BIODIVERSITY RESEARCH

Taking the heat: distinct vulnerability to thermal stress of central and threatened peripheral lineages of a marine macroalga

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ABSTRACT

Aim Although many studies have reported the effects of climate change on species' distributions, most of them consider each species as a physiologically homogenous unit. However, different lineages or populations inhabiting distinct bioregions within a species' distributional range can retain unique genetic diversity that could result in distinct adaptive capacities. A recent, large, climate-correlated distributional range contraction occurred at the southern edge of the intertidal macroalga *Fucus vesiculosus*, causing loss of genetic diversity unique to the southern clade. We tested for differential selective constraints and signs of local adaptation to thermal stress in the two genetic lineages.

Location Iberian Atlantic shores.

Methods We performed a series of common garden experiments and a field reciprocal transplant.

Results In the laboratory, southern *F. vesiculosus* showed higher resilience to heat stress than northern individuals. On the southwest coast of Portugal, local individuals grew more than those transplanted from the northern range; in the north of Portugal, growth rates did not differ significantly between lineages.

Conclusions We present evidence for unique adaptive traits at the retreating edge of the species' distribution that could be lost if warming trends persist. The loss of the distinct southern genetic heritage could end potential ongoing diversification or speciation processes and impoverishes the adaptive potential of the species as a whole.

Keywords
climate change, *Fucus vesiculosus*, rear-edge.

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INTRODUCTION

Global patterns of species distribution and abundance are strongly influenced by climate (Hoegh-Guldberg & Bruno, 2010; Burrows *et al.*, 2011; Poloczanska *et al.*, 2013). Climate-related range shifts have been documented in various terrestrial and marine species (Sorte *et al.*, 2010, 2011; Chen *et al.*, 2011), including extensions of the leading edges at higher latitudes and/or contractions of the rear trailing edges of species distribution ranges (e.g. Perry *et al.*, 2005; Sorte *et al.*, 2010; Fernández, 2011).

Genetic and phylogeographic consequences of millennial-scale climate oscillations have been assessed in several studies (Hewitt, 2004; Hampe & Petit, 2005). However, while many studies have examined the effects of ongoing climate change on biodiversity, most consider species as homogenous units, therefore missing the importance of intraspecific genetic and phenotypic variation.

For species with geographically homogeneous genetic diversity, the impact of range contraction does not depend on which portion of the species distribution range is lost (Ehrich *et al.*, 2007; Alsos *et al.*, 2012). In contrast, in species

with geographically structured genetic diversity, the attention to genetic divergence below the species level is important. For example, distribution margins at lower latitudes, which acted as past refugia preserving species through multiple glacial cycles, are often inhabited by populations that harbour the majority of species genetic diversity (reviewed in Hewitt, 2004; Hampe & Petit, 2005). Such low-latitude populations are often considered more vulnerable to warming than central populations because of the warmer environment they experience (Hampe & Petit, 2005). Consequently, risks of extinction in trailing populations facing the immediate threat of climate change at low latitudes (e.g. Nicastro *et al.*, 2013; Neiva *et al.*, 2015) or lower elevation limits (e.g. Rubidge *et al.*, 2012) expose species to the potential loss of unique pools of genetic diversity. However, recent studies highlighting the effects of local adaptation and phenotypic plasticity on forecasts of climate-driven range shifts have shown that edge and central populations can be equally sensitive to warming (Valladares *et al.*, 2014; Bennett *et al.*, 2015).

Despite accumulating evidence that the maintenance of genetic diversity is critical to the persistence of populations and the adaptive potential of the species (e.g. Reed & Frankham, 2003; Zardi *et al.*, 2015a), whether, and to what degree, range contractions and consequent loss of genetic diversity affect the overall adaptive potential of species remains a challenging question that is largely unexplored.

In this study, we selected the intertidal macroalga *Fucus vesiculosus* as an ideal model species to test the general hypothesis that climate-driven extirpation of characteristics unique to trailing edge populations hampers the species' adaptive potential against stressful environments. *F. vesiculosus* is a canopy-forming bioengineer abundant along northern Atlantic shores. Over the past 30 years, this species has suffered a remarkable contraction of the southern range edge along eastern Atlantic shores, with a northward latitudinal shift of approximately 11° consistent with recent sea surface temperature (SST) warming (Nicastro *et al.*, 2013). Species distributional modelling has identified extreme SST (maximum summer and minimum winter temperatures) as the most relevant environmental predictor for the distribution of this species (Assis *et al.*, 2014). Importantly, the assessment of extant and extinct (previously sampled) populations indicates that genetic diversity is geographically structured in this species and two lineages are distinguishable along this stretch of coast with putatively neutral (microsatellite) markers (Nicastro *et al.*, 2013; Assis *et al.*, 2014), 13 protein coding genes (Canovas *et al.*, 2011a) and 35 SNP markers (Canovas *et al.*, 2011b). This rapid range shift has resulted in severe genetic erosion caused by the extinction of most of the populations comprising the southern genetic lineage (Nicastro *et al.*, 2013).

We tested for signs of local adaptations between the northern Iberian lineage (hereafter N lineage) and the nearly extinct clade at the trailing edge of the species distribution (hereafter S lineage). To this end, we carried out an interlineage field transplant experiment, complemented with records of thermal profiles in each region, and performed a laboratory common garden experiment to evaluate lineage resilience to thermal selective constraints.

METHODS

Study area

The Atlantic Iberian coastline is characterized by a strong north-to-south gradient of increasing water and air temperature, which is persistent throughout the whole year (Lima & Wethey, 2012; Zardi *et al.*, 2015b). Notably, over the last three decades, coastal water temperatures have increased significantly along the entire coastline, averaging 0.20 °C/decade (Nicastro *et al.*, 2013). For the laboratory common garden and field transplant experiments, four estuarine sites were selected along the west coast of the Iberian Peninsula. From northern Portugal northwards, *F. vesiculosus* occurs both on the open coast and in sheltered habitats (estuarine and coastal lagoons). From northern Portugal southwards towards Morocco, it comprises a distinct genetic lineage (Nicastro *et al.*, 2013) and occurs only in estuaries and coastal lagoons (Ladah *et al.*, 2003). Estuarine sites were chosen to minimize habitat variation between lineages. Environmental conditions (salinity, water temperature, depth and sediment composition) can vary considerably in west Iberian estuaries; however, a clear latitudinal thermal gradient exists in estuaries, mirroring that on the open coast (e.g. Cabral *et al.*, 2007). Additionally, intertidal sites inhabited by *F. vesiculosus* within Portuguese estuaries are largely marine dominated (Zardi *et al.*, 2015b). In general, they are characterized by smaller amplitude thermal fluctuations compared to the open coast. However, importantly, *in situ* measurements along the intertidal distributional range of *F. vesiculosus* have shown that air and water temperatures do not differ significantly between the open coast and estuaries (Zardi *et al.*, 2013).

Two sites were within the distributional range of the N *F. vesiculosus* lineage and two within that of the S lineage (Fig. 1a). The N sites were Redondela (VG; 42°17′16.83″ N, 8°37′25.15″ W) in the Redondela river estuary (Vigo) and Viana do Castelo (VC; 41°41′5.37″ N, 8°49′57.08″ W) in the Lima River estuary. The S sites were Carrasqueira (CS; 38°24′46.73″ N, 8°45′26.23″ W) in the Sado River estuary and Alcochete (AL; 38°45′29.49″ N, 8°57′33.27″ W) in the Tejo River estuary. All of these sites are mudflats where *F. vesiculosus* is abundant, attached to rock or hard debris throughout the mid-intertidal.

Field experiment

Non-reproductive juvenile individuals, average length of 5.4 ± 1.5 cm, were used in the field transplant experiment. Individuals were tagged using lightweight tags carrying a unique sequence of colour-coded beads threaded onto dental floss. The experiment was performed following a reciprocal transplant design with *n* = 20 for each treatment at
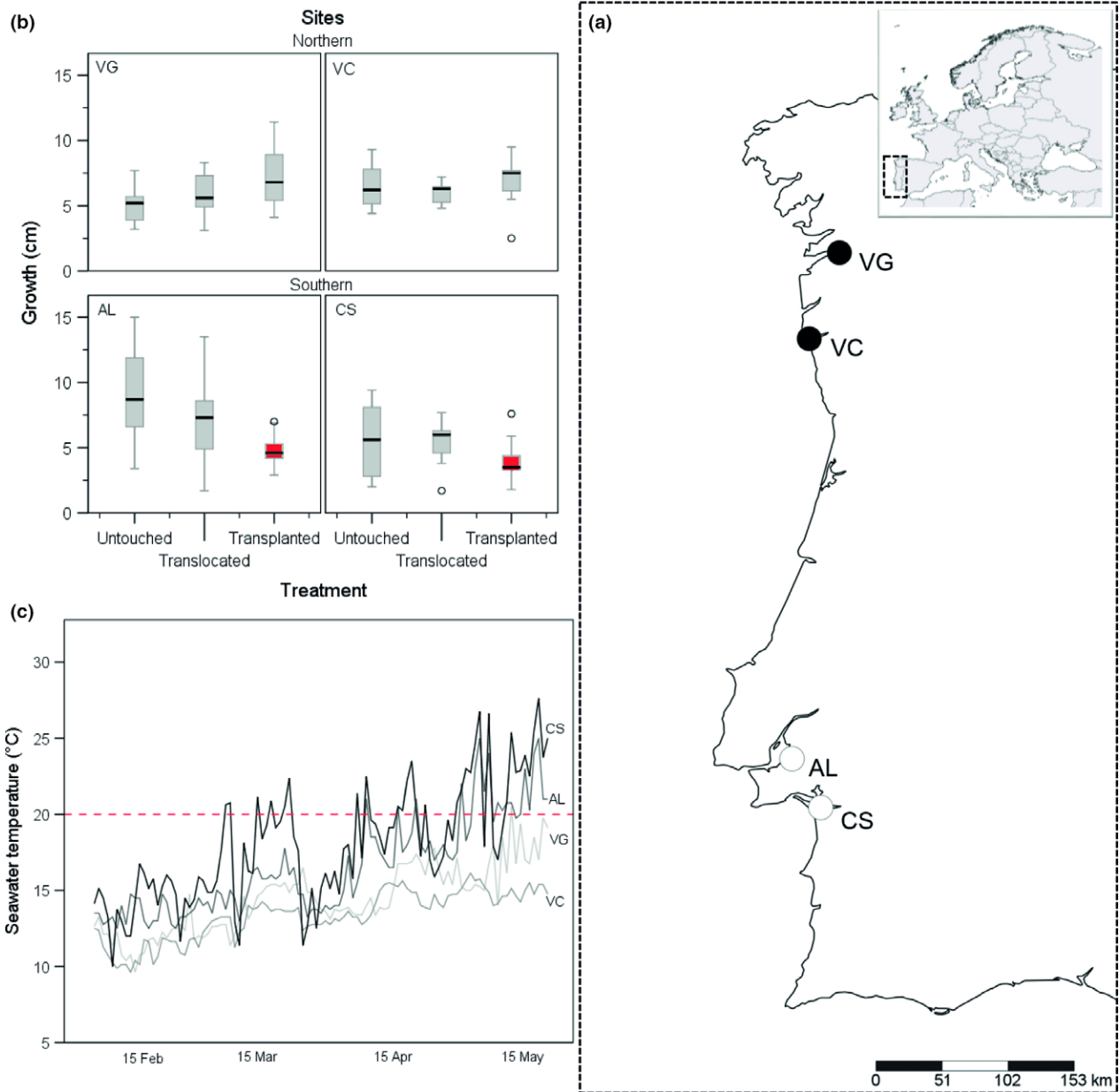
Figure 1 Field experiments. (a) Map of the study area with codes for sites generated using SimpleMappr (http://www.simplemappr.net), northern and southern locations in black and white circles. (b) Growth rates recorded at end of the reciprocal transplant experiments (n = 10, 7, 13 and 9 for VG, VC, AL and CS, respectively); in red, the treatment that was significantly different across pairwise comparisons. (c) Daily seawater temperature series, to illustrate the thermal range recorded at each site during transplant experiments.

each site: individuals transferred beyond the distributional range of that lineage (Transplant, S to N region and N to S region), individuals transferred within the distributional range of a lineage (Translocation, control for manipulation and relocation effects) and individuals that were left undisturbed (Untouched; unmanipulated control). A small portion of the substratum to which each individual was attached was carefully removed using a chisel and affixed to solid substrate at the host site with a fast-curing epoxy compound (Z-Spar Splash Zone Compound, Underwater Epoxy Putty, A-788). The host substratum was cleaned of

natural biological cover and mud prior to gluing and was selected among local *F. vesiculosus* patches (average density per m²: 302 ± 113). All individuals were cleaned of epibionts before being deployed in the field. After an *in situ* acclimation period of 2 weeks, the initial maximum length (i.e. from the holdfast to the furthest apex) of each experimental individual was measured. After 15 weeks (from 1 February 2014 to 17 May 2014), growth rates were calculated for each individual as the difference between initial and final maximum length. The experiment covered the period of maximum growth in individual length and

biomass for *Fucus* spp. in this region (Zardi *et al.*, 2015b). During summer, at these experimental locations, *Fucus* spp. do not show any significant growth and often, receptacles shrinkage and tissue breakage caused by the combined effects of desiccation and hydrodynamic stress result in negative growth (Zardi *et al.*, 2015b).

Temperature profiles during the experiment were measured for each site; temperature was monitored at 2 h intervals using data loggers (iButtons®, Maxim Integrated Products; Dallas Semiconductor, San Jose, CA 95134, USA, $n = 4$ per site), encased in plastic bottle caps, sealed with silicone sealant and glued to hard substrata using the same epoxy compound employed for the transplant experiments. Due to the loss of two loggers in AL, the values of two loggers from the other sites were randomly removed to have a balanced design. Temperature data obtained were averaged between loggers at each site. Seawater temperatures were obtained by selecting the closest value to the peak of daytime high tide (tides.mobilegeographics.com). When two tides occurred during daytime, the last tide of the day was selected.

Common garden experiments

At each experimental site, adult algae were collected and transported to the laboratory in cool boxes within 72 h. Non-reproductive apical tips were cut and acclimated for 10 days at a temperature of 13 °C, 100% humidity and in darkness. This is necessary to maintain the tissue in a healthy state (KRN pers. obs.). Two days prior to the stress experiment, tips were placed in closed 10 L tanks with filtered sea water (daily replaced; salinity $34 \pm 1‰$) under low photosynthetic photon flux density (low PPFD: 100–150 µmol m^{-2} s^{-1}) at 13 °C (average minimum seawater temperature recorded by *in situ* loggers).

Acclimated algae were exposed to four seawater temperatures under high photosynthetic photon flux density (high PPFD: 350–500 µmol m^{-2} s^{-1}, the average light regime experienced within *F. vesiculosus* canopies) for 3 h: 28, 33, 35 and 38 °C in a temperature-controlled reach-in chamber (Fitoclima 700 EDTU; Aralab, Lisbon, Portugal). These temperatures are representative of those commonly experienced by *Fucus* spp. in Portuguese mudflats, and previous studies, assessing thermal stress in fucoids, have shown that heat shock resilience is significantly impaired over this range of temperatures (Pearson *et al.*, 2009; Mota *et al.*, 2015). The length of stress exposure included a thermal ramping from 13°C to the target temperature with 15 min steps at 18, 23, 28, 33, 35 and 38 °C (± 0.5 °C). Controls were manipulated similarly to heat stress treatments but left at the acclimation temperature (13 °C). After the stress experiment, algae were returned to acclimation conditions to recover. To estimate post-stress recovery rates, the photoinhibition of PSII maximum quantum yield (F_v/F_m) was measured with a photosynthesis yield analyzer (Waltz, MINI-PAM-II) and used as a proxy for physiological performance. The F_v/F_m ratio is a measure of the relationship between the capacity for photochemical quenching $[F_v = (F_m - F_o)]$ and the total fluorescence emission of closed PSII reaction centres (F_m), and it is directly proportional to the quantum efficiency of PSII photochemistry (Butler & Kitajima, 1975). In brown algae, maximum F_v/F_m ratio values are usually between 0.7 and 0.8 and are reduced under stress (Bischof *et al.*, 1999). F_v/F_m values were measured immediately after stress (no recovery) and after 2 and 24 h of recovery using independent samples of tips for the three recovery periods ($n = 12$ per treatment per recovery period).

Data analyses

Data were processed using the ANOVA module in the IBM SPSS Statistic software suite (IBM Corp., Armonk, New York, USA), or with PERMANOVA stand-alone software (Anderson, 2001, 2005), when the ANOVA assumptions of homoscedasticity and normality (tested using Levene's test and the Shapiro–Wilk test, respectively) were not met even after transformation. Significant interactions or main effects with multiple levels were further explored with a *post hoc* Student–Newman–Keuls (SNK) test or pairwise tests when a PERMANOVA was used. The α-values in the pairwise test were adjusted using Bonferroni correction to reduce type I errors in multiple comparisons.

PERMANOVA analyses were run with 9999 permutations using Euclidean distances without restrictions on the permutation of raw data. To estimate the significance of this statistic, we used a Monte Carlo (MC) test, which is preferred when the number of unique permutations is low (Anderson, 2001, 2005). Pairwise comparisons were performed for significant factors. Not all individuals were recovered at the end of the field experiment, either because tagged individuals washed away or because the tag was lost or destroyed. To account for different sample sizes, datasets were balanced by randomly removing data to adjust sample sizes within each site (i.e. a sample size of 10, 7, 13 and 9 for VG, VC, AL and CS, respectively; implemented in SPSS). At each site, growth data were analysed with treatment (Transplanted, Translocated or Untouched) as a fixed factor.

For the common garden experiment, a series of analyses were carried out to determine the threshold at which recovery values were different from the control treatments for each lineage at each recovery time, with Temperature (13, 28, 33, 35 38 °C) as a fixed factor and Population (site 1, site 2) as a nested random factor. Outliers were removed prior to the analyses if their *z*-scores were above 3.5 (Barnett & Lewis, 1994).

RESULTS

Field experiment

There were no significant differences in growth rates among treatments in either of the two northern sites, VG (Untouched VG, Translocated VC, Transplanted CS; *P*(mc) > 0.05) and

VC (Untouched VC, Translocated VG, Transplanted AL; P(mc) > 0.05; Fig. 1b).

In contrast, there were significant effects of treatment at both southern sites, where transplanted northern individuals fared less well than southern lineage individuals. At AL, transplanted N Iberian lineage individuals (Transplanted VC) had significantly lower growth rates than S Iberian lineage individuals (Untouched AL or Translocated CS), with no significant difference between S Iberian individuals (Untouched = Translocated, Transplanted < Untouched or Translocated, P < 0.01 for all pairwise comparisons). Similarly, at CS, transplanted N individuals (Transplanted VG) had significantly lower growth rates than S Iberian lineage individuals (Untouched CS or Translocated AL), again with no significant differences among S Iberian lineage individuals (Untouched = Translocated, Transplanted < Untouched or Translocated, P < 0.05 for all pairwise comparisons).

Over the study period, the average seawater temperature recorded at CS was 18 °C, with a maximum peak of 27.6 °C, while temperatures regularly exceeded 20 °C from mid-April onwards (Fig. 1c). At AL, the average water temperature recorded was 16.5 °C, with a maximum of 25 °C, while temperatures reached regularly 20 °C in May.

In VG, average water temperature over the study period was 14.4 °C, with 1 day of 20.5 °C (maximum value recorded) in mid-May. In VC, average seawater temperature was 13.3 °C with a maximum value of only 16.1 °C; temperatures here never reached 20 °C.

Common garden experiments

Immediately after the stress (0 h; Fig. 2), there was a significant decrease in physiological performance from control values at 33 and 38 °C for N lineage individuals and only at 38 °C for the southern lineage algae [P(mc) < 0.01 in all cases]. After 2 h of recovery, the physiological performance of algae stressed at 38 °C was significantly lower than that of controls for both lineages [N lineage: P(mc) < 0.01; S lineage P(mc) = 0.001].

After 24 h of recovery, physiological performance was lower relative to control conditions for stressed northern lineage individuals at 33, 35 and 38 °C [P(mc) < 0.01], while for southern lineage individuals, the effect was significant only at 38 °C [P(mc) < 0.01].

DISCUSSION

Two main conclusions can be drawn from our study: (1) the southern lineage of *F. vesiculosus* is physiologically more tolerant of high seawater temperatures than the northern lineage and (2) the species shows signs of asymmetric, local adaptation with S lineage populations adapted to local environmental conditions at the retreating front of the species' distribution. Our results have far-reaching implications, as the loss of the rear-edge component of the species' genetic background could possibly hamper the adaptive potential of the species as a whole.

The importance of seawater temperature in setting distributional limits of intertidal species is a recurrent subject in the literature (e.g. Breeman, 1988; Lima *et al.*, 2007; Fernández, 2011; Smale & Wernberg, 2013). For a wide variety of taxa, it has been shown that SST is the most relevant environmental predictor over large spatial scales (e.g. Rivadeneira & Fernández, 2005; Jones *et al.*, 2010; Martínez *et al.*, 2012; Teske *et al.*, 2013; Assis *et al.*, 2014, 2015; Lourenço *et al.*, 2016). When submersed during high tide, the body
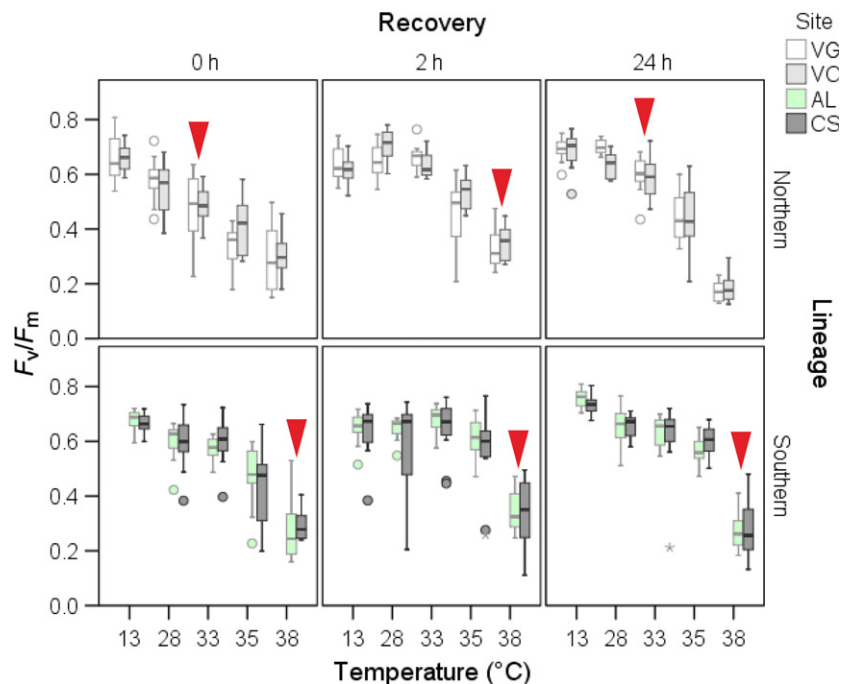

Figure 2 Common garden experiments. Box plots of photoinhibition of PSII maximum quantum yield measurements of acclimated algae exposed to four seawater temperatures under high photosynthetic photon flux density (high PPFD: 350–500 μmol m^{-2} s^{-1}) for 3 h followed by 1, 2 and 24 h of recovery (n = 12). Red arrows indicate the threshold at which recovery values were significantly different from the control treatments for each lineage at each recovery time. Site codes as in Fig. 1.

temperature of intertidal organisms is largely dictated by water temperature; in contrast, thermal conditions during low tide can be mediated by organismal traits (e.g. physiology, behaviour; Nicastro *et al.*, 2012) and/or habitat heterogeneity (e.g. shading, crevices; Fuller *et al.*, 2010; Nicastro *et al.*, 2010).

A species distribution modelling (SDM) approach applied to *F. vesiculosus* identified long-term average SST in the hottest and coldest months as the best predictors for the species' present range (Assis *et al.*, 2014). Here, we show that the biogeographic role of near-shore water temperature gradients is also relevant at the subspecific level and might be relevant in delineating the geographic distribution of intraspecific lineages.

Atlantic Iberian shores are characterized by a sharp north-to-south increase in SST (e.g. Lima *et al.*, 2007; Assis *et al.*, 2013; Zardi *et al.*, 2015b), and our *in situ* temperature loggers confirmed a strong dissimilarity in temperatures between the sites where the two lineages are found, with the differences between northern and southern sites being most pronounced during warm periods. Southern populations experienced the highest water temperatures, reaching nearly 28 °C on multiple days. The highest values recorded at the northern sites were 20 °C, while temperatures at the southern sites frequently exceeded 20 °C, particularly in the second half of the recordings (from May 2015).

Reciprocal transplant experiments detected asymmetric local adaptation. At the end of the field transplant experiments, we recorded lower growth rates in the N lineage transplants compared to indigenous and translocated individuals of the S lineage at sites located within the distributional range of the S lineage, while no difference in lineage performance was observed at locations within the distributional range of the N lineage. Seaweed growth is known to be affected by several climatically sensitive variables including temperature and desiccation (Davison & Pearson, 1996); stressful thermal conditions result in cellular and subcellular damage and significant metabolic costs in terms of reallocation of resources for repair (such as heat stress proteins production; Pearson *et al.*, 2009). These non-trivial energetic constraints reduce growth and reproduction, and thus fitness, and can eventually lead to mortality (e.g. Davison & Pearson, 1996). SST and air temperatures at southern locations during the experimental period (February–May) are comparable to those occurring at northern sites during summer (Zardi *et al.*, 2015b). Future surveys assessing growth rates at different locations over longer periods will be critical to further understand the implications of our findings under warming scenarios. For example, phenology is affected by environmental changes and several studies have reported climate-induced phenological shifts (Menzel *et al.*, 2006). In fucoid seaweeds, higher temperatures have strong effects on phenological events and trade-offs between life history traits. Specifically, *Fucus* spp. show lower reproductive investment and smaller size at maturity when facing high water and air temperature (Martínez *et al.*, 2012; Zardi *et al.*, 2015b).

Range margins often coincide with ecological margins; thus, species are expected to reach the limits of their environmental tolerance at a range boundary. Marginal populations are often small, fragmented and subjected to both loss of genetic diversity by drift, which reduces adaptive potential, and to high selective pressure that promotes the development of unique phenotypic and genetic traits (Kawecki, 2008). However, more recent studies stressing the importance of local adaptation have challenged this paradigm, indicating that sensitivity to warming does not necessarily follow latitudinal, edge-centre patterns (Valladares *et al.*, 2014; Bennett *et al.*, 2015); populations' thermal safety (defined in Bennett *et al.*, 2015 as 'the temperature buffer between an organisms upper thermal-tolerance limit and the maximum ambient temperatures it experiences') and climate vulnerability can be similar among all populations. Observational studies or common garden experimental approaches have suggested that, in similar intertidal systems, the balance between these two (opposing) effects can result in either maladaptation or local adaption of marginal populations (Pearson *et al.*, 2009; Araújo *et al.*, 2011; Jueterbock *et al.*, 2014). Our findings suggest that these trailing edge populations are locally adapted to conditions at the southern species margin, although longer-term studies, preferably involving progeny from controlled crosses, are required to confirm this and exclude the possibility that environmental history influences individual performance. However, there is evidence that developmental plasticity and maternal environmental effects are not determinant in shaping phenotypic differentiation across steep environmental gradients in fucoids; reciprocal transplants and laboratory trials have highlighted the critical role of genetic mechanisms (i.e. local adaptation) in generating phenotypic differences (e.g. physiological tollerance; Hays, 2007).

Comparative common garden experiments reinforced the conclusions of field experiments by detecting differences in physiological resilience between lineages exposed to high seawater temperatures. While both lineages recovered similarly from temperatures up to 33 °C, the N lineage displayed lower recovery rates than the S lineage at 35 and 38 °C. Although the temperatures used in the common garden experiments were higher than those recorded by spring *in situ* data loggers, *F. vesiculosus* is exposed to high temperatures comparable to those used in our laboratory experiments regularly in warmer months. For example, these temperature extremes have been recorded frequently in southern mudflats, during warm summer days, when the temperature of water in shallow channels or at the interface between air and mud often exceeds 36 °C (Mota *et al.*, 2015).

Over the last three decades, SST along north-east Atlantic shores has increased significantly and steadily, affecting the distributions of several marine species (e.g. Lima & Wethey, 2012; Neiva *et al.*, 2015; Lourenço *et al.*, 2016), including *F. vesiculosus*. In particular, a dramatic range contraction of the S lineage of *F. vesiculosus* has occurred, with a latitudinal reduction of more than 1200 km from southern Morocco to

central Portugal (Nicastro *et al.*, 2013). Presently, the S lineage, which is at the rear edge of the species' distribution, is represented by only a few isolated populations constrained within two degrees of latitude (Nicastro *et al.*, 2013). The disappearance of *F. vesiculosus* populations from extensive stretches of coastline is likely to have direct ecological consequences. The ecosystem engineering abilities of this habitat forming species affect coastal species richness by increasing spatial complexity (Fogel *et al.*, 2004; Hastings *et al.*, 2007). Thus, its large-scale loss may modify and reduce ecosystem structure, and the diversity and abundance of associated species (Duarte *et al.*, 2015), with knock-on effects extending to multiple trophic levels.

More important, however, may be the longer-term consequences. The loss of marginal populations from the low-latitude edge of a species' range could have significant genetic and evolutionary implications (Hampe & Petit, 2005; Rubidge *et al.*, 2012). Indeed, the results of our laboratory and field experiments indicate that this extensive climate-induced range contraction threatens unique portions of the species' genetic pool, possibly crippling its adaptive potential. Future climate scenarios predict a generalized warming of SST throughout the globe, including of the eastern Atlantic coastline. Abundant experimental and theoretical evidence indicates that the short-term adaptive potential of many organisms is unable to endure the rapidly increasing pressure of contemporary climate changes (Parmesan, 2006; Sinervo *et al.*, 2010), although it is also possible that genetic variation and epigenetic changes may help populations to adapt (Munday *et al.*, 2013 and references therein). The recent loss of most of the S lineage indicates that the adaptive limits of southern populations have already been exceeded. Indeed, during summer, seawater temperatures at the southern range expose *F. vesiculosus* to prohibitively damaging thermal conditions resulting in chronic heat stress without the possibility of recovery (Mota *et al.*, 2015). The loss of genetic diversity through the elimination of a southern lineage with unique, locally adapted physiological properties reduces the adaptive potential of the species as a whole and threatens its potential for recovery from the effects of extensive environmental change.tcaps 0

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