Canopy-forming species mediate the effects of disturbance on macroalgal assemblages on Portuguese rocky shores

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ABSTRACT: Understanding the relationship between biodiversity and stability is a central issue in ecology. This is particularly needed under current scenarios of biodiversity loss due to multiple anthropogenic stressors. In this study, we experimentally examined the combined effects of the loss of key functional species (canopy-forming macroalgae) and mechanical disturbance on macroalgal intertidal assemblages at 2 sites along the rocky coast of northern Portugal. We tested the model that the canopy may buffer the effects of disturbance on associated organisms, leading to the logical hypothesis that effects of mechanical disturbance would be lower where the canopy was left intact compared to patches where it was experimentally removed. The proposed model was supported by multivariate and univariate results, as both differences in the structure of whole assemblages and in the abundance of individual taxa between disturbed and undisturbed assemblages were reduced or prevented by the presence of the canopy, independently of the examined site. Specifically, only in the absence of the canopy did disturbance determine a decrease in the abundance of the red alga *Ahnfeltiopsis devoniensis* and an increase in articulated coralline algae of the genus *Corallina*. Present findings have relevant implications for understanding and predicting the consequences of multiple factors responsible for the erosion of biodiversity occurring globally in coastal areas, as current rates of loss of canopy-forming species in urban areas may be expected to exacerbate the effects of predicted climate change, including modifications in intensity and temporal patterns of storms.

KEY WORDS: Biodiversity · Multiple stressors · Canopy algae · Disturbance · Rocky intertidal

INTRODUCTION

Understanding the relationship between changes in biodiversity and ecosystem properties such as stability, nutrient and energy fluxes, or productivity is of increasing concern for ecology, policy makers, and the general public (Vitousek 1994, Costanza et al. 1997, Chapin et al. 1998, Hooper et al. 2005).

Theoretical and experimental research has documented strong links between diversity and stability, often with a direct relationship between diversity and resistance and resilience of communities (Pimm 1984, McCann 2000, Ives & Carpenter 2007, Griffin et al. 2009). However, to date, most research has been conducted in terrestrial systems (Hooper & Vitousek 1997, Tilman 1999, Hooper et al. 2005, van Ruijven & Berendse 2010), and relatively few examples of empirical marine studies are available (Stachowicz et al. 2007, Boyer et al. 2009). Additionally, most marine studies examining the diversity–stability hypothesis were carried out in the context of biological invasions, with few attempts to evaluate how diversity shapes the

ability of communities to resist perturbations. These include specific studies on macroalgal beds and thermal stress (Allison 2004), eelgrass meadows and grazing by geese (Hughes & Stachowicz 2004) or disturbance (Williams 2001, Reusch et al. 2005), and microalgal biomass and combinations of sediment types and varying temperatures (Worm et al. 2006). The ability of systems dominated by canopy-forming algae to resist disturbance needs further experimental evaluation. Moreover, changes in patterns of biodiversity, and their functional consequences, are affected by multiple biological and abiotic drivers (Paine et al. 1998, Halpern et al. 2008), leading to the need for examining how the effects of one stressor are modulated by those of concomitant others (Folt et al. 1999, Crain et al. 2008).

Species with particular morphological or physiological traits, whose extinction may have drastic consequences for relevant ecological processes, are of overwhelming importance for the study of the relationship between biodiversity and ecosystem functioning (Schwartz et al. 2000, Geider et al. 2001, Loreau et al. 2002, Smith & Knapp 2003). Such species include key habitat formers (ecosystem engineers, sensu Jones et al. 1994) occurring at different locations (Jenkins et al. 1999, Benedetti-Cecchi et al. 2001, Eriksson et al. 2006, 2007). These species modify the spatial complexity and provide a specific habitat for a number of organisms, so that their removal may cause drastic changes in the structure of associated assemblages, as it was documented for canopy-forming macroalgae (Benedetti-Cecchi et al. 2001, Schiel & Lilley 2007), sea-grasses (Ramage & Schiel 1999), and mussel beds (Seed 1996). Mechanisms responsible for such effects include modifications of light, temperature, local hydrodynamics, sedimentation, and competition for the substratum (Reed & Foster 1984, Duggins et al. 1990, McCook & Chapman 1991, Seed 1996), factors that can affect the associated assemblages both positively, for example by ameliorating physical conditions, and negatively, for example by monopolizing space (Bertness et al. 1999, Bulleri et al. 2002). These characteristics make algal canopies a key functional element of coastal habitats, in terms of production, cycling of nutrients, and food webs (Underwood 1998, 1999). There is evidence that algal canopies are particularly sensitive to anthropogenic disturbance and tend to decline globally in urban areas (Benedetti-Cecchi et al. 2001, Airoldi & Beck 2007, Connell et al. 2008, Mangialajo et al. 2008). Moreover, particularly in intertidal habitats, they are extremely exposed to multiple stressors, such as human trampling (Schiel & Taylor 1999, Araújo et al. 2009a), burial, and sediment scouring (Schiel et al. 2006) and to climate change (Thompson et al. 2002).

In intertidal habitats, mechanical disturbance due to intense storms may remove patches of algal canopies (Underwood 1998), with the consequent local extinction of understory species (Dayton 1975, Bertness et al. 1999, Jenkins et al. 2004, Lilley & Schiel 2006) and drastic direct and indirect effects on biological interactions (Underwood 1998, 1999). Furthermore, an increase in extreme storms is predicted by models of climate change (Emanuel 1987, Raper 1993, Michener et al. 1997, Easterling et al. 2000). Therefore, examining the relationship between the loss of algal canopies and physical disturbance is relevant to understanding and predicting the environmental impacts of human-related stressors on intertidal assemblages.

In this study, we experimentally examined the combined effects of the loss of canopy-forming macroalgal species and mechanical disturbance on macroalgal assemblages inhabiting the low rocky intertidal habitat of northern Portugal. The main hypothesis was that the presence of the canopy could buffer the effects of disturbance on the structure and diversity of understory assemblages and on patterns of abundance of individual algal organisms. Specifically, we tested the hypotheses that (1) mechanical disturbance would determine significant changes to assemblages and individual taxa where the canopy was experimentally removed, but not where it was left intact, (2) this pattern would be consistent between 2 sites located about 25 km apart along the Portuguese coast.

MATERIALS AND METHODS

Study site. The study was performed between January 2006 and April 2007 at 2 rocky sites, Viana do Castelo (41° 41' N, 08° 51' W) and Amorosa (41° 38' N, 08° 49' W), along the coast of northern Portugal, at low-tide level (between 0.5 and 1 m above Chart Datum (LAT)). This temporal scale is in most cases appropriate for detecting direct and indirect effects of the examined processes on intertidal assemblages (Menge 1997, Strong 1997, Benedetti-Cecchi et al. 2001). The tidal regime along the Portuguese coast is semidiurnal, with maximum spring tides of 3.5 to 4 m. The typical rocky shore is granitic, and the coast is exposed to prevailing northwest oceanic swells that are particularly intense during the winter (Araújo et al. 2005). With the exception of the most exposed sites, which are generally dominated by mussels *Mytilus galloprovincialis* Lamarck and encrusting algae, such as *Lithophyllum incrustans* Philippi, this level on the shore is characterized by highly diversified macroalgal assemblages. These are dominated by small canopy-forming species, such as the red algae *Mastocarpus stellatus* (Stackhouse) Guiry, *Chondrus crispus* Stackhouse, and

Gigartina pistillata (S.G. Gmelin) Stackhouse. Understory assemblages include turf-forming species, such as the red algae *Chondracanthus acicularis* (Roth) Fredericq, *Ahnfeltiopsis devoniensis* (Greville) P.C. Silva & DeCew, *Gymnogongrus crenulatus* (Turner) J. Agardh, the articulated coralline algae of the genus *Corallina*, and the brown algae *Bifurcaria bifurcata* R. Ross and *Himanthalia elongata* (Linnaeus) S.F. Gray. Large kelps, such as *Saccorhiza polyschides* (Lightfoot) Batters, *Laminaria ochroleuca* Bachelot de la Pylaie and *L. hyperborea* (Gunnerus) Foslie, are sparse at this height on the shore, being more abundant in the subtidal habitat and in rock pools, and were never found in experimental units. The most common grazing invertebrates are limpets (*Patella* spp.) and trochids of the genus *Gibbula* (Araújo et al. 2005, 2009b).

Experimental design and sampling. A total of 20 patches (30 × 30 cm, from tens of cm to a few meters apart) with a cover of algal canopy (mixtures of *Mastocarpus stellatus*, *Chondrus crispus*, and *Gigartina pistillata*) >70 % and 10 to 15 cm thick were identified at each site at the beginning of the study (January 2006) and marked with screws at the corners for subsequent relocation. This patch size was comparable to that of disturbed patches identified in a previous study in the same geographic area (Viejo et al. 2008). Since the 3 canopy-forming species were comparable in size, they likely had comparable abilities to create an understory habitat. We therefore assumed that the effects of the algal canopy manipulated in the present study were not affected by potential differences in the relative abundance of each species in patches assigned to each experimental treatment. Five patches were randomly assigned to each of the following treatments: canopy intact and undisturbed (+C, −D), canopy intact and disturbed (+C, +D), canopy removed and undisturbed (−C, −D), and canopy removed and disturbed (−C, +D). The experimental removal of the canopy from the whole area of 10 −C patches was done using a knife, taking care to leave the understory organisms undamaged. In patches assigned to the +D treatment, a mechanical disturbance was applied using a hand rake and scratching the rock surface in 2 orthogonal directions, a procedure able to create patches of bare space, interspersed within intact assemblages, in a range of sizes comparable to that documented for other rocky intertidal systems (Benedetti-Cecchi & Cinelli 1994). This treatment followed the removal of the canopy in −C, +D treatment, while it was applied on intact assemblages in the +C, +D treatment. In this last treatment, therefore, some individuals of canopy-forming species could have been removed or damaged by experimental disturbance. However, this effect was analogous to that of any mechanical disturbance naturally impacting the studied assemblages, and we logically assumed that this could not prevent our experimental treatments from testing the proposed model of a buffering effect of the canopy on disturbance. Half of the number of the scratches necessary, on average, to remove all biomass from the substratum, as shown by a pilot study, was established as the standard intensity of disturbance. In order to maintain the temporal scale of our treatments comparable to that of canopy loss and mechanical disturbance occurring naturally on the shore, the removal of the canopy was maintained throughout the study, by periodically removing the individuals of the canopy-forming species that recruited in experimental patches assigned to −C treatments, while disturbance was applied only once at the beginning of the experiment.

At each site, algal organisms were sampled visually at the beginning (January 2006, immediately before the start of the experiment) and at 5 dates over the period of the study (January 2006, April 2006, September 2006, February 2007, April 2007) by using a quadrat of 30 × 30 cm divided into 25 sub-quadrats of 6 × 6 cm. Given the size of the examined organisms and the small scales of variability documented for intertidal algal and invertebrate assemblages (Benedetti-Cecchi 2001, Fraschetti et al. 2005), the size of patches was considered appropriate to obtain representative estimates of abundance (Andrew & Mapstone 1987). Cover values were calculated by assigning each taxon in each sub-quadrat a value between 0 (absence of the taxon) and 4 (whole sub-quadrat covered) and expressing final values as percentages (Dethier et al. 1993). Organisms were identified to the most detailed level of taxonomic resolution achievable in the field, in some cases lumping different species into the same genus.

Analysis of data. Before performing experimental treatments, we assessed whether assemblages in experimental patches established at each site were similar, as initial differences might have affected their responses to experimental treatments. Not yet treated assemblages were compared through multivariate analysis of variance based on permutations (PERMANOVA, Anderson 2001), including 2 fixed and crossed factors, Canopy and Disturbance, and 5 replicates (the 5 patches assigned to each factorial combination of treatments), separately for each site.

To assess the effectiveness of experimental treatments, the percentage cover of the canopy over the period of the study (i.e. averaged over 5 dates of sampling) and that of bare rock at the first date of sampling were measured, separately for each site. In +C treatments, estimating the cover of bare rock in some cases required moving aside the canopy to make the understory habitat visible, analogously to sampling of associated assemblages at each time.

Separate and interactive effects of experimental treatments were tested on the whole assemblage and on individual taxa. Multivariate responses were examined by comparing disturbed and undisturbed assemblages in patches where the canopy was left untouched and in patches where it was removed over the course of the study. This was made by calculating centroids for assemblages sampled at each site in each of the 5 patches assigned to each combination of experimental treatments across the 5 sampling dates. Separate analyses of data from each sampling date were not performed in order to avoid the uncontrolled increase of the probability of Type I error occurring when repeating tests on data that are not temporally independent (Underwood 1997), such as in the present case. Since the average of raw abundance data of individual taxa is not an appropriate measure of the average assemblage across time (Legendre & Anderson 1999, McArdle & Anderson 2001), we first calculated principal coordinates (Gower 1966) from a Bray-Curtis dissimilarity matrix (Bray & Curtis 1957) among the full set of data, in order to place the observations into a Euclidean space, without affecting the Bray-Curtis measure (i.e. the distance between any pair of observations based on principal coordinates is equivalent to the dissimilarity between those observations obtained from the original data). Centroids were calculated as arithmetic averages of the principal coordinates over the 5 sampling dates (McArdle & Anderson 2001) using the computer program PCO (Anderson 2003). A matrix of Euclidean distances between each pair of centroids was then calculated, separately for each site. To provide a direct comparison of undisturbed and disturbed assemblages relatively to the presence or the removal of the canopy, we calculated Euclidean distances between 5 undisturbed assemblages paired at random with 5 disturbed assemblages, separately for +C and –C treatments. These distances were finally analyzed with a 2-way analysis of variance (ANOVA), including the crossed factors Site (random, 2 levels, Viana versus Amorosa) and Canopy (fixed, 2 levels, +C versus –C). A lower distance (corresponding to a larger similarity) between undisturbed and disturbed assemblages where the canopy was left intact compared to patches where it was removed was expected in order to support a buffering effect of the canopy on mechanical disturbance.

ANOVA was also used to examine responses of the total number of taxa (a surrogate measure of species richness) and the cover of the most abundant individual taxa over the period of the study. This was made by calculating average values of each response variable over 5 sampling dates, then analyzing them with a 3-way model, including the same 2 factors (Site and Canopy) as the multivariate analysis, crossed with Disturbance (fixed, 2 levels, +D versus –D).

When necessary, data were log-transformed to meet the assumption of homogeneity of variances (after Cochran's test). SNK tests were used for *a posteriori* comparisons of means ($\alpha = 0.05$).

RESULTS

PERMANOVA indicated that assemblages in patches assigned to each experimental treatment did not differ at the beginning of the study at both sites (Viana: $MS_{CANOPY} = 698.77$, pseudo-$F = 0.31$, p = 0.829; $MS_{DISTURBANCE} = 493.05$, pseudo-$F = 0.22$, p = 0.911; $MS_{CANOPY \times DISTURBANCE} = 1387.73$, pseudo-$F = 0.61$, p = 0.577; Amorosa: $MS_{CANOPY} = 485.57$, pseudo-$F = 1.37$, p = 0.188; $MS_{DISTURBANCE} = 315.10$, pseudo-$F = 0.89$, p = 0.552; $MS_{CANOPY \times DISTURBANCE} = 354.75$, pseudo-$F = 1.00$, p = 0.434).

Canopy cover averaged over 5 sampling dates was around 60 to 70% in +C treatments, while in –C treatments it was always below 10% (Fig. 1A). Disturbed
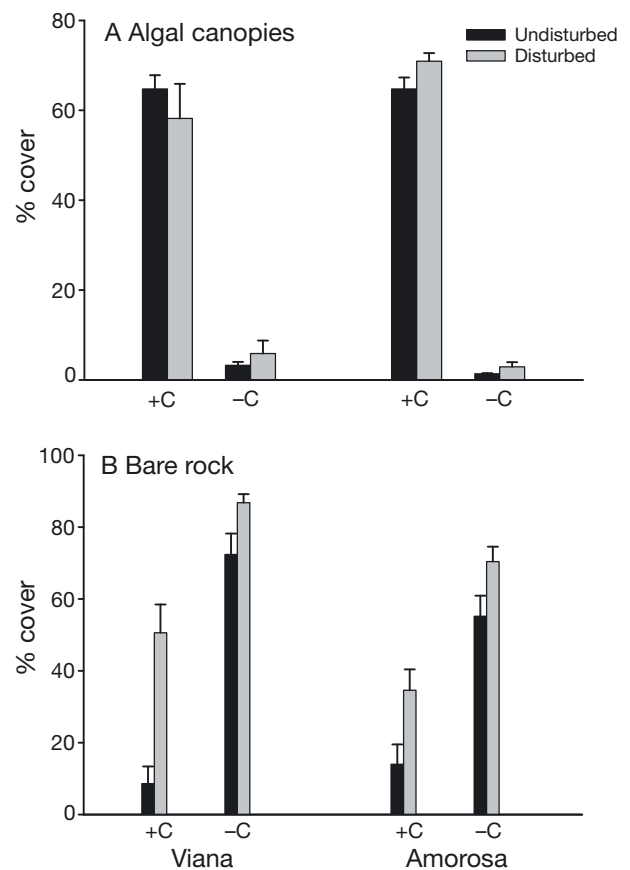

Fig. 1. Abundance of (A) algal canopies (mean +SE, n = 25) over the period of the study and of (B) bare rock (+SE, n = 5) at the first date of sampling in patches assigned to each combination of experimental treatments (+C and –C indicate the presence or the experimental removal of the canopy, respectively), separately for each site

Table 1. Analysis of variance examining the effects of site and algal canopies on the Euclidean distance between undisturbed and disturbed assemblages across 5 sampling dates. NS: not significant

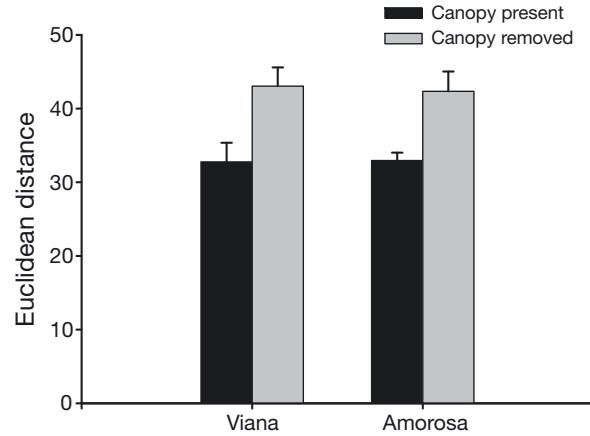| Source of variation	df	MS	F	p
Site (S)	1	0.34	0.01	0.912
Canopy (C)	1	483.99	490.32	0.028
S × C	1	0.99	0.04	0.851
Residual	16	27.07		
Cochran's C test	C = 0.336, NS			
Transformation	None			

Fig. 2. Euclidean distance (mean +SE, n = 5) between undisturbed and disturbed assemblages in patches where algal canopies were left intact or experimentally removed, separately for each site. Data averaged across 5 sampling dates

treatments were characterized by larger proportion of bare rock compared to undisturbed treatments, although these differences were emphasized in patches where the canopy was left intact compared to those where it was experimentally removed (Fig. 1B). The absolute highest covers of bare rock were consistently displayed by −C treatments (Fig. 1B), likely as a direct consequence of the removal of canopy-forming species primarily attached to the substratum.

The effects of disturbance on the structure of whole assemblages were reduced by the presence of the canopy (Table 1). Specifically, disturbed and undisturbed assemblages were more similar, with values of

Euclidean distance about 35% larger, in patches where the canopy was left untouched than in those where it was removed at both sites (Fig. 2).

The buffering effect of the canopy on disturbance was confirmed by responses of some individual taxa, such as *Ahnfeltiopsis devoniensis* and *Corallina* spp. (Table 2), although in taxon-specific directions. Inde-

Table 2. Analysis of variance examining the effects of site, algal canopies, and disturbance on the total number of taxa and the abundance of individual algal taxa across 5 sampling dates. NS: not significant

Source of variation	df	Number of taxa MS	F	p	*Ahnfeltiopsiss devoniensis* MS	F	p	*Calliblepharis jubata* MS	F	p	*Chondracanthus acicularis* MS	F	p
Site (S)	1	13.9	4.2	0.561	0.4	2.3	0.136	17.5	35.2	0.000	0.0	0.0	0.863
Canopy (C)	1	8.8	2.0	0.368	0.3	4.9	0.271	2.7	2.2	0.365	1.0	17.1	0.151
Disturbance (D)	1	4.4	1089.0	0.019	0.0	0.8	0.542	0.2	46.9	0.084	1.3	89.1	0.067
S × C	1	4.4	1.3	0.216	0.1	0.4	0.552	1.2	2.5	0.206	0.1	0.1	0.771
S × D	1	0.0	0.0	0.926	0.0	0.2	0.656	0.0	0.0	0.918	0.0	0.0	0886
C × D	1	0.5	0.3	0.633	14.5	136.3	0.049	0.0	0.3	0.663	1.2	1.5	0.437
S × C × D	1	1.4	0.4	0.540	0.1	0.5	0.450	0.1	0.6	0.470	0.8	1.2	0.275
Residual	32	3.3			0.2			0.2			0.7		
Cochran's C test		C = 0.276, NS			C = 0.186, NS			C = 0.270, NS			C = 0.256, NS		
Transformation		None			Ln(x+1)			Ln(x+1)			Ln(x+1)		

Source of variation	df	*Corallina* spp. MS	F	p	*Gymnogongrus crenulatus* MS	F	p	*Stypocaulon scoparium* MS	F	p	*Ulva* spp. MS	F	p
Site (S)	1	0.5	2.5	0.221	3.1	8.8	0.006	52.4	6.6	0.015	2.9	16.3	0.000
Canopy (C)	1	0.1	0.3	0.671	5.6	5.4	0.245	27.2	1.8	0.408	21.3	24.3	0.116
Disturbance (D)	1	4.7	109.8	0.061	0.0	0.1	0.844	14.2	2.4	0.366	0.7	7.0	0.189
S × C	1	0.2	1.1	0.305	1.0	2.9	0.084	15.1	1.9	0.179	0.9	4.9	0.068
S × D	1	0.0	0.2	0.649	0.3	1.0	0.355	5.9	0.7	0.396	0.1	0.6	0.541
C × D	1	2.7	394.4	0.032	0.0	0.0	0.801	22.2	1.9	0.397	0.1	2.9	0.431
S × C × D	1	0.0	0.0	0.815	0.2	0.7	0.360	11.4	1.4	0.240	0.1	0.3	0.541
Residual	32	0.2			0.4			8.0			0.2		
Cochran's C test		C = 0.357, NS			C = 0.295, NS			C = 0.689, 0.045			C = 0.367, NS		
Transformation		Ln(x+1)			Ln(x+1)			None			Ln(x+1)		

pendently of the site, the abundance of *A. devoniensis* was larger in undisturbed than in disturbed patches where the canopy was removed, while in +C patches, disturbance did not exert any significant effect on this species (Fig. 3, $SNK_{C \times D}$ = –C: –D > +D, +C: +D = –D, SE = 0.103). An opposite pattern was displayed by *Corallina* spp., with larger abundance in +D than in –D

patches combined with the removal of the canopy (Fig. 3, $SNK_{C \times D}$ = –C: +D > –D, +C: +D = –D, SE = 0.100). Although not significant, a trend towards a negative response to disturbance only in –C patches was shown at both sites by *Chondracanthus acicularis* and the brown alga *Stypocaulon scoparium* (Table 2, Fig. 3).
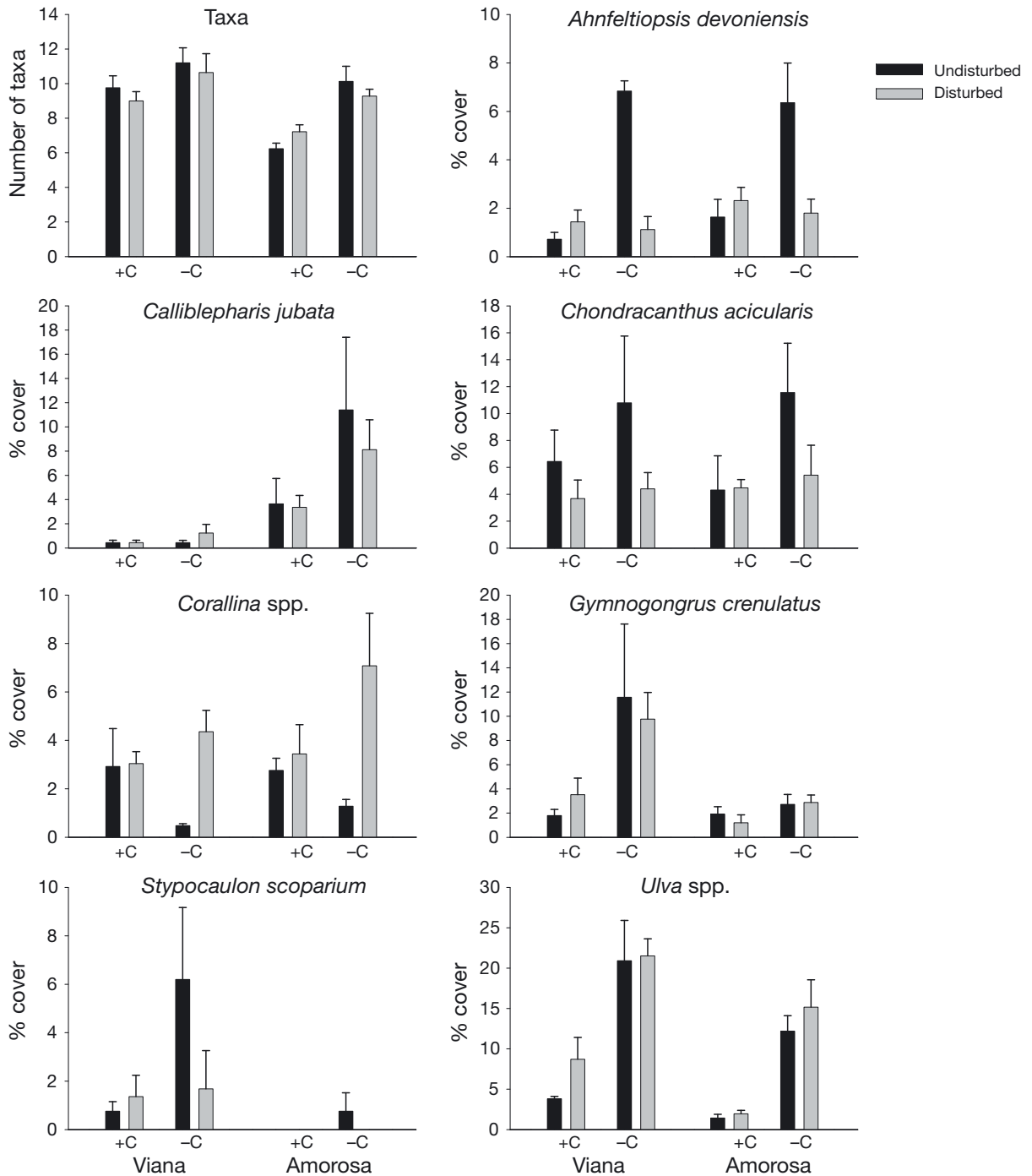

Fig. 3. Abundance of the total number of taxa and of individual taxa (mean +SE, n = 5) in patches assigned to each combination of experimental treatments (abbreviations as in Fig. 1), separately for each site. Data averaged across 5 sampling dates

No interactive effects of algal canopies and disturbance were observed for all other response variables examined (Table 2, Fig. 3). The total number of taxa was larger in −D than in +D patches independently of the site and the presence of the canopy (Table 2, Fig. 3). We also found some differences in local floras, independently of any effect of the manipulated factors: the red alga *Calliblepharis jubata* was more abundant at Amorosa than at Viana, while the opposite pattern was displayed by *Gymnogongrus crenulatus* and the green foliose algae *Ulva* spp. (Table 2, Fig. 3).

DISCUSSION

We hypothesized that algal canopies could buffer the effects of physical disturbance on intertidal algal assemblages and that this pattern was consistent between 2 sites along the coast of northern Portugal. These hypotheses were supported by our findings. The multivariate analysis showed that at both sites, undisturbed and disturbed assemblages were more similar in patches where the canopy was left untouched than in those where it was removed. Significant effects of disturbance only in the absence of the canopy were also documented for some of the individual algal taxa examined, such as *Ahnfeltiopsis devoniensis*, *Corallina* spp. and, less strongly, *Chondracanthus acicularis* and *Stypocaulon scoparium*, although with taxon-specific patterns.

It has been indicated that canopy-forming algae may mitigate the impact of stressing abiotic and biological factors on the associated assemblages through combinations of direct and indirect mechanisms (Bertness & Leonard 1997, Jenkins et al. 1999, Schiel & Lilley 2007). This model has been repeatedly invoked to explain the replacement of canopy-forming species by opportunistic turf-forming algae documented at several locations, particularly in urban areas (Benedetti-Cecchi et al. 2001, Bulleri et al. 2002, Mangialajo et al. 2008). In fact, harsher environmental conditions following the loss of the canopy may facilitate turf-forming species over more sensitive species, as was indicated for beds of *Hormosira banksii*, where the removal of the canopy determined a drastic reduction of other fucoid algae and smaller branched algae unable to survive without the protective canopy layer (Lilley & Schiel 2006). The larger abundance of turf-forming algae in the genus *Corallina* in disturbed compared to undisturbed patches after the removal of the canopy documented in the present study could be explained according to such a mechanism, i.e. as a consequence of their greater ability to live under the most severe experimental conditions. An inverse relationship between the canopy cover and the abundance

of coralline algae has been found in intertidal (Benedetti-Cecchi & Cinelli 1992) and subtidal (Melville & Connell 2001) habitats. Moreover, there is ample evidence that coralline algae tend to become dominant in sites subject to intense disturbance, including wave exposure (Bacchiocchi & Airoldi 2003, Bulleri & Airoldi 2005, Vaselli et al. 2008) and anthropogenic pressures (Airoldi et al. 1995, Boyra et al. 2004). The combination of reduced competition with other understory species more sensitive to the removal of the canopy and disturbance might explain the observed response of *Corallina* spp.

Direct effects of mechanical disturbance were likely responsible for the reduction of *Ahnfeltiopsis devoniensis* and, less strongly, *Chondracanthus acicularis* and *Stypocaulon scoparium* after the removal of the canopy. In particular, physical disturbance applied in the less protected habitat generated by the removal of the canopy might have negatively affected these species, analogously to what has been documented for other sources of mechanical stress, such as ice (McCook & Chapman 1991) and sediment scouring (Connell 2003). Previous studies have indicated that these species tend to attain lower abundances on wave-exposed than on protected shores (Araújo et al. 2005, Tuya & Haroun 2006).

Alternatively, but not mutually exclusively, the loss of canopies may drastically modify the responses of associated assemblages by altering trophic interactions. For instance, the removal of a canopy of *Ascophyllum nodosum* determined an increase in grazing intensity by limpets with consequent increase of barren areas (Jenkins et al. 1999, 2004), while the removal of *Hormosira banksii* was followed by a reduced abundance of whelks, leading to an increase in the abundance of their prey, i.e. barnacles (Underwood 1998, 1999). Grazing and carnivorous invertebrates were virtually absent from our experimental units at each sampling date, thus preventing us from hypothesizing that analogous mechanisms were responsible for our results.

Several studies have indicated that the loss of algal canopies causes drastic changes in the species richness of associated assemblages, whose direction depends on complex interactions between abiotic and biological factors (reviewed by Airoldi et al. 2008). For example, the removal of a canopy-forming species may increase the free space available for colonization by other species, thus increasing the total diversity of the system (Jenkins et al. 1999, 2004), while in other cases it can determine the opposite outcome through the dominance by a few opportunistic species, particularly under conditions of enhanced nutrient loads (Eriksson et al. 2006). In the present study, we did not find any interactive effects of experimental treatments on the

total number of taxa (a proxy for species richness). This suggests that the responses of the studied assemblages likely depended on changes in patterns of abundance of individual taxa, i.e. on the identity of organisms exposed to experimental treatments, rather than absolute richness (O'Connor & Crowe 2005, Cardinale et al. 2006, Stachowicz et al. 2007, Maggi et al. 2009). Our findings only indicated a consistently larger number of taxa in undisturbed than in disturbed patches, potentially suggesting that our experimental intensity of disturbance might be considered severe, although discrete, in terms of its effects on the diversity of the intertidal assemblages studied (sensu Connell 1978, Sousa 1979). Absolute differences of richness between undisturbed and disturbed assemblages, however, were small (about 1 taxon, on average); thus, the ecological relevance of the significant effect detected by the analysis should be interpreted with caution. This could simply be due to the large proportion of the total number of taxa represented by 1 taxon (respectively, 16.7% and 9% of mean values between 6 and 11, in different treatments).

This study indicated that algal canopies may increase the resistance of intertidal assemblages to physical disturbance, adding to the evidence that this functional trait of assemblages may be drastically affected by the loss of habitat-forming species (Kennelly 1987, Kiirikki 1996, Bertness et al. 1999, Eriksson et al. 2007, Gamfeldt et al. 2008). Moreover, it suggests that multiple stressors operating simultaneously may interactively affect the structure of intertidal assemblages. Such complex effects cannot be inferred from studies on single disturbances (Paine et al. 1998, Darling & Côté 2008). Therefore, our findings have important implications for predicting the responses of organisms to combined factors responsible for the global erosion of coastal biodiversity (Elmqvist et al. 2003, Bellwood et al. 2004, Micheli & Halpern 2005), adding to the evidence that canopy-forming species cannot be replaced by functional equivalents once lost (Schiel 2006, Airoldi et al. 2009). Although further research is needed to evaluate the effects of different types of multiple stressors and their generality across a range of spatial and temporal scales and under sets of abiotic and biological circumstances larger than those examined here (Solan et al. 2004, Naeem 2008), this study will improve our ability to understand and predict the consequences of biodiversity loss due to concomitant human-related factors, including climate change and urbanization, and to implement conservation and management actions aimed at preserving the functioning of marine systems.

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