

# Canopy microclimate modification in central and marginal populations of a marine macroalga

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## Abstract

The effects of environmental changes on species distribution are generally studied at large geographical scales. However, aggregations of individuals can significantly moderate the impact of the environment at smaller, organismal scales. We focused on the intertidal macroalga *Fucus guiryi* and carried out field and laboratory common garden experiments to evaluate how the different individual morphologies and canopy densities typical of central and peripheral populations modify microhabitat conditions and associated levels of stress. We show that *F. guiryi* canopies significantly alter environmental conditions (i.e., temperature, humidity and light regimes) and mitigate the levels of stress experienced by individuals within the group. Southern algae are more branched and form denser canopies but, unexpectedly, despite these considerable differences, the mitigating effects of northern and southern canopies did not differ significantly. Microhabitat conditions beneath canopies were more stressful at marginal locations, indicating that southern populations are not more effective than northern algae at mitigating the harsher climate at the edge of the species distribution. Our findings highlight the importance of assessing structural changes in aggregating species across their distribution and relating these to local climates to understand the impact of environmental changes at scales relevant to individual organisms.

**Keywords** Aggregation · Intertidal temperature · Environmental stress · *Fucus* spp. · Algal canopy · Trailing edge

## Introduction

There is ample evidence that contemporary climate change is affecting the abundance and distribution of life on Earth (Harley et al. 2006; IPCC 2007; Parmesan and Yohe 2003; Root et al. 2003; Walther et al. 2002). When species distributional limits are set by physical factors, responses to large-scale environmental change are often particularly critical for populations inhabiting the periphery of the species' distribution, where the immediate pressure of climate change forces

the species to develop novel adaptive strategies or face local extinction (Barry et al. 1995; Hampe and Petit 2005).

Towards such distributional edges, the general expectation is that as physiological stress levels increase, individual performance is negatively affected. As a result, populations become smaller, more isolated and patchily distributed to the point at which regional population dynamics can no longer buffer local extinction events (Brown et al. 1995; Guo et al. 2005).

However, several empirical studies question the generality of the 'benign centre' view (Sagarin and Gaines 2002). It is now increasingly recognised that abundance patterns and demographic dynamics are less predictable than originally thought because they are affected by complex interactions of multiple factors that alter in space and time (Tam and Scrosati 2011; Viejo et al. 2011). In particular, although the effects of changing climate on species distribution limits are generally investigated at large temporal and geographical scales, local small-scale effects and interactions within the ecosystem can compensate or even reverse the impact of climate (Helmuth et al. 2002; Helmuth et al. 2008). Within-system effects are

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particularly noticeable for organisms living in aggregations. Evidence from a wide variety of taxa describes aggregations as evolutionarily advantageous arrangements that grant individual members several benefits including significant amelioration of environmental conditions, reduced predation risk and increased reproductive success, but at the price of reduced resources (e.g., Krause and Ruxton 2002).

The beneficial effects of an aggregate lifestyle largely depend on the physical organisation of the aggregation and on the characteristics of the organism(s) composing the aggregation (e.g., abundance and individual morphology; Hawkins et al. 2009; Kordas et al. 2011; Moore et al. 2007). What is more, the degree of amelioration at the aggregation level is likely to vary across climatic clines through environmentally mediated dynamics (Bertness and Leonard 1997; Cole and McQuaid 2010, 2011; Crain and Bertness 2006).

In this study, we hypothesise that fundamental structural differences in algal aggregations at the trailing edge and the centre of the distributional range of a dominant canopy-forming macroalga will result in distinct aggregation benefits in terms of micro-climate mitigation and thus the individuals' experience of environmental stress.

Macroalgae are important structural and functional components of marine intertidal ecosystems. Their three-dimensional structures provide shelter for numerous other organisms (Benedetti-Cecchi 2001; Bulleri et al. 2002; Schiel and Lilley 2007) with important effects of algal morphology and density on the sub-canopy microclimate. For example, a greater thallus thickness decreases the rate of desiccation, while more branching results in greater desiccation rates and higher heat dissipation (Norton 1991; Bell 1995). At the aggregation level, different frond sizes and shapes produce distinct temperature and humidity microclimates while the degree of branching significantly affects the light regime within the canopy (Jorve 2008).

We used *Fucus guiryi* as the focal species. Plant density and the morphology of this keystone intertidal brown macroalga differ significantly but gradually across the north–south distribution of the species (Zardi et al. 2015); individuals inhabiting the centre of distribution are more elongated and have wider fronds than specimens from the southern (equatorial) edge. There, the species has a bushy morphology; i.e., individual algae are shorter with more branching. In general, at the southern edge, inter-individual distances are reduced, but patches are more scattered (Zardi et al. 2015). This core-to-margin gradient in both algal morphology and the nature of algal patches mirrors a north–south gradient of increasing air temperature which has become more intense over recent decades due to significant coastal warming [average of 0.214 °C/decade; National Aeronautics and Space Administration (NASA), Goddard Earth Sciences (GES), Data and Information Services Center (DISC); Acker and Leptoukh 2007; Lima and Wethey 2012; Nicastro et al. 2013].

In the present study, we carried out field and laboratory common garden experiments to address the following questions: 1) Do the individual morphologies and canopy densities of *F. guiryi*, typical of central and peripheral populations, generate distinct, within-aggregation microclimatic conditions? 2) Do different microclimatic conditions affect levels of stress experienced by individuals composing the aggregation?

## Materials and methods

### Study sites

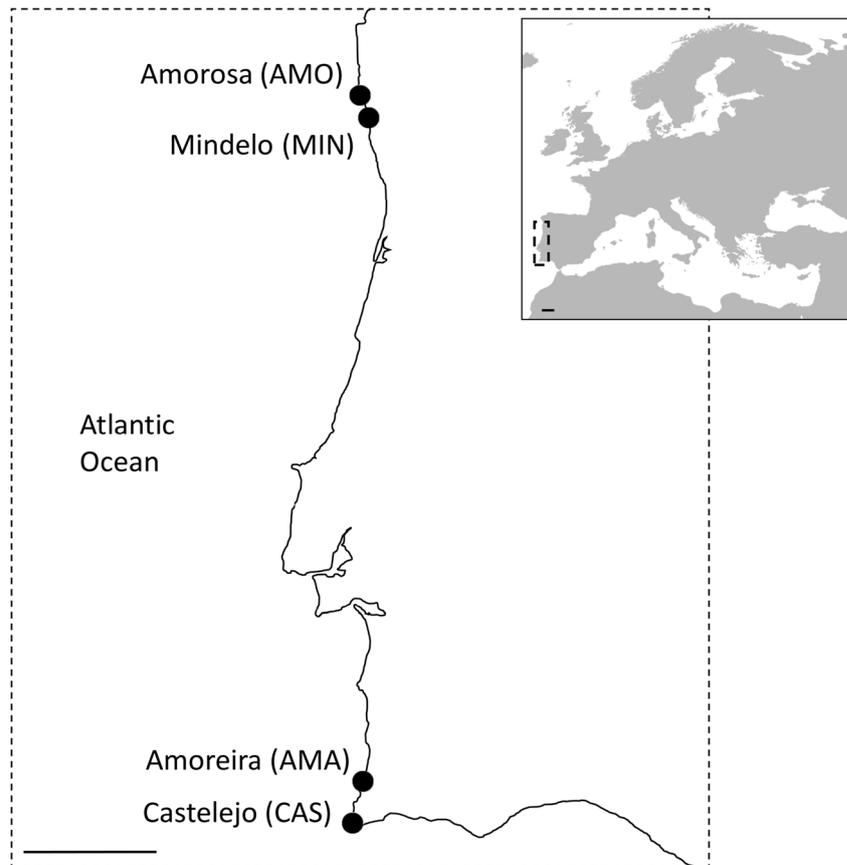
Two sites were chosen (Fig. 1; Table 1SM): north Portugal (N Portugal) at the core of *F. guiryi* distribution and south Portugal (S Portugal) at the southern edge. At each site, two replicate rocky intertidal locations were selected haphazardly. In Iberia, *F. guiryi* is continuously distributed with a north-eastern margin in the warm waters of the Bay of Biscay and a southern limit in southern Portugal (Zardi et al. 2015). The distributional centre lies in north-west Iberia (northern Portugal-Galicia). South of southern Portugal, isolated populations can be found restricted within centres of upwelling (Lourenço et al. 2016). North of the Bay of Biscay, the species has been reported (as *F. spiralis* var. *platycarpus*; Batters 1902) in the English Channel and in Scotland. These areas are separated by hundreds to thousands of km from the continuous Iberian environmental and distributional gradients and were not considered in our study.

### Laboratory common garden experiments

At each site, 4 independent 30 × 30-cm patches were haphazardly chosen in the middle of the vertical range of the species. In each patch, maximum frond length (i.e., measured as the length of the longest frond from tip to holdfast) and maximum circumference (i.e., widest part of the frond) were measured for five individuals and the distance between five neighbouring individuals was recorded (Table 1SM). A representative subsample of algae was carried back to the laboratory for further processing. These individuals were initially acclimated at 12 °C, 100% humidity in darkness for 10 days, followed by 2 days in seawater at low (50–100 μmol m<sup>-2</sup> s<sup>-1</sup>) photosynthetic photon flux density (PPFD) supplied by fluorescence lamps at 12 °C under a 12:12 h light:dark (L:D) photoperiod.

For laboratory common garden experiments, we measured the physiological resilience to emersion stress of apical tissue of *F. guiryi* individuals ( $n = 6$ ). To do this, we collected samples of apical tissue (hereafter 'tips') from the two populations and exposed them to emersion conditions under artificial canopies. Canopies were constructed by tying live algae to a

**Fig. 1** Map of the study area with codes for sites in brackets. Scale bars are 100 km



framed, partially rigid, white PVC net ( $50 \times 30$  cm; mesh size 2 cm). Individuals collected from the south were positioned 2 cm apart from each other while the distance between individuals from the north was 4 cm, mirroring the average distance between individuals assessed in the field (Table 1SM and see also Zardi et al. 2015). Canopy areas were  $24 \times 16$  cm. Solitary individuals were also attached to the same white plastic net ( $8 \times 4$  cm). Framed solitary individuals and canopies were kept under acclimation conditions for 12 h before starting the experiment.

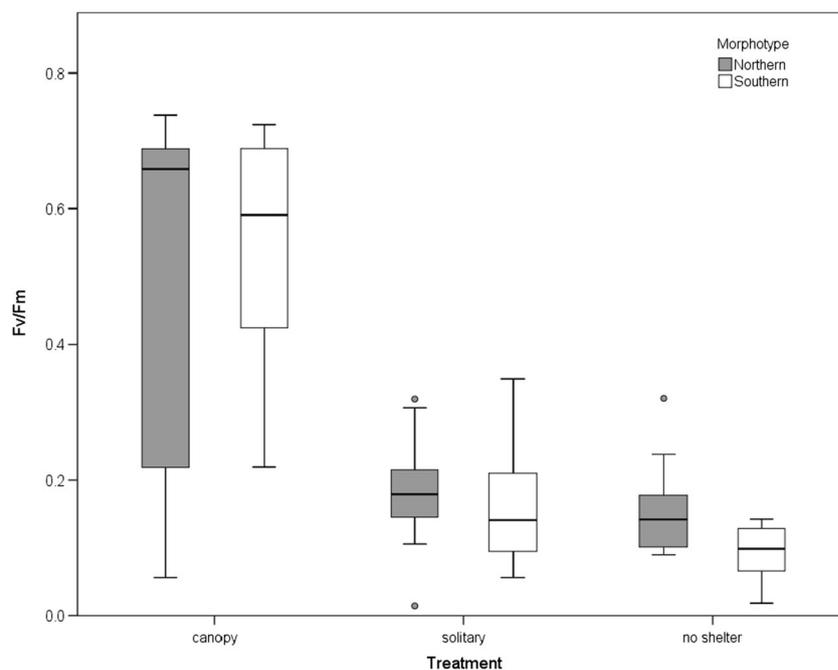
For each morphotype (southern or northern), the experimental treatments were (a) below artificial canopies and (b) below solitary individuals. In addition, a no-shelter treatment was included, i.e., tips placed on bare substratum. Tips were exposed to air beneath framed solitary individuals and canopies and on bare substratum at  $35^\circ\text{C}$  for 6 h, under  $330 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD. After 24 h recovery under acclimation conditions, the Fv-to-fm ratio was determined using a pulse amplitude modulated (PAM) fluorometer (Junior-PAM, Heinz Walz GmbH, Germany) on dark-adapted (5 min) tissue. The Fv-to-fm ratio is a measure of the maximum efficiency of the PSII reaction center (Maxwell and Johnson 2000). Values of 0.7–0.8 are considered to reflect healthy tissue, while lower values indicate stress (Büchel and Wilhelm 1993; Ting and Owens 1993).

Control values of the Fv-to-fm ratio were obtained from tips that were not exposed to emersion and were kept under acclimation conditions until the end of the experiment.

### Field measurements

During summer (July and August 2013), environmental conditions within the microhabitat formed by *F. guiryi* canopies and at empty patches (no shelter) next to canopies were assessed at each location over two separate days. Days were selected as examples of typical summer stressful periods and complied with the following filters: spring tides with low tide between 11–14 h and typical sunny atmospheric conditions for the season and the region (Table 1SM). Temperature and relative humidity were measured using data loggers ( $n = 4$ ; iButtons®, Maxim Integrated Products, Dallas Semiconductor, TX, USA) at 1-min intervals for 4 hours, 2 hours before and 2 hours after minimum tidal height (tide table at <http://tides.mobilegeographics.com>). Photosynthetically active radiation (PAR) was measured during the same period at 20-min intervals using a light meter with a spherical micro-quantum sensor (ULM-500, © Heinz Walz GmbH, Germany). To calculate a sheltering index (SI) for each

**Fig. 2** Common garden experiments. Measurements of photoinhibition of PSII maximum quantum yield of acclimated algae (apical tissue) air exposed at 35 °C for 6 h under 330  $\mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD followed by 24 h of recovery



day/location, the value under the canopy (c) for each measurement was calculated as a percentage of the values recorded under conditions of no shelter (ns) using this equation:  $SI = (c - ns) / ns * 100$ .

## Data analyses

Data did not fulfil the prerequisites of parametric analyses even after transformation, and were therefore analysed using PERMANOVA v 1.6 (Anderson 2001). Distance-based homogeneity of dispersion tests, tests of main effects and pair-wise tests on significant interactions were performed using 999 permutations. Bonferroni correction was applied to all pair-wise comparisons. Analyses were performed using SPSS Statistics 21.0.

Physiological resilience to air exposure was analysed with a three-way PERMANOVA with treatment (canopy, solitary, no shelter) and morphotype (northern, southern) as orthogonal, fixed factors and location (1 or 2) as a random factor nested within the two orthogonal factors. Significant differences among control values were tested with a two-way PERMANOVA with morphotype (northern, southern) as an orthogonal, fixed factor and location (1 or 2) as a random factor nested.

The effect of morphotype (fixed, orthogonal; southern, northern) and location (nested, random, 1, or 2) on each sheltering index was tested with a two-way PERMANOVA (days pooled).

## Results

### Laboratory common garden experiments

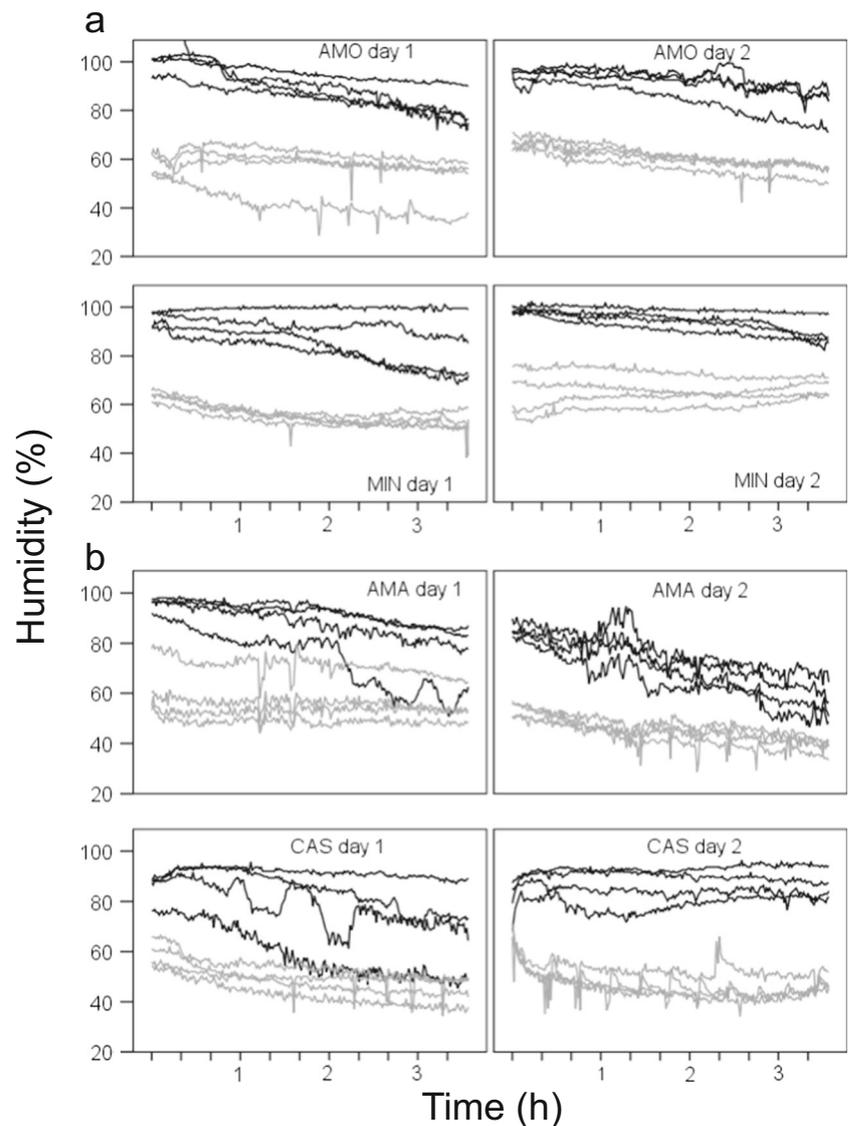
After 24 h of recovery, the Fv-to-fm ratio under canopies was significantly greater than below solitary individuals or with no shelter [treatment  $P$  (Monte Carlo; MC) < 0.01; Table 2SM; Fig. 2], although Fv-to-fm values beneath canopies from the two northern locations were significantly different [location (type)  $P$  (MC) < 0.01]. There was no effect of morphotype [ $P$  (MC) = 0.97]. Variability of under-canopy Fv-to-fm values was greater than under solitary individuals, most likely due to the spatial cover complexity of canopies.

Control values were all indicative of healthy tissue and no significant differences in Fv-to-fm ratios were detected between types [ $P$  (MC) = 0.08; Table 3SM; data not shown] or locations [ $P$  (MC) = 0.79].

### Field measurements

In both the north and south, temperatures and PAR were lower, and relative humidity was higher below canopies than with no shelter (Figs. 3, 4, 5) but the temperatures recorded were higher in the south than in the north. Compared to the no-shelter condition, average temperature below canopies was 7.2 and 9.4 °C at northern and southern locations, respectively. On average, below-canopy humidity was 35% higher than that recorded on rocks. Below canopies, PAR never reached values higher than 70  $\mu\text{mol}$

**Fig. 3** Humidity trends in under-canopy (in black) and no-shelter (in grey) conditions during low tide at (a) northern and (b) southern sites. Site codes as in Fig. 1



$\text{m}^{-2} \text{s}^{-1}$ , while outside canopies, values ranged between 933 and 2683  $\mu\text{mol m}^{-2} \text{s}^{-1}$  PPF. D.

For humidity, temperature and PAR, the shelter offered by the canopy was consistently, non-significantly different between morphotypes [ $P$  (MC) = 0.71, 0.1 and 0.53, respectively; Tables 4, 5 and 6SM; Fig. 6a–c]. There were significant differences among locations [ $P$  (MC) = 0.02] but all pair-wise comparisons were non-significant when further explored.

## Discussion

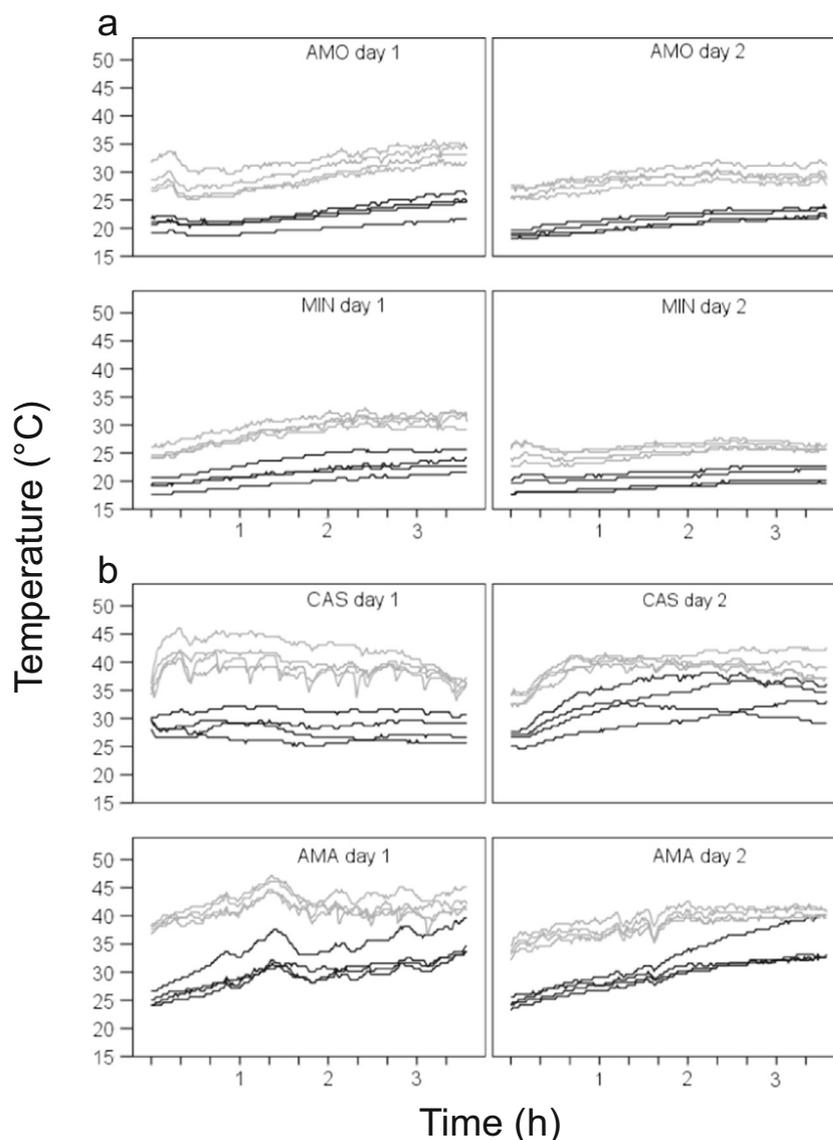
Aggregations can strongly modify environmental factors; thus, changes in their physical organisation are expected to disproportionately alter the physical habitat at scales that are relevant to individual organisms within the group (e.g., Moore

et al. 2007; Nicastro et al. 2012). Our results show that *Fucus guiryi* canopies significantly ameliorate environmental conditions. However, along the species' distributional range, morphological differences and differences in plant densities between northern and southern canopies did not result in distinct microclimates.

Environmental mitigation is particularly critical in the intertidal where species live at the interface of land and sea, and are subject to strong abiotic stressors that place them close to their thermal limits (Harley and Helmuth 2003; Nicastro et al. 2010; Martínez et al. 2012). During low tide, emersion leads to desiccation, extreme temperatures, nutrient limitation, high irradiance and osmotic stresses that are enhanced at species' intertidal upper limits (Davison and Pearson 1996).

The spatial complexity provided by the canopies of *Fucus* spp. can ameliorate harsh conditions in stressful environments (Watt and Scrosati 2013; Duarte et al. 2015).

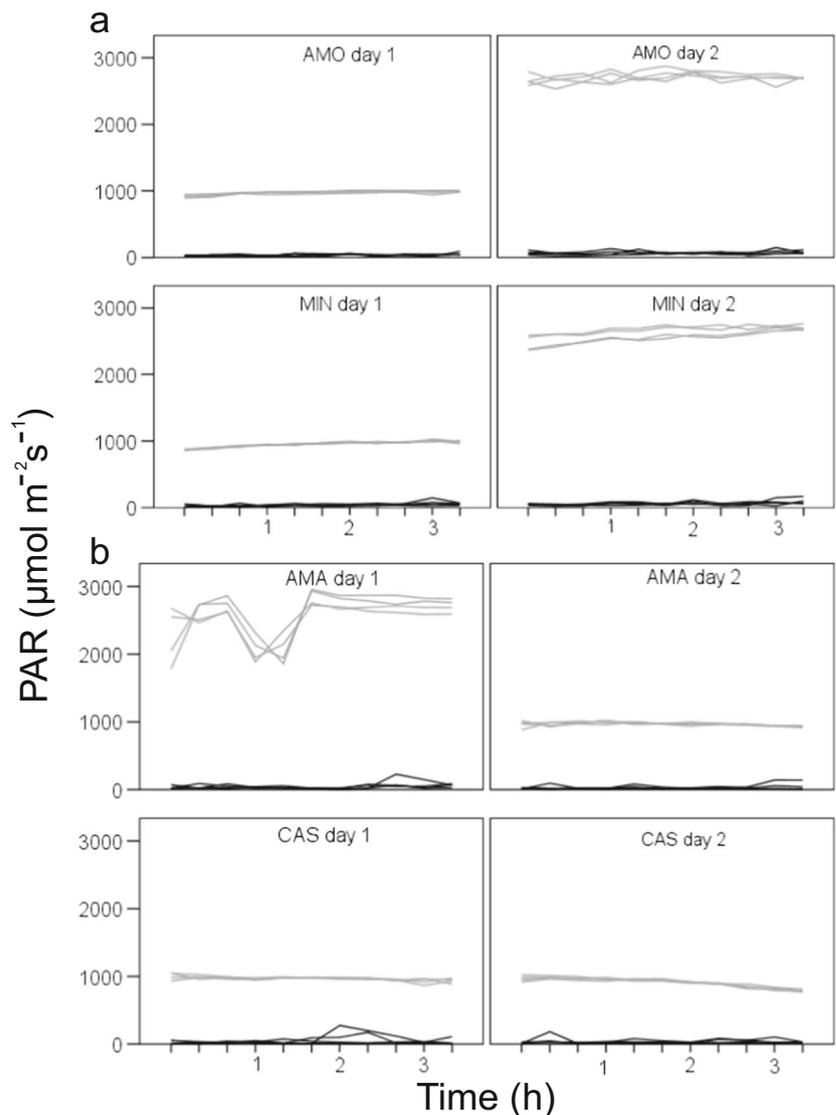
**Fig. 4** Temperature trends in under-canopy (in black) and no-shelter (in grey) conditions during low tide at (a) northern and (b) southern sites. Site codes as in Fig. 1



Such beneficial influences are particularly effective for its own recruits and juveniles as the gametes usually settle close to the parents, resulting in a high proportion of juveniles experiencing sub-canopy conditions (Wahl et al. 2011). Since juveniles are especially susceptible to emersion stress (Schoenwaelder et al. 2003; Wahl et al. 2011), canopies act as a refuge and considerably increase juvenile survival (Lamote et al. 2007). Furoid germling survival rates can be close to 100% beneath the canopy, as opposed to near-zero on bare rock (Brawley and Johnson 1991), although field experiments along the physically stressful Iberian coast show variable but low (i.e., <30%) survival of *Fucus* spp. germlings (Ladah et al. 2003). In addition, embryos protected by the canopy can maintain photosynthetic activity longer than individuals that are exposed during emersion (Lamote et al. 2007). Our physiological results validate the tempering effect of the canopy on light, humidity and temperature stress.

Apical tissue that was not sheltered did not show any signs of regaining physiological capacity after 24 h of recovery. PSII maximum quantum yield values were far from the range regarded as healthy (Fv-to-fm ratio 0.7–0.8; Büchel and Wilhelm 1993; Ting and Owens 1993), suggesting that the damage was permanent. In contrast, apical tissue placed below canopies showed good recovery from the stress of exposure. Interestingly, Fv-to-fm values showed high variability compared to previous studies with *Fucus* spp. where only apical tissue was compared (Pearson et al. 2009; Zardi et al. 2011), indicating a high level of heterogeneity in the sub-canopy habitat. Because of the intrinsically complex arrangement of *Fucus* aggregations, modulation of environmental conditions and the stress experienced by organisms that form canopies is not homogeneous, with very different physiological consequences at the center versus edge versus top of the canopy (Mota et al. 2014). This is supported by the larger variability in

**Fig. 5** Light intensity (PAR) trends in under-canopy (in black) and no-shelter (in grey) conditions during low tide at (a) northern and (b) southern sites. Site codes as in Fig. 1



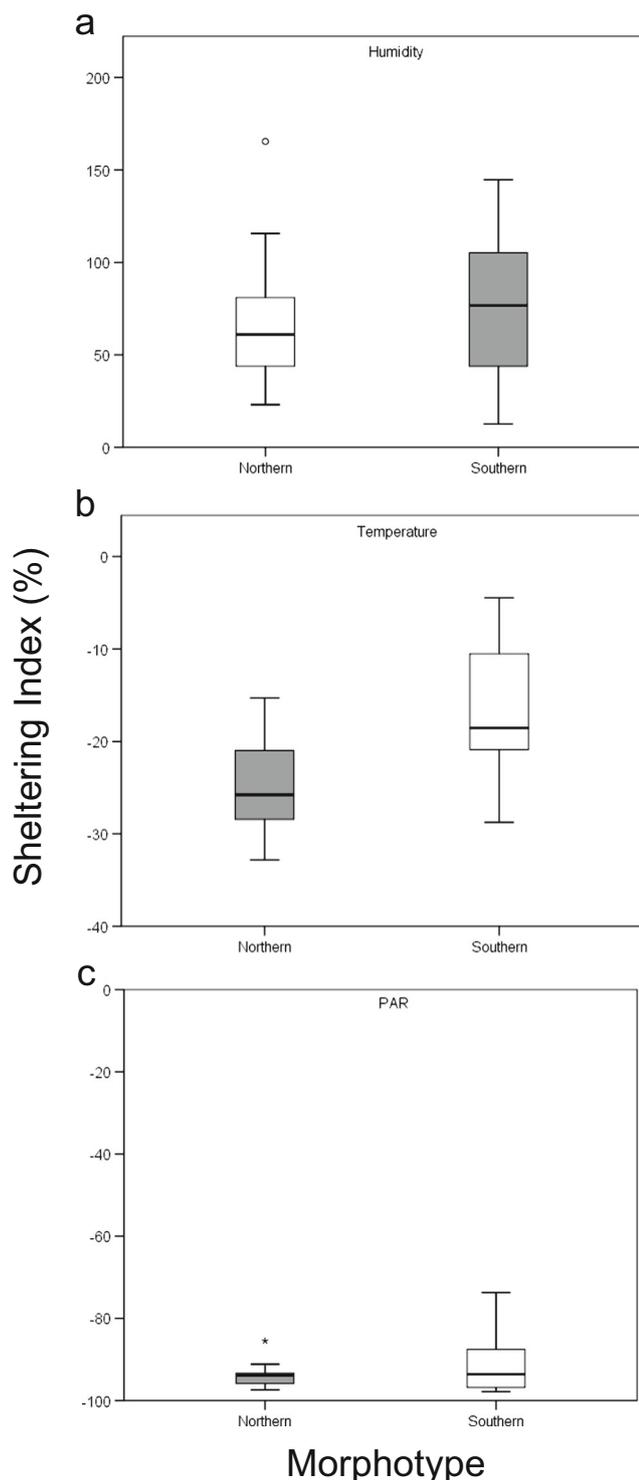
Fv-to-fm values under northern canopies; in southern, marginal populations, individuals are bushier (i.e., higher maximum circumference-to-length ratio) and canopies are significantly denser than in northern, central locations (Zardi et al. 2015), thus providing more uniform cover.

Previous studies have found that the structural variability of individuals and aggregations (i.e., size, shape and degree of branching) of intertidal algae significantly alters the sub-canopy microclimate (i.e., temperature, humidity and light regimes) and that the relationship between morphology and microclimate is not affected by seasonal fluctuations in climate or inter-seasonal variations in algal morphology (e.g., *Spartina anglica*, van Hulzen et al. 2007; *Mastocarpus* spp., Jorve 2008).

Unexpectedly, we found that, despite marked structural differences between northern and southern canopies (Zardi et al. 2015), their habitat-modifying abilities did not differ significantly. This indicates that the southern compact, bushy

specimens (short and wide) that form dense canopies do not compensate for the more severe impact of climate experienced at the rear edge of the species' distribution. This is critical for understanding range contraction at the southern edge, where the distribution of intertidal fucoids is limited by low recruit survivorship (Ladah et al. 2003). There, thermal stress is both harsher than in northern locations and conditions are deteriorating due to a warming climate (Nicastro et al. 2013).

It is still unclear whether the unique morphologies and densities displayed at the rear edges of species distributions are the result of adaptation or phenotypic plasticity, so that the evolutionary significance of these differences is unclear (Merilä and Hendry 2014). Morphological traits could solely mirror non-adaptive variation caused by distinct environmental conditions and, thus, micro-habitat modification would simply be a non-adaptive by-product. Alternatively, diverse morphotypes would allow higher tolerance of specific environmental conditions and moderation of environmental



**Fig. 6** Sheltering indexes for (a) humidity, (b) temperature and (c) light intensity (PAR) at northern and southern morphotypes

conditions could be viewed as a direct consequence of extended phenotypes that increase the fitness of the canopy-forming species (Dawkins 1982; Wright and Jones 2006). Whatever the driver of local morphotypes, a large reshuffling of species' distributions (contraction and expansion) and abundances has occurred along shores inhabited by rear-edge *F. guiryi* (e.g.,

Lima et al. 2007; Lourenço et al. 2012; Nicastro et al. 2013; Rubal et al. 2013; Assis et al. 2014). A more extensive understanding of how trailing edge morphologies do or do not alter the environment's moderating effects of species such as *F. guiryi* is important for predicting how the impact of contemporary climate change may lead to cascading effects on the associated ecosystem.

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#### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflicts of interest.

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