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structuring kelp communities, highlighting the role of large-scale, low-frequency episodic changes in the oceanographic climate. More recently, increases in the frequency of oceanographic events have been related to changes in the structure of nearshore communities (Johnson et al. 2011, Schiel 2011). However, changes in frequency imply variation in both overall intensity and temporal patterns (i.e. temporal variance) of disturbance (Benedetti-Cecchi 2003), making it difficult to distinguish the relative contribution of each component to effects on natural communities.

Increases in the temporal variance of weather events (Michener et al. 1997, Muller & Stone 2001) have the potential to alter natural regimes of disturbance (Bertocci et al. 2005, D'Odorico et al. 2005). In the marine environment, disturbance due to physical factors such as waves and currents (Dayton 1971, Sousa 2000) is a driver of patterns of abundance and distribution of intertidal and shallow subtidal benthic organisms (e.g. Lubchenco & Menge 1978, Dayton et al. 1992, Benedetti-Cecchi & Cinelli 1996, Connell et al. 1997). Nonetheless, there has been little effort to experimentally assess the ecological effects of alterations in the temporal variance of disturbance events (Molinis & Donohue 2010), in particular in the context of climate change (Bertocci et al. 2005, 2007, Benedetti-Cecchi et al. 2006, Vaselli et al. 2008, Incera et al. 2010).

An even smaller effort has been made to assess how the alterations in the regime of disturbance (i.e. mean intensity and temporal variance) generated by large-scale climate changes can be modified by other human perturbations that generally take place at smaller spatial scales. Current theory predicts, in fact, that the ability of natural systems to resist to and to recover from disturbance is largely dependent on life-history traits of dominant species (e.g. Dayton 1975, Callaway 1995, Bertness et al. 1999). Under these circumstances, the ongoing decline of species playing key ecological roles, such as top predators (Heithaus et al. 2008) or foundation species (Dayton 1972, Bruno & Bertness 2001, Ellison et al. 2005), caused by human perturbations operating at local to regional scales (such as harvesting, pollution, habitat fragmentation), can be predicted to enhance the susceptibility of natural communities to altered regimes of disturbance.

The aim of the present study was to investigate the compounded effects of changes in the mean intensity and temporal variance of storms and loss of dominant species (i.e. canopy-forming macroalgae) on the abundance and diversity of benthic assemblages in

rockpools. Perennial canopy-forming species can buffer understory organisms from physical stress (Bertness et al. 1999, Lilley & Schiel 2006, Bertocci et al. 2010), although they can be damaged or dislodged by very large storms (Underwood 1998). Anthropogenic disturbances, including organic and inorganic pollution and enhanced rates of sediment deposition, are, however, the major causes of the global decline of canopy-forming species (Tegner et al. 1995, Benedetti-Cecchi et al. 2001, Gorman & Connell 2009, Perkol-Finkel & Airoidi 2010). In general, the loss of canopy-forming macroalgae results in the dominance of opportunistic taxa and, ultimately, in less productive communities (Eriksson et al. 1998, Benedetti-Cecchi et al. 2001, Bulleri et al. 2002, Steneck et al. 2002, Gorman & Connell 2009 and references therein).

We predicted that events of disturbance would have no effect on understory organisms in the presence of canopy-forming macroalgae, except for the extreme case in which intense disturbance events, aggregated in time (i.e. at high intensity and temporal variance), would result in the elimination of the canopies. In addition, we predicted that the experimental removal of macroalgal canopies would promote dominance by fast-growing algal turfs in the absence of disturbance. However, we expected that increasing the intensity and/or temporal aggregation of events of disturbance would dampen such positive effects (since algal turfs are largely susceptible to mechanical disturbance; Lubchenco & Menge 1978), indirectly facilitating species that are more resistant to mechanical disturbance (but less competitive in acquiring space), such as encrusting algae or invertebrates (Lubchenco & Menge 1978, Bulleri 2006).

MATERIALS AND METHODS

Study system

We studied rockpool assemblages dominated by dense stands of the canopy-forming macroalgae of the genus *Cystoseira* (Fucales). These algae are firmly attached to the substratum through a coriaceous holdfast, can reach 40 cm in height and form dense canopy stands, thus providing shade and shelter for understory assemblages (Bertness et al. 1999, Jenkins et al. 1999, Leonard 2000, Bulleri et al. 2002). It is worth noting, however, that previous studies showed that *Cystoseira* spp. should not be considered a foundation species in these rockpools (sensu Dayton 1972); in fact, although its displace-

ment induces a switch towards a turf-dominated system, this displacement does not affect the general pattern of distribution of the other understory species, which can probably find suitable conditions in the turf matrix as well (Benedetti-Cecchi & Cinelli 1992). Populations of *Cystoseira* spp. are declining along Mediterranean rocky coasts, as a consequence of the intensification of human activities in coastal areas (Seapy & Littler 1982, Rodríguez-Prieto & Polo 1996, Benedetti-Cecchi et al. 2001, Mangialajo et al. 2008) and competition from exotic seaweeds (Bulleri et al. 2010).

A field experiment was carried out along the west coast of Italy (Calafuria, Livorno; 43° 30' N, 10° 20' E) from April 2003 to June 2005. Rockpools had a surface area ranging from 1.4 to 8 m² (mean depth \pm SD: 40 \pm 14.4 cm) and were located from 0.1 to 0.3 m above the mean low-water level. Since water exchange between these low-shore pools and the open sea occurs even during calm sea conditions, fluctuations in physical-chemical variables (e.g. temperature, salinity, oxygen, pH) are likely to be smaller than in pools at higher levels on the shore. In the low-shore rockpools, the provision of open space (defined as bare rock or barren patches monopolised by encrusting corallines) is mostly due to mechanical removal of erect species during storms (Benedetti-Cecchi & Cinelli 1996). Experimental removal of boulders from rockpools for 1 yr has shown that the rolling of boulders on the sloping sides during storm events is one of the main causes of mechanical disturbance (average percentage of open space \pm SE: rockpools without boulders = 8.83 \pm 2.23%; rockpools with boulders = 14.83 \pm 3.16%; n = 24; E. Maggi unpubl. data). Measures taken in rockpools before the start of the experiment indicate that the weight per unit area of boulders ranged between 0 and 19 kg m⁻² (median: 8 kg m⁻²), likely reflecting wide fluctuations in the intensity of disturbance during storms. Grazing by sea urchins *Paracentrotus lividus* Lam. and *Arbacia lixula* L. can also be an important source of disturbance in these rockpools, but it is generally restricted to narrow areas in front of herbivore refuges (Benedetti-Cecchi & Cinelli 1995) and does not influence the availability of open space within stands of *Cystoseira* spp. (Benedetti-Cecchi & Cinelli 1996).

Algal mosaics in rockpools were composed by stands of *Cystoseira* spp. (mainly *C. brachycarpa* var. *balearica* (Sauvageau) Giaccone, but also *C. compressa* (Esper) Gerloff & Nizamuddin and *C. crinita* Bory), which are the dominant canopy-forming algae, with an understory assemblage made of erect

and encrusting algae. Small-sized erect forms include filamentous (e.g. *Ceramium* spp., *Cladophora* spp.), coarsely branched (e.g. *Gelidium* sp., *Hypnea musciformis*, *Laurencia obtusa*, *Rytiphloea tinctoria*), thin tubular sheet-like (e.g. *Dictyota dichotoma*, *Dictyopteris membranacea*, *Padina pavonica*) and articulated coralline algae (e.g. *Corallina elongata*, *Jania* sp.). These algae form a complex matrix (a common feature in Mediterranean intertidal rocky habitats; see e.g. Benedetti-Cecchi et al. 2001) which is hereafter referred to as 'turf'. Encrusting algae comprised both red corallines (mostly *Lithothamnion* sp.) and brown algae. Sessile invertebrates included the tube-forming gastropod *Vermetus triqueter* Bivona-Bernardi, serpulids, spirorbids, the barnacle *Balanus glandula* Darwin, mussels and, occasionally, sponges and didemnid tunicates. In addition to sea urchins, grazers were represented by limpets (*Patella ulyssiponensis* Roding and *P. caerulea* L.).

Experimental design

We assumed that changes in temporal variability of disturbance generated by the scouring of boulders inside rockpools would realistically simulate the effects of changes in temporal variability of disturbance due to large storm events. To manipulate temporal variability of events of disturbance by boulders, we created 3 different temporal sequences of presence/absence of boulders inside pools, intended to reflect increasing temporal variance: continuous presence of boulders; a sequence of boulder presence/absence distributed almost regularly in time; and a sequence of boulder presence/absence more irregularly distributed. In the last 2 cases, boulders were present inside rockpools for 13.5 mo over a total of 27 mo (Fig. 1, Table 1). Four rockpools were randomly assigned to each sequence. Two out of these 4 rockpools were then randomly assigned to each of 2 levels of intensity of disturbance: small and large, defined as the weight of boulders per unit area, and consisting of 8 kg m⁻² (the median of the observed distribution) and 16 kg m⁻², respectively. In the continuous sequence, the 2 levels of intensity were halved (resulting in 4 and 8 kg m⁻², respectively), since boulders were present twice as long in this treatment. This resulted in a realised total intensity of disturbance comparable across sequences, for each level of intensity (Table 1). Care was taken in minimising differences in weight among boulders (we always chose boulders of about 7 to 9 kg in weight) to avoid confounding effects due to a differ-

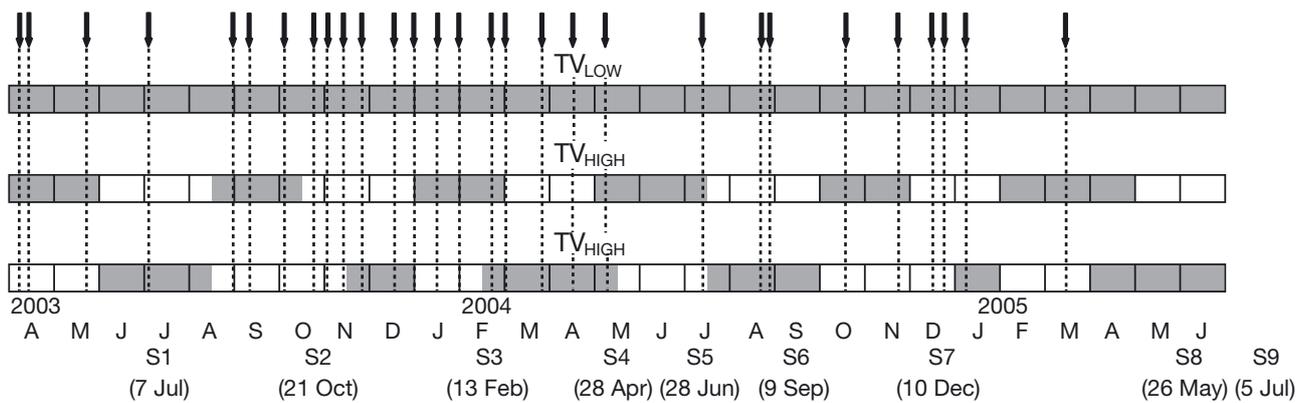


Fig. 1. Distribution of disturbance events over the course of the experiment, for each sequence of presence (grey) and absence (white) of boulders. Storm events able to move boulders inside pools are indicated (black arrow). S1 to S9: sampling dates. TV_{LOW} and TV_{HIGH}: low and high temporal variance, respectively

ent probability of being overturned during storms (Sousa 1979, McGuinness 1987). Events of disturbance due to boulders occurred only in association with rough seas. We therefore calculated *a posteriori* the values of realised temporal variance for the different experimental conditions, as the sum of the squared differences of the time interval between consecutive events (i.e. storms) from the mean time interval over the whole period of the experiment. Data on storms at the study site were collected from the Istituto Superiore per la Protezione e la Ricerca Ambientale (ISPRA, www.idromare.it; meteorological station located in Livorno). A storm was defined as the occurrence of on-shore winds (with an orientation between 180° and 360°) with daily average speed >8 m s⁻¹ (corresponding to waves at least 1.5 m in height, according to the Beaufort scale, and considered strong enough to move boulders inside rock-

pools; E. Maggi pers. obs.) for at least 2 consecutive days, or >12 m s⁻¹ if blowing only for 1 d. A total of 29 storm events occurred throughout the study. All 29 events acted on assemblages of rockpools where boulders were continuously kept, while about half of these events occurred when boulders were present in regular and irregular sequence pools (Table 1, Fig. 1), resulting in different realised temporal variances of disturbance (Table 1). We defined the continuous presence of boulders as low temporal variance of disturbance (TV_{LOW}). Due to the negligible difference between the temporal variances in rockpools with regular or irregular boulder presence, we considered data from these rockpools as having the same (high) level of temporal variance of disturbance (TV_{HIGH}). We therefore averaged the effects of the regular and irregular sequences of boulder presence and contrasted this mean effect against the effect of continuous presence (i.e. TV_{HIGH} vs. TV_{LOW}).

Table 1. Applied disturbance in rockpools with continuous presence of boulders or with boulders present at regular or irregular intervals (see Fig. 1). I_{SMALL} and I_{LARGE}: small and large intensity, respectively; TV_{LOW} and TV_{HIGH}: low and high temporal variance, respectively. Numbers separated by a comma refer to regular and irregular treatments, respectively

	Continuous TV _{LOW}		Regular/irregular TV _{HIGH}	
	I _{SMALL}	I _{LARGE}	I _{SMALL}	I _{LARGE}
Presence of boulders (mo)	27	27	13.5	13.5
Weight of boulders per unit area (kg m ⁻²)	4	8	8	16
No. of storms acting on assemblages	29	29	14,16	14,16
Realised total intensity of disturbance (kg m ⁻² × no. of storms)	116	232	112,128	224,256
Realised temporal variance of disturbance		0.48		2.05,2.56

continuous presence (i.e. TV_{HIGH} vs. TV_{LOW}). Since the 2 sequences belonging to the TV_{HIGH} treatment were characterised by almost complementary temporal events of presence/absence of boulders inside rockpools (Fig. 1), their mean effect over the entire study was comparable to that of a continuous presence of half-weighted boulders; as a consequence, the contrast 'TV_{HIGH} vs. TV_{LOW}' estimated the difference in the effect of treatments differing only in terms of temporal variance.

Thus, crossing temporal variance (2 levels, low and high) and intensity (2 levels, small and large) generated 4 experimental combinations (Table 1).

This experimental design allowed us to separate the effects of the temporal variance of events from those of their intensity (Benedetti-Cecchi 2003). In order to represent the entire range of natural intensities of disturbance, boulders were also removed from 2 additional rockpools throughout the duration of the experiment (treatment 'No Boulders').

Experimental treatments were checked and, when necessary, re-established after each storm event, as soon as weather conditions made it feasible. In each of the 10 rockpools, six 10 × 10 cm quadrats, 10s of cm apart, were randomly identified within the canopy of *Cystoseira* spp. and marked at their corners with epoxy-putty (Subcoat S, Veneziani). In 3 quadrats, canopies were left untouched (+Canopy treatment), while both canopies and holdfasts of *Cystoseira* spp. were removed from the others throughout the study period, using a paint scraper and a knife (-Canopy treatment). Care was taken to avoid damaging the surrounding and understory organisms or altering the topography of the substratum.

Sampling and analyses of data

Pools were sampled 9 times during the study period (Fig. 1). Percentage covers of organisms were estimated using a plastic frame of 8 × 8 cm (smaller than the marked plots, to avoid edge effects) divided into 16 sub-quadrats of 2 × 2 cm that were given a score from 0 to 4 (0 ≈ 0% coverage, 1 ≈ 25%, 2 ≈ 50%, 3 ≈ 75%, 4 ≈ 100%) for each taxon in each sub-quadrat. Final covers were obtained by summing scores over the 16 sub-quadrats (Dethier et al. 1993), for a maximum score of 64. Values were then expressed as percentages. Organisms were identified to the highest level of taxonomic resolution achievable in the field. Given the low cover of individual species and genera, these were lumped into morpho-functional groups for statistical analyses (i.e. turf-forming species, encrusting algae and sessile invertebrates). Finally, diversity of species was estimated as the total number of taxa in each 8 × 8 cm quadrat.

Since experimental levels of intensity of disturbance were comparable among levels of temporal variance only over the entire duration of the study (Table 1), data were analysed as mean temporal values of covers and diversity over the 9 sampling dates using asymmetric ANOVAs. Rockpools without boulders (No Boulders) were initially compared to all other treatments; this contrast (No Boulders vs. Boulders) was crossed with the canopy treatment (fixed, 2 levels: +Canopy, -Canopy). Variability asso-

ciated with the other treatments (Boulders) was then partitioned among 2 factors: the contrast 'TV_{HIGH} vs. TV_{LOW}' (fixed, 2 levels) and Intensity (fixed, 2 levels). These 2 factors and Canopy were analysed as 3 fixed, crossed factors. The factor Rockpool (2 levels, i.e. 2 pools per treatment) was included as a random effect, nested within each type of treatment, and crossed with Canopy.

Data met the assumptions of homoscedasticity (Cochran *C* test), except for sessile invertebrate percent cover, which was $\ln(x+1)$ transformed to make variances homogeneous. Student-Newman-Keuls (SNK) tests were used for *a posteriori* comparisons of the means after a significant effect was detected by ANOVAs (Winer 1971, Underwood 1997).

RESULTS

The removal of *Cystoseira* spp. was effective in reducing canopy cover (Canopy: $F = 1386.26$, $p < 0.0001$; mean temporal percentage cover of *Cystoseira* spp. ± SE: +Canopy = $64.29 \pm 1.70\%$, -Canopy = $7.52 \pm 0.66\%$; $n = 378$). Intensity and temporal variance of disturbance interactively affected the cover of *Cystoseira* spp. (Intensity × TV_{HIGH} vs. TV_{LOW} × Canopy: $F = 14.41$, $p < 0.01$). In particular, in the +Canopy treatment, the cover of *Cystoseira* spp. was significantly reduced by a disturbance of large intensity and low temporal variance (Fig. 2).

The removal of the canopy affected the cover of turf-forming species and encrusting algae in interaction with rockpools (Rockpool × Canopy; Table 2). In particular, percentage cover of turf-forming species increased after the removal of *Cystoseira* spp. in 12 out of 14 rockpools (Fig. 3). The same effect of canopy removal was observed on cover of encrusting algae, but only in 4 out of 14 rockpools (SNK tests, $p < 0.05$).

Intensity and temporal variance of disturbance by boulders, and canopy presence interactively influenced the cover of sessile invertebrates (Intensity × TV_{HIGH} vs. TV_{LOW} × Canopy; Table 2). In particular, large intensity of disturbance determined an increase in cover of these animals, except when the canopy was present (i.e. in the +Canopy treatments) and temporal variance of events was low (Fig. 4). In addition, a significant variability among rockpools was observed (Rockpools; Table 2)

Removal of *Cystoseira* spp. significantly increased the diversity of taxa in the absence of boulders, but not in their presence (No Boulders vs. Boulders × Canopy; Table 2, Fig. 5). A significant variability among rockpools was also detected (Table 2).

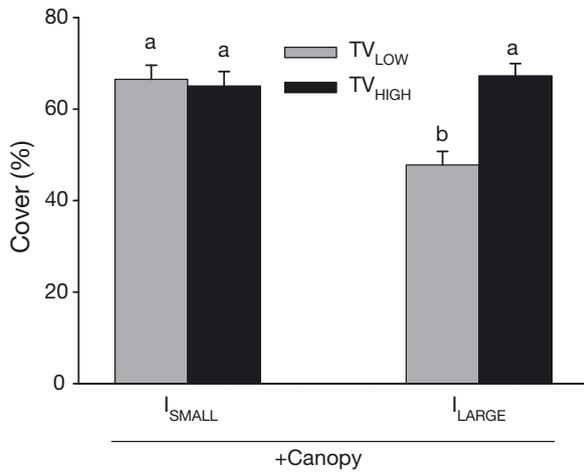


Fig. 2. *Cystoseira* spp. Mean temporal abundance in the presence of canopy (+Canopy) in rockpools with boulders at low (TV_{LOW}) and high (TV_{HIGH}) temporal variance of disturbance, both at small (I_{SMALL}) and large (I_{LARGE}) intensity. Data are means (+1 SE) over 3 replicate plots pooled between the 2 TV_{LOW} or 4 TV_{HIGH} replicate rockpools and 9 sampling dates. Shared lowercase letters indicate treatments that do not differ significantly (Student-Newman-Keuls tests, p > 0.05)

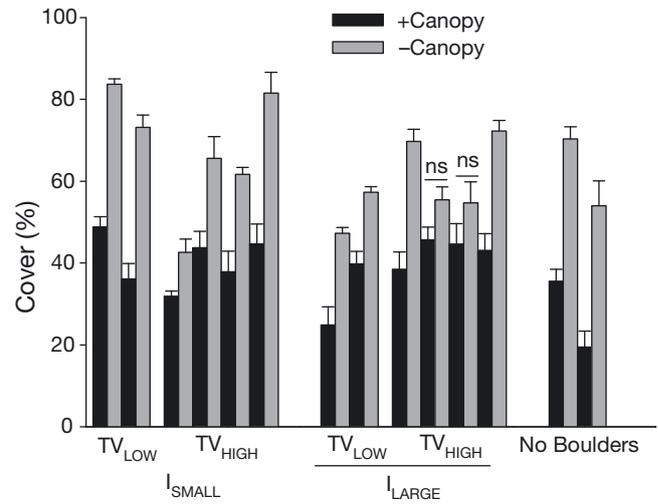


Fig. 3. Mean temporal abundance of turf-forming species in the presence (+Canopy) or absence (-Canopy) of canopy in each rockpool assigned to the different disturbance treatments. Data are means (+1 SE) over 3 replicate plots pooled among 9 sampling dates. I_{SMALL} and I_{LARGE}: small and large intensity, respectively; No Boulders: boulders were continuously removed; TV_{LOW} and TV_{HIGH}: low and high temporal variance, respectively. ns: treatments that do not differ significantly (Student-Newman-Keuls tests, p > 0.05)

DISCUSSION

Contrary to our expectations, macroalgal canopies did not buffer understory assemblages from disturbance. In fact, the mean cover of both turfs and encrusting algae was not affected by disturbance at all, even in the absence of a canopy. Indeed, the cover of sessile invertebrates increased under some combinations of intensity and temporal variance of disturbance.

Disturbance negatively affected *Cystoseira* spp., in particular when disturbance events were characterised by large intensity and low temporal variance.

While the effect of intensity is intuitive (i.e. the larger the intensity, the larger the biomass removed), the negative effect exerted by high-intensity disturbances with low temporal variance is unexpected. A low variance implies that events of disturbance are more regularly distributed over time, in comparison to high temporal variance, when events are more clustered but separated by relatively long periods of absence of disturbance. This suggests that the negative response of *Cystoseira* spp. was likely due to the lack of sufficient time to recover, rather than by a clustering of disturbance events. A similar result has

Table 2. ANOVAs on percentage covers and diversity of understory organisms. Only sources of variability of interest are shown. Data are F-values. TV_{LOW} and TV_{HIGH}: low and high temporal variance, respectively. *p < 0.05; ***p < 0.001

Source of variability	Turf-forming algae	Encrusting algae	Sessile invertebrates	Diversity of taxa
No Boulders vs. Boulders	1.06	0.45	0.69	0.79
Canopy	109.42***	3.89	0.00	15.03*
No Boulders vs. Boulders × Canopy	2.44	0.19	0.22	8.01*
Intensity	0.88	3.34	6.97*	0.06
TV _{HIGH} vs. TV _{LOW}	0.02	1.08	0.00	1.07
Intensity × TV _{HIGH} vs. TV _{LOW}	3.34	0.58	0.26	0.01
Intensity × Canopy	2.04	0.01	0.17	0.05
TV _{HIGH} vs. TV _{LOW} × Canopy	1.27	0.19	0.56	0.04
Intensity × TV _{HIGH} vs. TV _{LOW} × Canopy	1.33	0.63	6.86*	0.54
Rockpool	11.43***	5.66***	4.11**	13.25***
Rockpool × Canopy	2.96*	5.75***	1.68	2.07

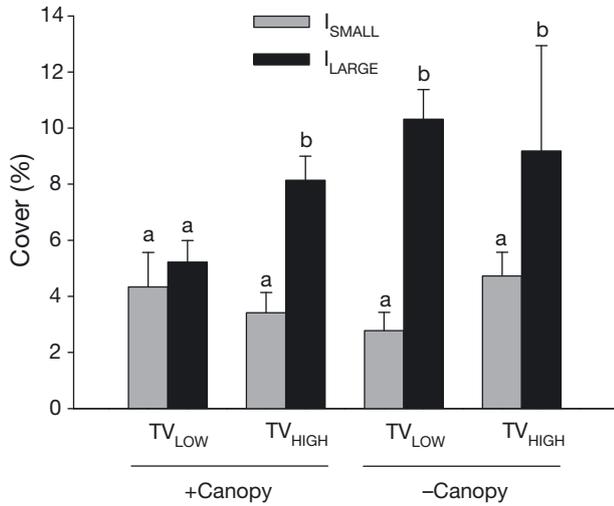


Fig. 4. Mean temporal abundance of sessile invertebrates in rockpools with boulders at small (I_{SMALL}) and large (I_{LARGE}) intensity of disturbance, for low (TV_{LOW}) and high (TV_{HIGH}) temporal variance of events, both in the presence (+Canopy) and absence (-Canopy) of canopy. Data are means (+1 SE) over 3 replicate plots pooled between the 2 TV_{LOW} or 4 TV_{HIGH} replicate rockpools and 9 sampling dates. Shared lowercase letters indicate treatments that do not differ significantly (Student-Newman-Keuls tests, $p > 0.05$)

recently been obtained by simulating the effect of hurricanes on coral reefs (Mumby et al. 2011). In that study, average coral cover was always greater under clustered hurricanes than with random independent events, likely because with clustered hurricanes, greater recovery could take place between subsequent events of disturbance.

In general, removal of canopy resulted in an increase in the cover of species composing algal turfs, in accordance with previous experimental findings (Benedetti-Cecchi & Cinelli 1992, Benedetti-Cecchi et al. 2001, Bulleri et al. 2002, Gorman & Connell 2009). We found no effect of disturbance on turf-forming species. This morphological group is mostly composed of species that reproduce vegetatively (e.g. filamentous algae; Lubchenco & Menge 1978), which are likely able to rapidly recover after disturbance.

No direct negative effect of canopy removal emerged for encrusting macroalgae or sessile invertebrates, although these organisms have been repeatedly shown to rely on the modification of environmental conditions generated by larger brown macroalgae in other systems (Benedetti-Cecchi et al. 2001, Bulleri et al. 2002, Connell 2003a,b, Mangialajo et al. 2008). Here, in contrast, encrusting algae increased after removal of the canopy in some rockpools, suggesting the occasional occurrence of a

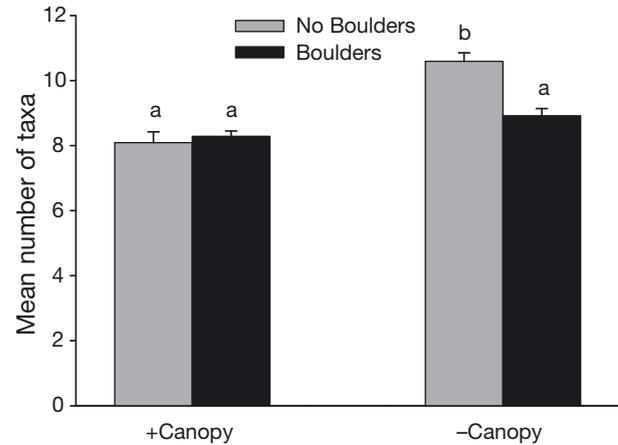


Fig. 5. Mean temporal diversity of taxa in rockpools where boulders were continuously removed (No Boulders) or a disturbance was applied (Boulders), in the presence (+Canopy) or absence (-Canopy) of canopy. Data are means (+1 SE) over 3 replicate plots pooled among 9 sampling dates and between 2 No Boulders or 12 Boulders replicate rockpools. Shared lowercase letters indicate treatments that do not differ significantly (Student-Newman-Keuls tests, $p > 0.05$)

direct negative effect of *Cystoseira* spp., probably through shading. Red algal crusts can withstand overgrowth by erect forms (e.g. Steneck 1986, Kendrick 1991, Airoidi 2000, Underwood 2006), but not indefinitely (Bulleri 2006). Reduced ability of algal crusts to survive overgrowth by canopy-forming species could be due to the greater stability in cover of macroalgal canopies compared to algal turfs. In addition, coalescence of holdfasts of *Cystoseira* spp. might entirely block solar irradiance over a large proportion of the surface underneath the canopy. It is worth noting, however, that the increase in the cover of encrusting algae after the removal of the canopy could be, at least in part, due to the ease of spotting them during samplings. As expected, both encrusting algae and sessile invertebrates were resistant to mechanical stress and were not directly negatively affected by events of disturbance by boulders. Indeed, percent cover of sessile animals slightly increased in our study when intensity of disturbance was high, except in the presence of the canopy at low temporal variance of disturbance. This was possibly an indirect effect caused by a small decrease (maybe cumulative) in cover of other species or, alternatively, a small increase in bare rock.

The loss of canopy also resulted in a slight increase in the number of taxa, in the absence of disturbance. This effect was, however, counteracted by the scouring of boulders during storms. A possible explanation is that some taxa (likely algal turf) were not able to

live in the presence of *Cystoseira* spp., due to lower competitive ability in acquiring space or tolerance to shading. These species were probably also the most susceptible to the mechanical stress due to the rolling of boulders, and this negative effect was as large as the positive effect of removing *Cystoseira* spp.

Like *Ecklonia radiata* along Western Australian coasts (Toohey et al. 2007), *Cystoseira* spp. is competitively dominant inside rockpools. The removal of the canopy would, therefore, promote the abundance of sessile animals (Connell 2003b) and algal turfs (Connell 2003a). The reduction in availability of light under the canopy is probably one of the most important factors negatively affecting understory primary producers (Toohey et al. 2004). Nevertheless, it is important to note that *Cystoseira* spp. can also represent a direct competitor for space in this system. In some rockpools, due to the large density of holdfasts and short length of thalli, *Cystoseira* spp. monopolised primary space (E. Maggi pers. obs.). Thus, *Cystoseira* spp. would be able to depress the abundance of both opportunistic, fast-growing species, such as algal turfs, and less competitive forms, such as encrusting algae.

As suggested by Bertocci et al. (2010), the ability of macroalgal canopies to protect associated benthic organisms from adverse environmental conditions is not limited to physical stressors (sensu Grime 1977) such as light or temperature (Bertness et al. 1999, Leonard 2000), but can extend to mechanical disturbance (i.e. the removal of biomass; sensu Grime 1977). Nevertheless, our results show that this ability is probably species-specific, likely due to a specific resistance to mechanical stress. Species manipulated along the Portuguese coast (*Mastocarpus stellatus*, *Chondrus crispus* and *Gigartina pistillata*) were not affected by disturbance (see Fig. 1A in Bertocci et al. 2010), probably due to their small size and morphology; in contrast, the cover of *Cystoseira* spp. was significantly reduced by regimes of large intensity and high temporal variance of storm events in the present study.

In summary, the loss of canopy-forming species was more important than changes in intensity or temporal variance of events of disturbance per se, in regulating the abundance and diversity of sessile assemblages inside rockpools. Algal turfs increased in cover as a consequence of the loss of *Cystoseira* spp. Contrary to our expectation, less competitive species, such as encrusting algae, were not indirectly influenced by changes in abundance of algal turfs, but were directly affected by the competitive ability of *Cystoseira* spp. to occupy primary space and/or

prevent light penetration. Therefore, due to the lack of negative effects of scouring by boulders on turf-forming species, predicted changes in intensity and temporal variance of disturbance related to storm events would not have the potential to counteract the expected shift of assemblages towards a system dominated by algal turfs, once *Cystoseira* spp. are lost from rockpools. Importantly, other human perturbations are likely to enhance further the ability of algal turfs to achieve dominance in rocky habitats. For example, enrichment in nutrients and CO₂ of coastal waters can ultimately foster the shift from canopy 'forests' to turf-dominated habitats (Eriksson et al. 2002, Österblom et al. 2007, Connell et al. 2008, Mangialajo et al. 2008, Connell & Russell 2010). New evidence that canopies (and hence interactions with turfs) may be able to resist the synergistic effects of these sources of pollution (Falkenberg et al. 2012) further emphasises the need to preserve marine forests.

The almost complete lack of a direct effect of temporal variance of disturbance on understory assemblages does not rule out its important effects inside rockpools. In the present study, intense disturbance events characterised by low temporal variance were able to remove the canopy of *Cystoseira* spp.; although favouring algal turfs, canopy loss generally implies a dramatic loss of standing biomass (Toohey et al. 2007). In addition, the persistence in rockpools of a diverse assemblage of mobile organisms (e.g. fish and crustacean amphipods; E. Maggi pers. obs.) could rely on the presence of the canopy for shelter and food (Gibbons 1988, Connolly 1994). Following the loss of canopy-formers, increased intensity and/or temporal aggregation of disturbance events could directly influence patterns of distribution and abundance of these mobile species.

The importance of positive species interactions is predicted to increase along a gradient of physical stress (the stress gradient hypothesis; Bertness & Callaway 1994). A general negative effect of the canopy-forming *Cystoseira* spp. on understory organisms was observed in the present study, but we cannot exclude that levels of intensity or temporal variance higher than those investigated in the present study could turn competition into facilitation. Although the climate is changing gradually in terms of average conditions (e.g. mean temperature, mean precipitation), temporal variance increases more rapidly, resulting in the temporal clustering of extreme climate events such as heat waves and intense precipitations (Mitchell et al. 2006). The potential effects of such extremes on people and ecosystems

are substantial (Mitchell et al. 2006, Mills 2009), and ecologists have been urged to increase efforts in understanding the consequences of changes in disturbance regimes (Turner 2010). In addition, the duration of the present study (about 2 yr) might have been too short to disclose a community response to climatic changes, such as the cascading competitive consequences on kelp communities associated with La Niña events (i.e. large-scale, low-frequency episodic changes in nutrient enrichment; Dayton et al. 1999), that occur at larger time-scales. This suggests that considering different characteristics of a disturbance regime (e.g. Bertocci et al. 2005, Benedetti-Cecchi et al. 2006, Molinos & Donohue 2011) could largely improve our predictive abilities, in particular on the consequences of global climate change.

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