# Effects of loss of algal canopies along temperature and irradiation gradients in continental Portugal and the Canary Islands

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ABSTRACT: We examined the hypothesis that the loss of canopy-forming macroalgae from rock pools would have stronger effects on associated algal assemblages along gradients of harsher climate conditions (i.e. higher sea and air temperatures and irradiation) occurring in continental Portugal and the Canary Islands. The study was carried out at 'cool' and 'warm' regions in both systems (N and SW Portugal and Lanzarote and El Hierro Islands, respectively), using a comparative approach involving the same manipulative experiment simultaneously conducted at multiple locations. Canopy-forming macroalgae were experimentally removed, and the structure (abundance and distribution) of associated algal assemblages (in terms of morpho-functional groups) was compared between treated and unmanipulated plots 6 and 12 mo after removal of the canopy. In both continental Portugal and the Canary Islands, warmer conditions were associated with a larger Euclidian distance in the structure of assemblages between canopy-removed and unmanipulated plots 6 mo, but not 12 mo, after the removal treatment. Responses of morpho-functional algal groups varied depending on the system, in addition to the environmental gradient. Although the present findings could not be unequivocally ascribed to causal effects of climate conditions alone, they indicate that the effects of algal canopy loss were enhanced along gradients of harsher environmental conditions at even supposedly very different continental and island systems over the short term. The studied systems were potentially able to recover about 1 yr after the disturbance, but this might not happen under current or predicted scenarios of natural or anthropogenic disturbances able to drive a persistent loss of foundation species.

KEY WORDS: Biological interactions · Canopy-forming algae · Disturbance · Island ecology · Large-scale experiments · Latitudinal gradients · Rockpools

## INTRODUCTION

Foundation species (Dayton 1972) play an important role in primary production and habitat provision, critically driving patterns of distribution, abundance and diversity of associated assemblages in terrestrial (e.g. Ellison et al. 2005) and marine (Bertness et al. 1999, Benedetti-Cecchi et al. 2001, Steneck et al. 2002, Bruno et al. 2003) systems and contributing to ecosystem services of extremely high economic value (Costanza et al. 1997).

There is evidence that habitat-forming macroalgae are declining worldwide as a consequence of a range of human-related stressors (Airoldi & Beck

2007, Connell et al. 2008), including terrestrial runoff and sedimentation (Irving et al. 2009, Shepherd et al. 2009), sewage discharges (Bellgrove et al. 2010), coastal development (Mangialajo et al. 2008), storm disturbance (Dayton & Tegner 1984, Schiel 2011) and high temperatures (Schiel et al. 2004, Wernberg et al. 2010). Kelp and fucoid species, in particular, can dominate temperate habitats in both hemispheres (Benedetti-Cecchi et al. 2001, Steneck et al. 2002) and are sensitive to warming, tending to be reduced in abundance and possibly to retreat in their distribution as a consequence of local temperatures approaching or exceeding their tolerance limits (Hawkins et al. 2009, Wernberg et al. 2011). Within such tolerance limits, however, it could be expected that the ecological importance of habitat-forming macroalgae will increase under global warming, as they can mitigate environmental stress and maintain the functioning of associated assemblages (Bruno et al. 2003, Halpern et al. 2007, Bertocci et al. 2010, Bulleri et al. 2012). In fact, effects of canopy-forming macroalgae on associated organisms have been shown to shift from positive to negative when moving northward in the northern hemisphere, due to differences in maximum daily temperatures (Leonard 2000) and according to the general idea that the strength of positive biological interactions should increase along gradients of increasing stress (Bertness & Callaway 1994, Richardson et al. 2012). Understanding the role of habitat-forming species under different temperature conditions is thus crucial for predicting the effects of climate warming (Harley et al. 2006, Poloczanska et al. 2007).

Logistic difficulties in manipulating temperature in the field are responsible for the general scarcity (Richardson & Poloczanska 2008), or limitation to laboratory or small-scale field experiments (Moore et al. 2007, Russell et al. 2009, Lathlean et al. 2013), of studies able to examine cause and effect relationships between changes in temperature, or other bottom-up factors, and ecological processes. A good alternative method to investigate the possible effects of sea surface temperature (SST) on community structure is to simultaneously perform analogous experiments in regions under different temperature regimes (Wernberg et al. 2010, 2012a). This 'comparative experimental approach' (Menge et al. 2002) is also critically important to examine links between ecological processes operating over a range of scales, including biotic interactions usually responsible for small-scale spatial patchiness and oceanographic and climate conditions driving

regional patterns of biodiversity (Underwood & Chapman 1996, Thrush et al. 2000).

Islands are useful systems on which to test hypotheses about large-scale ecological processes, particularly when examined in comparison with the same processes on the mainland (e.g. Benedetti-Cecchi et al. 2003, Ceccherelli et al. 2005, da Cruz & Calado 2012, González-Castro et al. 2012). Variable patterns of colonization and extinction dependent on the distance from sources of colonists and on the size of islands have been indicated as responsible for unique traits in species assemblages on islands, according to the classical 'island biogeography theory' (MacArthur & Wilson 1967, Whittaker et al. 2008). Insular environments may also differ from mainland ones due to historical traits, physical processes, natural and human disturbance and biotic interactions (Brown & Lomolino 2000, Lomolino 2005, Meiri et al. 2011).

Here, we took advantage of environmental gradients occurring along the coasts of continental Portugal and the Canary Islands, to examine the effects of the loss of canopy-forming macroalgae on associated seaweeds under different climatic variables (air and sea temperatures and irradiation levels). The Portuguese continental coast is about 800 km long and is characterized by a clear latitudinal gradient in ocean and atmospheric variables, including SST, air temperature and irradiation, with a northern 'cool' region and a central and southern 'warm' region (Lemos & Pires 2004, Tuya et al. 2012). This is likely responsible for the overlapping distributions of species of boreal and Lusitanian origin along the coast (Lima et al. 2007), for the occurrence of southern and northern limits of distribution of cold- and warm-water species, respectively (Lima et al. 2007), and for latitudinal clines in the abundances of other species (Boaventura et al. 2002, Lima et al. 2006, Tuya et al. 2012). The Canarian Archipelago comprises 7 major islands and a group of small islets (Chinijo Archipelago). The interaction between the cold Canary Current, flowing from NNE to SSW, and the Northwestern African upwelling (Pacheco & Hernández-Guerra 1999) creates a longitudinal climatic gradient associated with a transition from 'cooler' temperate to 'warmer' subtropical conditions, which extends from the easternmost (Lanzarote, Chinijo Archipelago, Fuerteventura) to the westernmost islands (La Gomera, La Palma and El Hierro) (Barton et al. 1998, Davenport et al. 2002). This gradient is coupled with shifts in patterns of distribution and abundance of temperate and tropical/subtropical

algal species (Tuya & Haroun 2006), as well as rocky-reef fishes and intertidal invertebrates (Tuya et al. 2004, 2006).

In temperate marine systems, however, causal effects of temperature gradients are difficult to unequivocally disentangle from those of co-varying factors, such as variations in the availability of nutrients due to upwelling events, or in patterns of distribution and consequent pressure by consumers (e.g. Dayton & Tegner 1984). For example, Fiúza (1983) described a particular spatial pattern of variability in upwelling along the Portuguese coast, with the flat shelf north of the Nazaré Canyon characterized by fairly homogeneous upwelling alongshore, the southern half of the Portuguese west coast characterized by an offshore separation of upwelling waters north of the Bay of Setúbal likely due to deep physical features represented by the Lisbon and the Setúbal Canyons, the steep area south of Cape Sines characterized by events occurring closer to the shore, and the southernmost coast (Algarve) directly affected by upwelling only as a consequence of occasional westerly winds. The possible contribution of such latitudinal gradients could prevent interpreting the findings from our study as being unambiguously determined by temperature/irradiation patterns. Nevertheless, recent evidence of a general relaxation of the upwelling intensity along the Portuguese coast (Lemos & Pires 2004, Santos et al. 2011) suggests that the relative contribution of such climatic variables could at least increase in the near future. We thus took advantage of the clear gradients in oceanographic and climate conditions occurring along the studied continental and island regions to experimentally examine the links between the loss of canopy-forming macroalgae and its possible consequences in a 'warmer' climate.

As our study system, we used the algal assemblages associated with dominant canopy-forming macroalgae in rock pools. We predicted that such organisms would become subject to environmental stress (e.g. due to the exposure to increased UV radiation and temperatures) after the loss of the canopy, which would be harsher in 'warm' than in 'cool' regions from both continental Portugal and the Canary Islands. Specifically, we tested the hypotheses that (1) the experimental removal of the algal canopy would cause a dissimilarity between treated and unmanipulated plots in the structure of algal assemblages and in the abundance of morpho-functional groups that would be larger at the 'warm' compared to the 'cool' region; (2) this effect would be consistent across the studied continental and insular systems.

## MATERIALS AND METHODS

### Study sites

A manipulative field experiment was set up at the 'cool' and 'warm' regions of continental Portugal (north and southwest coast, respectively) and the Canary Island Archipelago (Lanzarote and El Hierro islands, respectively). Two locations (ca. 5 to 20 km apart) in each region were selected: Moledo (41° 48′ 51.66″ N, 11° 28′ 0.55″ W) and Vila Praia de Âncora (41° 47′ 52.87″ N, 11° 27′ 58.28″ W) in N Portugal; Oliveirinha (37° 53′ 12.38″ N, 8° 47′ 47.97″ W) and Queimado (37° 49′ 20.46″ N, 8° 47′ 36.93″ W) in SW Portugal; Punta Mujeres (29° 09′ 30.18″ N, 13° 25′ 38.04″ W) and La Santa (29° 07′ 27.96″ N, 13° 38′ 48.86″ W) at Lanzarote; La Estaca (27° 46′ 44.35″ N, 17° 54′ 19.19″ W) and Tacorón (27° 40′ 16.14″ N, 18° 01′ 37.47″ W) at El Hierro. A map of the locations sampled is given in Supplement 1 at www.int-res.com/articles/suppl/m506p047_supp. All locations provide large rocky (limestone, sandstone, shale or granitic in continental Portugal; mostly basaltic in the Canary Islands) platforms extending across the intertidal zone. The tidal regime is semidiurnal, with maximum spring tides of 3.5 to 4 m along the Portuguese coast and about 3 m in the Canaries. 'Cool' locations at both systems were characterized by lower SST and air temperatures and reduced levels of photosynthetically active radiation (PAR) compared to 'warm' locations (see Supplement 2 at www.int-res.com/articles/suppl/m506p047_supp).

The study was performed on macroalgal assemblages from rock pools located at mid-intertidal heights (i.e. between ca. 1 and 2.5 m above chart datum). These were characterized by stands of dominant canopy-forming brown algae, mostly *Cystoseira humilis* Schousboe ex Kützing (Canary Islands and SW Portugal) and *Bifurcaria bifurcata* Ross (N Portugal). Both species present branched thalli, 10s of cm in length, that provide a 3-dimensional habitat hosting diverse algal organisms belonging to the same morpho-functional groups (e.g. Otero-Schmitt & Pérez-Cirera 1996, Sánchez & Fernández 2006). Therefore, we assumed that the different identity of the canopy and associated algae could not confound the experimental test of our hypotheses (see also Bulleri et al. 2012).

### Experimental design and sampling

At each location, the same experiment was carried out over a period of 1 yr (between May 2012 and May 2013) in 5 independent rock pools, selected at random out of those dominated (i.e. with the canopy virtually covering the whole extent of the pool) by a large *C. humilis* or *B. bifurcata* canopy, interspersed along a gently sloping rocky platform extending for hundreds of metres. The mean size of pools was larger in N Portugal (length, width: 5.4, 2.8 m) than in SW Portugal (3.1, 1.6 m) and the Canary Islands (3.2, 1.6 m). However, all pools included in this study had similar depth (maximum value varying, on average, between 0.23 m in N Portugal and 0.36 m in SW Portugal), which was considered more relevant due to the expectable larger influence of this dimensional characteristic on the severity of temperature, irradiation and desiccation. Six 25 × 25 cm plots were established in each pool in May 2012, with initial mean cover of the canopy-forming species between 87 and 96 %. Three of the 6 plots were allocated at random to the experimental treatment of removal of the erect portion of the canopy, while the other 3 were left unmanipulated as controls. The treatment was applied by hand with scissors and a knife to minimize disturbance to associated organisms. The canopy was removed only at the beginning of the experiment; all quadrats were then left untouched to examine the effects of our treatment on associated algae during the first year of recovery of the canopy. Resource limitations made it unfeasible to conduct multiple experimental trials starting at different times with the aim of examining whether response variables were consistent depending on the timing of disturbance responsible for the loss of the canopy. Therefore, we chose to start our single trial before the summer in order to expose organisms deprived of the canopy to the presumed harshest environmental conditions of high temperature and irradiation.

The percentage cover of each algal taxon was visually estimated in each plot at 6 and 12 mo after the experimental removal of the canopy (November 2012 and May 2013, respectively). Sampling was carried out by means of a 20 × 20 cm frame overlaid on the centre of each plot (to avoid edge effects) and divided into 25 sub-quadrats of 4 × 4 cm. Cover values were calculated by assigning to each taxon in each sub-quadrat a value between 0 (absence) 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 or higher taxonomic categories. In the presence of the canopy, the cover of associated organisms was estimated by moving aside the canopy-forming species, in order to expose the understory assemblages (e.g. Bertocci et al. 2010).

### Analysis of data

To test the hypothesis of larger dissimilarities in the structure of algal assemblages between canopy-removed and unmanipulated plots under 'warm' compared to 'cool' climate at each date of sampling, treated (T) and control (C) plots in each rock pool were paired according to the following procedure. First, after removing the canopy-forming species from the dataset, a principal coordinate analysis (PCO, Gower 1966) was applied to the Bray-Curtis matrix of dissimilarities among all samples. This allowed us to place the original observations into a Euclidean space, preserving the relationships quantified by the Bray-Curtis measure, i.e. the Euclidean distance between paired observations in the principal coordinates matrix was equivalent to the Bray-Curtis dissimilarity between those observations calculated from the original variables. Second, Euclidean distances were calculated for all 9 combinations of T-C paired plots in each pool and averaged to obtain a mean value of T-C distance for each pool in each location and system at each date of sampling. Finally, these resulting mean distances were analysed, separately for each sampling date and the continental and Canary Islands datasets, with a 2-way ANOVA, including the factors Climate (fixed, 2 levels: 'cool' versus 'warm') and Location (random, 2 levels, nested in Climate), with 5 pools providing the replicates.

To examine whether changes in T-C distances in the structure of assemblages were driven by analogous responses of species belonging to morphologically and likely ecologically similar algal groups, the sampled taxa were *a posteriori* collapsed into 6 morpho-functional groups (adapted from Steneck & Dethier 1994; see Supplement 3 at www.int-res.com/articles/suppl/m506p047_supp.pdf): articulated calcareous algae (e.g. *Corallina* spp.), foliose algae (e.g. *Ulva* spp.), corticated algae (e.g. *Gymnogongrus* spp.), filamentous algae (e.g. *Ceramium* spp.), leathery algae (e.g. small, non-canopy-forming fucoids such as *Cystoseira compressa*) and encrusting algae (e.g. *Lithophyllum* spp.). Percentage cover values (in some cases exceeding 100 % due to multi-layered assemblages) of each group were analysed with a 4-way

ANOVA, including the same factors as the previously described analysis, plus Pool (random, 5 levels, nested in each Climate × Location combination of levels) and Treatment (fixed, 2 levels: T versus C; fully crossed).

The 2 dates of sampling were analysed separately due to the temporal non-independence of data collected from the same plots. The continental Portugal and Canary Islands datasets were also analysed separately, as the absolute larger mean values of climatic variables, such as SST and air temperatures (hypothesized as being more stressful for exposed assemblages after the removal of the canopy) at the latter compared to former system (see Supplement 2) could have confounded differences between them. Nonetheless, increased T-C dissimilarities under 'warm' compared to 'cool' regions, eventually documented for both N versus SW Portugal and Lanzarote versus El Hierro separately, would have provided support to our hypothesis of consistency of canopy-removal versus environmental gradient effects over the studied continental and insular system.

Before each ANOVA, homogeneity of variances was checked with Cochran's $C$-test. When possible, data were log-transformed to meet this assumption. When this was not possible, untransformed data were analysed and significance tests considered robust if $p < 0.01$ (instead of $p < 0.05$, to compensate for the increased probability of a Type I error) or there were a large number (i.e. 40) of independent estimates of residual variance (Underwood 1997). When appropriate, SNK tests were used for post hoc comparisons (at $\alpha = 0.05$) of means.

## RESULTS

### Recovery after 6 mo

Six months after the removal treatment, the canopy-forming species had partially recovered in disturbed plots at all study sites, attaining mean ± SE cover of 23.6 ± 3.0% in N Portugal, 35.4 ± 3.8% in SW Portugal, 18.4 ± 2.5% at Lanzarote and 31.3 ± 3.5% at El Hierro.

In both continental Portugal and the Canary Islands, the climatic gradient was associated with significant differences in the Euclidean distance of algal assemblages between control and treated plots (Table 1). In particular, T-C mean distances were larger in the 'warm' compared to the 'cool' region at all locations from both systems (Fig. 1).
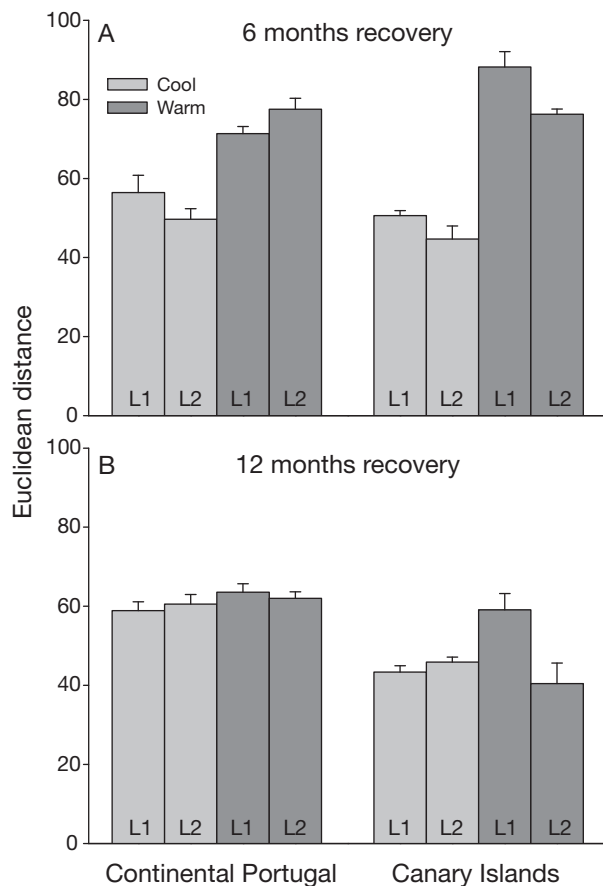
In continental Portugal, articulated calcareous algae were significantly more abundant in treated than in control plots, independently of the climatic region (Table 2, Fig. 2A). In the Canary Islands, a similar response of these algae to the removal of the canopy occurred only in the 'cool' region (Lanzarote Island), while in the 'warm' region (El Hierro Island), they were not present in either the treated or the control plots (Table 2, Fig. 3A).

Larger cover in treated than in control plots in the 'cold' region were documented for both the foliose and the filamentous algae from continental Portugal (Table 2, Fig. 2B,D). In the Canary Islands, both algal groups showed varying responses to the loss of the canopy between locations (Table 2). The cover of foliose forms was larger in treated than in control plots only at La Estaca on El Hierro Island, while it showed a non-significant opposite trend at the other location from the same island and very low or null effect at Lanzarote Island (Fig. 3B). Filamentous forms, instead, significantly increased in abundance after the removal of the canopy at both locations on Lanzarote Island, while at El Hierro Island they were found only in unmanipulated plots at La Estaca (Fig. 3D).

Corticated algae were the only group showing a significant Climate × Treatment interaction, in the direction of a reduction in cover after the removal of the canopy in continental Portugal. Specifically, such a response was observed in the 'cool', but not in the 'warm' region (Table 2, Fig. 2C). Effects of the removal treatment on these algae were also detected

Table 1. ANOVA examining the effects of climate and location on Euclidean distances of algal assemblages between canopy-removed and control plots at 6 and 12 mo after the removal of the canopy. Significant effects are presented in **bold**

| Source of variation | df | 6 mo | | | | | | 12 mo | | | | | |
| | | Continental Portugal | | | Canary Islands | | | Continental Portugal | | | Canary Islands | | |
| | | MS | $F$ | p | MS | $F$ | p | MS | $F$ | p | MS | $F$ | p |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Climate | 1 | 2280.96 | 21.85 | **0.043** | 5973.66 | 26.77 | **0.035** | 46.82 | 7.51 | 0.111 | 134.27 | 0.30 | 0.637 |
| Location(Climate) | 2 | 104.40 | 2.26 | 0.137 | 223.12 | 6.04 | **0.011** | 6.24 | 0.27 | 0.764 | 442.25 | 7.37 | **0.001** |
| Residual | 16 | 46.17 | | | 36.92 | | | 22.72 | | | 60.02 | | |
| Cochran's $C$-test | | $C = 0.516$, $p > 0.05$ | | | $C = 0.517$, $p > 0.05$ | | | $C = 0.328$, $p > 0.05$ | | | $C = 0.556$, $p > 0.05$ | | |
| Transformation | | None | | | None | | | None | | | None | | |

Fig. 1. Euclidean distances (mean + SE) of algal assemblages between treated (canopy removal) and control plots from 2 locations in the 'cool' and 2 locations in the 'warm' regions of continental Portugal (L1 and L2 are Moledo and Vila Praia de Âncora in the 'cool' north region and Oliveirinha and Queimado in the 'warm' southwest region, respectively) and the Canary Islands (L1 and L2 are Punta Mujeres and La Santa in the 'cool' Lanzarote region and La Estaca and Tacorón in the 'warm' El Hierro region, respectively) at (A) 6 mo and (B) 12 mo after the removal of the canopy. Data averaged across 5 rock pools

at the Canary Islands, but they were related to patterns specific to individual rock pools rather than to the climatic condition (Table 2). However, at all island locations except Tacorón on El Hierro Island, corticated algae tended to reach relatively larger values in treated plots (Fig. 3C).

The abundance of leathery and encrusting algae in continental Portugal varied between sampled pools and between locations, independently of the presence/removal of the canopy and the climatic condition (Table 2, Fig. 2E,F). In the Canary Islands, both groups were affected by the removal of the canopy with a location-specific pattern (Table 2), viz. significantly larger cover in treated compared to control plots, only at Punta Mujeres (Lanzarote Island), while they were completely absent on El Hierro Island (Fig. 3E,F).

Table 2. Summary of significant results from ANOVA on abundance of morpho-functional groups of algae sampled 6 mo after the removal of the canopy in continental Portugal (CP) and the Canary Islands (CI). $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

| Morpho-functional algae group | System | Test | $MS_{NUM}$ | $MS_{DEN}$ | df | $F$ | Transformation |
|---|---|---|---|---|---|---|---|
| Articulated calcareous | CP | Treatment | 2.76 | 0.10 | 1, 2 | 27.38$^*$ | $\ln(x+1)$ |
| | | Pool(Location(Climate)) | 4.52 | 0.57 | 16, 80 | 7.95$^{***}$ | |
| | CI | Climate × Treatment | 78.76 | 5.21 | 1, 2 | 15.12$^*$ | None[a] |
| | | Pool(Location(Climate)) | 50.48 | 17.10 | 16, 80 | 2.95$^{***}$ | |
| Foliose | CP | Climate × Treatment | 5.58 | 0.53 | 1, 2 | 10.62$^*$ | $\ln(x+1)$ |
| | | Pool(Location(Climate)) | 3.65 | 0.22 | 16, 80 | 16.60$^{***}$ | |
| | CI | Treatment × Location(Climate) | 2199.02 | 389.21 | 2, 16 | 5.65$^{**}$ | None[a] |
| | | Climate | 5890.50 | 379.14 | 1, 2 | 15.54$^*$ | |
| | | Pool(Location(Climate)) | 650.20 | 65.99 | 16, 80 | 9.85$^{***}$ | |
| Corticated | CP | Climate × Treatment | 104.53 | 3.75 | 1, 2 | 27.88$^*$ | None |
| | CI | Treatment × Pool(Location(Climate)) | 172.70 | 14.63 | 16, 80 | 11.80$^{***}$ | None[a] |
| Filamentous | CP | Climate × Treatment | 9.76 | 0.86 | 1, 2 | 11.29$^*$ | $\ln(x+1)$ |
| | CI | Treatment × Location(Climate) | 3422.14 | 541.86 | 2, 16 | 6.32$^{**}$ | None[a] |
| | | Treatment × Pool(Location(Climate)) | 541.86 | 34.36 | 16, 80 | 15.77$^{***}$ | |
| Leathery | CP | Location(Climate) | 3.43 | 0.85 | 2, 16 | 4.01$^*$ | $\ln(x+1)$ |
| | | Pool(Location(Climate)) | 0.85 | 0.20 | 16, 80 | 4.32$^{***}$ | |
| | CI | Treatment × Location(Climate) | 83.33 | 21.54 | 2, 16 | 3.87$^*$ | |
| Encrusting | CP | Location(Climate) | 6.14 | 1.28 | 2, 16 | 4.79$^{**}$ | $\ln(x+1)$ |
| | | Pool(Location(Climate)) | 1.28 | 0.57 | 16, 80 | 3.46$^{***}$ | |
| | CI | Treatment × Location(Climate) | 988.49 | 290.44 | 2, 16 | 3.40$^*$ | None |

[a]Variances were heterogeneous (after Cochran's $C$-test) and could not be stabilised by transformations
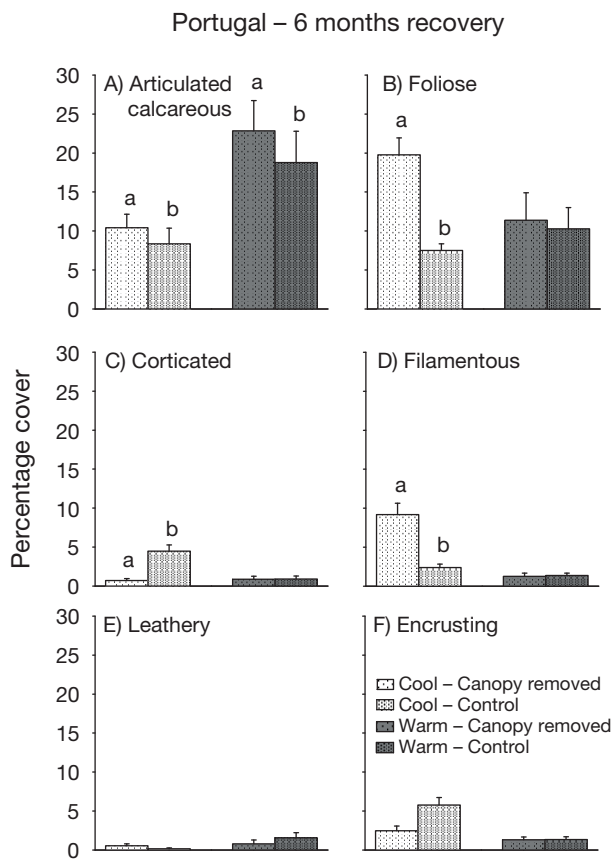
## Portugal – 6 months recovery



Fig. 2. Abundance (mean % cover + SE) of morpho-functional groups of algae in treated and control plots from 'cool' and 'warm' regions of continental Portugal at 6 mo after the removal of the canopy. Data averaged across 3 replicate plots, 5 pools and 2 locations. Different letters above bars represent treatments significantly different at p < 0.05 (SNK test; note that in panel A, only comparisons between treatments across 'cool' and 'warm' conditions are appropriate due to the significant main effect of Treatment)

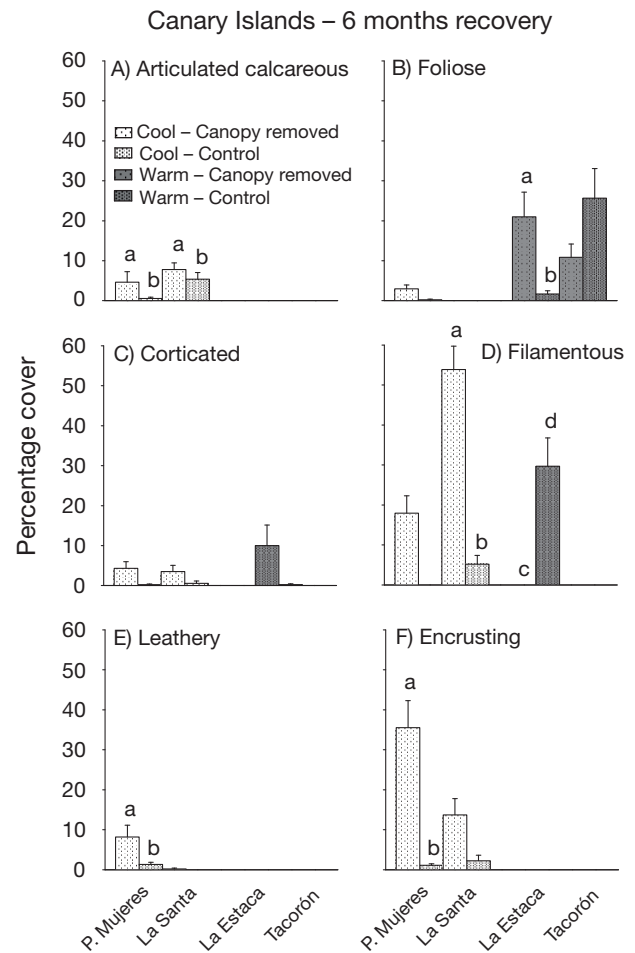## Canary Islands – 6 months recovery



Fig. 3. Abundance (mean % cover + SE) of morpho-functional groups of algae in treated and control plots from 'cool' and 'warm' regions of the Canary Islands at 6 mo after the removal of the canopy. Data averaged across 3 replicate plots and 5 pools. Letters above bars as in Fig. 2

## Recovery after 12 mo

Twelve mo after the start of the experiment, the mean ± SE cover of the canopy-forming species had further increased in treated plots from continental Portugal (N Portugal: 82.5 ± 2.22%; SW Portugal: 72.2 ± 6.7%) and Lanzarote (54.5 ± 5.7%), while it had remained comparable at El Hierro (26.5 ± 4.5%). In contrast to the 6 mo sampling, T-C distance values were now consistent across the climatic gradient and the examined system (Table 1, Fig. 1).

In continental Portugal, apart from significant variability among pools for most response variables, no significant effects were detected on articulated calcareous, foliose, corticated and filamentous algae (Table 3, Fig. 4A–D), whereas leathery and encrusting algae showed a significant Climate × Treatment

interaction (Table 3), but with different patterns. While both groups had very low and comparable covers in N Portugal, in SW Portugal leathery algae increased in treated compared to control plots (Fig. 4E), and encrusting algae showed the opposite response (Fig. 4F).

Responses to the treatment depending on the climate were documented at the Canary Islands for articulated calcareous, corticated and filamentous algae (Table 3). All of these groups were not found in pools sampled at El Hierro Island, while at Lanzarote Island their abundance was larger in treated than in control plots (Fig. 5A,C,D).

Foliose, leathery and encrusting algae were affected by the removal of the canopy depending on the sampled island location (Table 3). Foliose forms were relatively more abundant in treated than in

Table 3. Summary of significant results from ANOVA on abundance of morpho-functional groups of algae sampled 12 mo after the removal of the canopy in continental Portugal (CP) and the Canary Islands (CI). *p < 0.05, **p < 0.01, ***p < 0.001

| Morpho-functional algae group | System | Test | $MS_{NUM}$ | $MS_{DEN}$ | df | F | Transformation |
|---|---|---|---|---|---|---|---|
| Articulated | CP | Pool(Location(Climate)) | 673.46 | 89.85 | 16,80 | 7.50*** | None |
| calcareous | CI | Climate × Treatment | 187.55 | 1.03 | 1,2 | 182.01** | None[a] |
| | | Pool(Location(Climate)) | 66.94 | 9.90 | 16,80 | 6.76*** | |
| Foliose | CP | Pool(Location(Climate)) | 279.75 | 79.41 | 16,80 | 3.52*** | None[a] |
| | CI | Treatment × Location(Climate) | 6.37 | 0.70 | 2,16 | 9.08** | ln(x+1) |
| | | Pool(Location(Climate)) | 8.78 | 0.50 | 16,80 | 17.67*** | |
| Corticated | CI | Climate × Treatment | 94.86 | 7.08 | 1,2 | 13.40** | None[a] |
| | | Pool(Location(Climate)) | 54.50 | 19.45 | 16,80 | 2.80** | |
| Filamentous | CP | Pool(Location(Climate)) | 24.81 | 11.37 | 16,80 | 2.18* | None[a] |
| | CI | Climate × Treatment | 509.31 | 40.18 | 1,2 | 12.67* | None[a] |
| Leathery | CP | Climate × Treatment | 330.01 | 2.81 | 1,2 | 117.51** | None[a] |
| | | Pool(Location(Climate)) | 248.93 | 104.63 | 16,80 | 2.38** | |
| | CI | Treatment × Location(Climate) | 333.58 | 24.33 | 2,16 | 13.71*** | None[a] |
| Encrusting | CP | Climate × Treatment | 246.53 | 4.17 | 1,2 | 59.17** | None[a] |
| | | Pool(Location(Climate)) | 259.56 | 91.02 | 16,80 | 2.85** | |
| | CI | Treatment × Location(Climate) | 442.98 | 128.21 | 2,16 | 3.46* | None |

[a]Variances were heterogeneous (after Cochran's C-test) and could not be stabilised by transformations
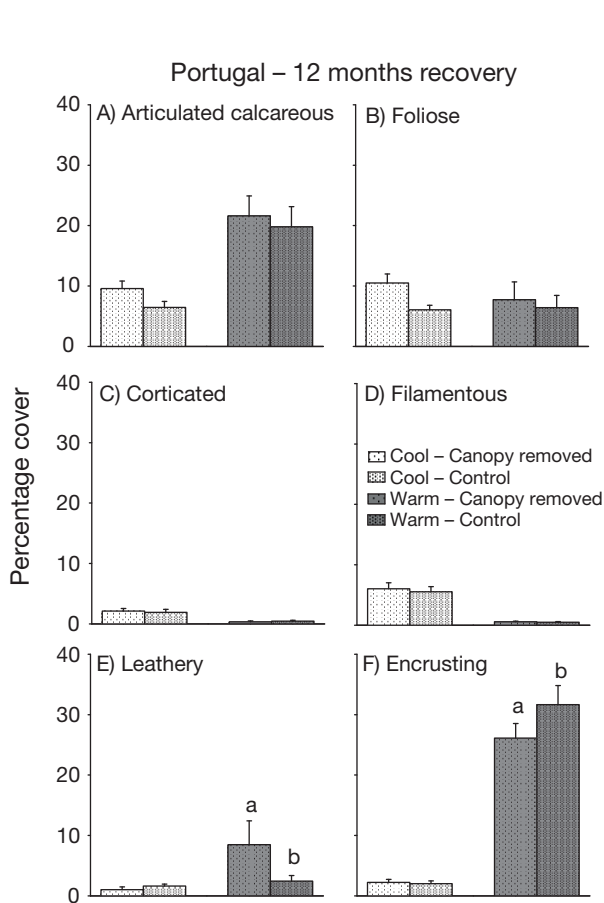


Fig. 4. Abundance (mean % cover + SE) of morpho-functional groups of algae in treated and control plots from 'cool' and 'warm' regions of continental Portugal at 12 mo after the removal of the canopy. Data averaged across 3 replicate plots, 5 pools and 2 locations. Letters above bars as in Fig. 2
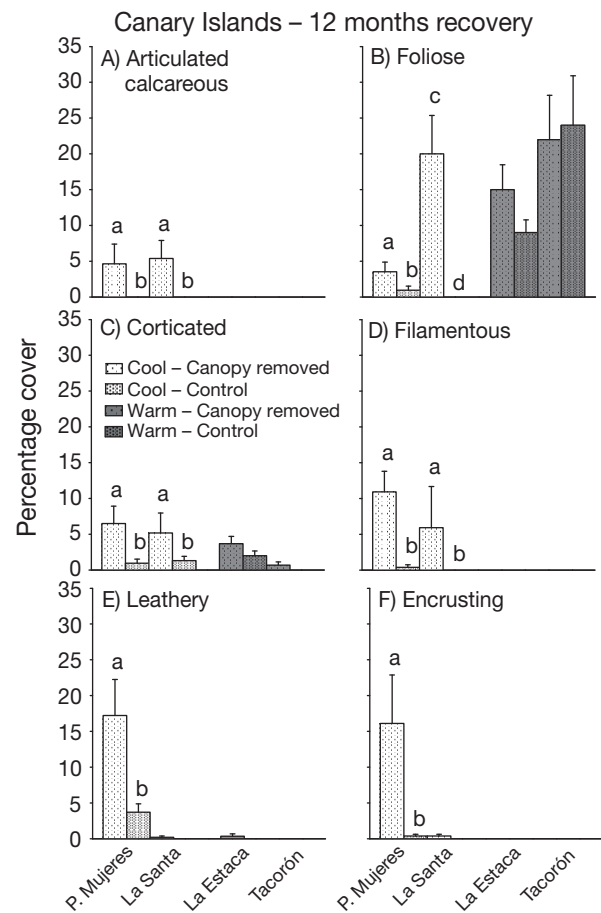


Fig. 5. Abundance (mean % cover + SE) of morpho-functional groups of algae in treated and control plots from 'cool' and 'warm' regions of the Canary Islands at 12 mo after the removal of the canopy (= treatment). Data averaged across 3 replicate plots and 5 pools. Letters above bars as in Fig. 2

control plots at Lanzarote Island, but the difference in cover was much larger at La Santa than at Punta Mujeres. On El Hierro Island, they attained relatively large and comparable cover at all locations, independently of the treatment (Fig. 5B). Leathery and encrusting forms were almost, or completely, absent on El Hierro Island and at La Santa (Lanzarote Island), while they clearly increased in abundance in treated compared to control plots at the other location (Punta Mujeres, Lanzarote Island) (Fig. 5 E,F).

## DISCUSSION

The present study was based on the assumption that canopy-forming macroalgae ameliorate the effects of a range of disturbances on understory assemblages (Bertness et al. 1999, Benedetti-Cecchi et al. 2001, Lilley & Schiel 2006, Bertocci et al. 2010). Thus, algal canopies would enhance the resistance of associated systems, i.e. their ability to remain unchanged under concomitant perturbations. As a direct consequence, the loss of canopies could exacerbate the effects of present or predicted harsh environmental conditions. Although true cause–effect relationships could not be identified and tested in the present study, this led us to hypothesize that, under higher irradiation, SST and air temperatures, rock pool assemblages experimentally deprived of protection by the canopy would become more different than unmanipulated assemblages. This hypothesis was supported by multivariate findings documented 6 mo after the removal of the canopy in both continental Portugal and the Canary Islands.

A main ecological outcome of the loss of canopy-forming macroalgae and of the consequent increased environmental stress on associated organisms (Bertness & Leonard 1997, Jenkins et al. 1999, Schiel & Lilley 2007, Bertocci et al. 2010) is the documented shift towards 'simpler' assemblages dominated by algal turfs (Benedetti-Cecchi et al. 2001, Bulleri et al. 2002, Mangialajo et al. 2008). This shift could be driven by a drastic reduction or local extinction of understory species unable to survive without the protective canopy, followed by the facilitation of turf-forming species less competitive for space, but more resistant to the new harsher conditions (e.g. Lilley & Schiel 2006, Schiel & Lilley 2011). A similar mechanism could explain the increased cover of articulated calcareous algae in canopy-removed, compared to undisturbed, plots documented in both regions in continental Portugal and in the 'cool' region of the Canary Islands. In fact, this is in agreement with the

known inverse relationship between the abundance of algal canopies and that of coralline algae from both intertidal and subtidal habitats (Benedetti-Cecchi & Cinelli 1992, Melville & Connell 2001, Bell-grove et al. 2010). At the same time, articulated coralline algae are known to be resistant to natural (Bulleri & Airoldi 2005) and human disturbances (Airoldi et al. 1995). Analogously, in the 'cool' region of continental Portugal, filamentous and foliose algae, including several opportunistic species among the most common (e.g. *Cladophora* spp. and *Ulva* spp., respectively), could have benefited from the concomitant reduction of competitive corticated algae in the canopy-removed plots. The abundance of algae such as *Chondracanthus acicularis* (Roth) Fredericq and *Ahnfeltiopsis devoniensis* (Greville) P.C. Silva and DeCew, both represented here within the corticated group, is demonstrably reduced after the removal of algal canopies (Bertocci et al. 2010) and under severe disturbance (Tuya & Haroun 2006).

Overall, our multivariate results suggest that the ecological mechanisms involved in the responses of associated assemblages to the loss of macroalgal canopies could be similar in the examined systems, despite a range of expectable biological (e.g. Santelices & Ojeda 1984, Konar 2000, Benedetti-Cecchi et al. 2000, 2001) differences, including the different identity of the algal canopies involved, and the abiotic (Brown & Lomolino 2000) differences between systems. Nevertheless, the inconsistencies in patterns of responses of individual algal groups between continental Portugal and the Canary Islands and between regions within the same system suggest a number of issues potentially important for the present, and possibly future, biogeography of the studied areas, presented below.

Deep modifications of the functional structure of natural assemblages under changing environmental conditions can drastically alter ecosystem functions, including their resilience to disturbance (Tilman 1999, Navarrete & Berlow 2006, Hooper et al. 2012). In this context, examining patterns of variation in the distribution and responses to local disturbances of the functional structure of assemblages across biogeographic breaks is of overwhelming importance. For instance, major changes in patterns of abundance of functional groups of organisms in coincidence with biogeographic transitions have been documented along the coasts of South Africa (Bustamante & Branch 1996), the west coast of North America between Alaska and Baja California (Blanchette et al. 2008) and the whole coast of New Zealand (Schiel 2011). Analogously, the continental coast of Portugal is

characterized by a biogeographic discontinuity in the distribution of intertidal algae (Lima et al. 2007) and subtidal kelp and fish species (Tuya et al. 2012). This is likely due to the effects of the Nazaré Canyon (39.6° N, crossing the Portuguese continental margin from the coast to about 4500 m depth) on geological and present abiotic and biological processes (e.g. Tuya et al. 2012). In the present study, however, such discontinuity was not as evident at the level of morpho-functional groups of algae, as these were all represented with comparable abundances in both the north and the southwest region, thus lacking abrupt changes coincident with the known biogeographic boundaries. Analogous findings were documented along the Pacific coast between Oregon and California (Connolly & Roughgarden 1998) and along the Atlantic coast of South America between the Argentinean and Magellanic Provinces (Wieters et al. 2012). Such patterns can be explained assuming, in general, that processes driving the structure of morpho-functional groups on the studied mainland coast are distinct from those shaping the boundaries of species ranges. While the variability in the distribution and abundance of species over biogeographic scales is mostly driven by patterns of dispersal drastically affected by oceanographic conditions (Broitman et al. 2001, Schiel et al. 2004), changes in the abundance of functional groups can be explained by regional differences in recruitment of key species (Connolly et al. 2001). At the same time, despite biogeographic changes in the distribution of species, homogeneity of functional groups at the regional scale can be maintained through a convergence of species with different geographic distributions on life traits providing similar overall group functions. For example, along the Argentinean coast, the mussel *Perumytilus purpuratus* forms extensive beds up to a northern range limit located at Punta Mejillon, where this habitat-forming species is replaced by another mussel, *Brachidontes rodriguezii*, with very small changes to the structure of associated assemblages (Wieters et al. 2012). The 2 examined regions of continental Portugal were characterized by different species, but these were to some extent 'interchangeable' (e.g. *Cladophora* spp. and other green algae were common filamentous forms in SW Portugal, while the red *Ceramium* spp. were much more abundant in N Portugal) in terms of supporting comparable patterns of distribution and abundance of morpho-functional groups over a biogeographic scale.

Much more variable patterns were documented at the Canary Islands, where several groups of algae showed drastic changes in their occurrence between regions. Articulated calcareous, leathery and encrusting algae were present at Lanzarote Island and completely absent from El Hierro Island, while an opposite trend was observed for foliose algae. In comparison with continental Portugal, a larger variability was also documented between locations within each region in the Canaries. These results would support the view that patterns of biodiversity at a range of scales differ between and within systems depending on a number of processes, and not necessarily due to climatic differences directly. For example, a comparison of patterns of species richness and algal composition at several archipelagos, including the Canary Islands, indicated that the inter-archipelago variability was mostly explained by differences in the distance from the nearest continental shore, while the intra-archipelago variability was greatly affected by the size of each island (Tuya & Haroun 2009). In addition, different historical events, local oceanographic and climatic conditions and levels of natural and anthropogenic disturbance could further contribute to differences in heterogeneity of habitats, populations and assemblages between continental Portugal and the Canary Islands and between individual islands (Brown & Lomolino 2000). In addition to biogeographic and climate-related differences, the islands of Lanzarote and El Hierro in particular are characterized by different size (806 and 279 km$^2$, respectively), distance from the mainland (ca. 130 and 380 km off the African coast, respectively) and by the different geological age characterizing the 'old' eastern and the 'young' western Canary Islands, associated with the generally larger extent of rocky intertidal platforms at Lanzarote compared to El Hierro (e.g. Ramírez et al. 2009). All of these traits could have been, to some extent, responsible for differences in the abundance of algal groups between islands, making it difficult to tease apart the relative contribution of each source. At the same time, however, a larger heterogeneity of some algal groups between locations on islands compared to the mainland has been previously reported, such as for encrusting coralline algae from the Tuscany Archipelago in the Mediterranean Sea (Benedetti-Cecchi et al. 2003). Again, the specific causes of such variation could not be assessed in the present study, but they likely involve interactions among physical and biological processes (Underwood 1985).

Our findings are also relevant for understanding, and possibly predicting, responses of associated assemblages to worldwide documented shifts in range distributions of key species (e.g. Last et al.

2011, Philippart et al. 2011, Wernberg et al. 2012b). Along the Atlantic coast of the Iberian Peninsula, in particular, several cool-water species have recently shown northward retractions of their ranges of distribution (Lima et al. 2007, Fernández 2011, Tuya et al. 2012). Climate warming has been invoked as a major cause of these shifts, as well as of the globally observed trend towards a poleward retreat of cool-water species (Helmuth et al. 2002, Wernberg et al. 2011). Our findings indicate that the loss of a canopy-forming species with an affinity for cool temperatures, such as the fucoid *Cystoseira humilis*, can determine changes in the associated assemblages, and that such changes are larger when the local environmental conditions are harsher. Although our study cannot exclude that different patterns of recovery might occur after disturbances removing the canopy at other times of the year (e.g. Oliveira et al. 2011), after a pulse disturbance, such as our removal treatment, and under the current environmental conditions, the studied assemblages showed the potential to considerably recover over a relatively short period in both continental and insular study systems. In contrast, it could be expected that chronic disturbances, including further increases of sea and air temperatures (e.g. Gómez-Gesteira et al. 2008) and decreases in the intensity of upwelling (Lemos & Pires 2004, Santos et al. 2011), would be able to drive persistent losses of such habitat-forming algae and alterations of their associated biodiversity, with possible drastic modifications of current biogeographic patterns. In such a context, however, there is an important difference between the 2 canopy-forming species examined here. Southward expansions of the range of distribution of *Bifurcaria bifurcata* have been observed along the Atlantic coast of northern Portugal (Lima et al. 2007) and in the English Channel (Mieszkowska et al. 2006) coincidentally with climate warming. Moreover, recent model projections have suggested that future warming could determine a further increase of the occurrence of this species in the Iberian Peninsula (Martínez et al. 2012). Such observations and predictions are clearly in contrast with those regarding fucoid canopies. Nevertheless, analogously to other canopy-forming seaweeds (Airoldi & Beck 2007, Connell et al. 2008, Mangialajo et al. 2008), *B. bifurcata* is particularly sensitive to environmental degradation, including chemical pollution (Díez et al. 2009) and biological invasions (Sánchez et al. 2005). As well as SST, air temperature and irradiation, all of these disturbances are expected to increase in the future, particularly in coastal areas. Although with different mechanisms and species-specific responses, their overall effects will most likely be towards a general retraction of the ranges of distribution of the studied algal canopies. Our results provide experimental evidence suggesting, for the near future, considerable changes in associated assemblages from both continental Portugal and the Canary Islands. These could be maintained over time scales exceeding the recovery ability of organisms and be directly related to and exacerbated by the harshness of local natural or anthropogenic environmental conditions.

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