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Response of kelps from different latitudes to consecutive heat shock

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ABSTRACT

Although extensive work has focused on kelp responses to constant temperature, little is known about their response to the consecutive temperature shocks they are often exposed to in the shallow subtidal and intertidal pools. Here we characterized the responses of the two southernmost forest-forming kelp species in the Northeast Atlantic, *Laminaria ochroleuca* De La Pylaie and *Saccorhiza polyschides* (Lightf.) Batt. to multiple cycles of thermal stress. Individuals from the upper vertical limit of the geographical distribution edges where the two species co-occur forming forests, France and Portugal, were exposed to 4 consecutive cycles of thermal shock simulating a spring tide. A 24 h cycle consisted of culture at 15 °C, plus 1 h heat shock at one of five levels (20, 22.5, 25, 27.5 or 30 °C). The maximum quantum yield (Fv/Fm) of chlorophyll fluorescence of photosystem 2 (PS2) was used to detect impaired reaction center function, as a proxy for individual fitness costs, during recovery from heat shock. Both species showed resilience to temperatures from 20 to 25 °C. While exposure to 27.5 °C caused no inhibition to Fv/Fm of *S. polyschides*, a threshold was met above this temperature and exposure to 30 °C caused the death of all individuals. In contrast, *L. ochroleuca* from France was damaged but able to survive 30 °C shocks and individuals from Portugal showed complete resilience to this treatment. In both species, blade elongation decreased with increasing temperature, with necrosis surpassing growth at higher temperatures. Resilience to high temperature exposure may confer an advantage to *L. ochroleuca* to colonize intertidal pools on the Portuguese coast, in agreement with the observation that both species recruit in tide pools but only *L. ochroleuca* reach adulthood. Our results indicate that as summer temperatures increase with climate change, the disappearance of *S. polyschides* from intertidal pools and a decrease in the density of *L. ochroleuca* can be expected.

1. Introduction

Temperature is a major factor influencing species geographical distribution, and has increased over the last decades due to anthropogenic pressure (Hampe and Petit, 2005; IPCC, 2007). Since 1980, mean sea surface temperature increased by 0.2–0.3 °C per decade in southern Europe, and by 0.3–0.7 °C in the Norwegian and North seas (Lima and Wethey, 2012). Moreover, projections indicate that warming rates may increase further in the coming decades (IPCC, 2007). These changes have the potential to cause local extinctions and poleward distribution shifts for several species (Hampe and Petit, 2005; Hiscock et al., 2004; Wernberg et al., 2010), as has been observed for several species of plankton (Beaugrand and Reid, 2003), gastropods (Mieszkowska et al., 2006), fish (Sabatés et al., 2006) and macroalgae (Nicastro et al., 2013), including kelps (Díez et al.,2012; Fernández 2011; Müller et al., 2009; Tuya et al., 2012; Voerman et al., 2013). However, just as terrestrial species' distribution shifts often occur in altitude (Franco et al., 2006; Kelly and Goulden, 2000), on marine shores the effects of climate change may be first observed in local species distribution on the shore, before geographical shifts are perceived (Cheung et al., 2009; Pehlke and Bartsch, 2008). Species populating shallower areas such as the intertidal and upper subtidal will be the first to experience the effects of global warming, as they're more exposed to temperature extremes, UV and excessive light, desiccation and osmotic stresses, and are more exposed to storm-induced wave surge. Indeed, intertidal species have been reported to suffer shifts in their geographical distribution faster than most terrestrial species (Helmuth et al., 2002). To persist as extreme environmental conditions become more frequent, populations will have to adjust to the new conditions and compensate for the elevated losses typical of populations near distributional boundaries (Guo et al., 2005). As such, the resilience of recruits and early stages to repeated cycles of heat shock is likely to be a determining factor in persistence of populations in the intertidal.

Kelps are habitat structuring species. They modify the area they populate, its environment and resources, and are fundamental for the

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survival of several other species (Bruno et al., 2003; Wernberg et al., 2010). Thus, variations in kelp species composition, size and canopy density will impact ecological and oceanographic processes. Although extensive work has been done on the temperature limits of kelp species (Bolton and Lüning, 1982; Fortes and Lüning, 1980; Izquierdo et al., 2002; Pang et al., 2007; Pereira et al., 2011; tom Dieck, 1993), nothing is yet is known about their ability to cope with consecutive cycles of stress exposure associated with low tides. In this study, we aimed to recreate the conditions experienced by recruiting individuals during typical summer spring tides, where individuals may be exposed daily to repeated cycles of thermal stress during low tides, and which may be decisive for population persistence. Experiments were performed to compare the two southernmost kelp-forest species in the Northeast Atlantic: *Laminaria ochroleuca* and *Saccorhiza polyschides*. Since, as reported for several species of animals and plants, individuals from different latitudes may be locally adapted or acclimated to different conditions (Liu and Pang, 2010; Zippay et al., 2010), we compared the responses of individuals from the higher and lower latitude ranges where these two species coexist: Brittany, France and Northern Portugal. The results of such experiments can provide clues as to whether temperature is likely to be a decisive factor influencing the distribution, persistence and composition of these populations in the near future.

2. Material and methods

2.1. Model species and collection

L. ochroleuca and *S. polyschides*, a perennial and an annual species, respectively, are two important Northeast Atlantic species. They both have their southernmost populations in isolated spots in the upwelling region of west Morocco and some very deep areas in the Mediterranean and Atlantic seamounts and islets, south of their coastal distributional range which ranges from the Portuguese coast to Brittany (France), and the English and Bristol Channels (Birkett et al., 1998; Braud, 1974; Lüning, 1990; Norton, 1977; Titley and Neto, 2000; Van den Hoek, 1982). *S. polyschides* has a wider northern distribution, found as far north as the west coast of Norway.

Sporophytes of the two species have similar upper temperature limit of around 24 °C (Birkett et al., 1998; Norton, 1977). Although no records of lower temperature limits were found for either species, at their northern distribution limit average winter sea surface temperatures (SST) are 4 °C and 10 °C, for *S. polyschides* and *L. ochroleuca* respectively (Braud, 1974; Norton, 1977). Moreover, these two species have an overlapping range of optimum temperatures. *L. ochroleuca* is described as growing better between 15 and 18 °C, while *S. polyschides* seems to perform better at temperatures from 10 to 17 °C (Biskup et al., 2014, Izquierdo et al., 2002; Norton, 1977). As such, despite their distinct life strategies, the two species have overlapping niches and are potential competitors.

This study is focused on the distributional range where the two species overlap, from northwest Iberia to the English Channel. Recruits of *L. ochroleuca* and *S. polyschides* ca. 15 cm length were collected near the northern distribution limit of *L. ochroleuca*, in Brittany, France (48°41′55.26″N 3°56′28.50″W), and in Northern Portugal (41°42′27.80″N 8°51′45.30″W), the southern distribution limit where both species are able to form forests. In Brittany, the vertical distribution of both species extends as high as the upper subtidal, being out of water only during the lowest spring tides of the year. In Northern Portugal they can be found in tidal pools and although their base is usually immersed, their blades may get exposed during spring tides. In both areas, collections were made in the upper distribution limit and were transported in cold seawater inside refrigerated boxes. In Brittany, samples were collected on the 13th of July 2011, arriving in the lab within 48 h of collection. In Northern Portugal, collections were made on the 29th of March 2012, reaching the laboratory within 12 h of collection. Experiments were done at slightly different times of the year to coincide with the recruitment peak of each area. Average SST during the month prior to collection was 14.1 °C in Brittany and 13.3 °C in Northern Portugal (Aqua MODIS SST, NASA). The same protocol and experimental conditions were used for both populations.

2.2. Experimental design

Immediately upon arrival, each individual was placed in 0.5 L individual tanks with 0.2 μm filtered seawater (FSW) and aeration at 15 °C for 5 days of acclimation, so they could recover from eventual stress caused by collection and transportation. This temperature close to the conditions during the month of collection and small sporophytes and other microscopic forms of both species grow efficiently at 15 °C (Izquierdo et al., 2002; Norton, 1977; Pereira et al., 2011). These conditions were also used as control during the experiment. Throughout the acclimation and experimental periods, sporophytes were exposed to a 12 h day photoperiod, with a photon flux density of 40 μmol m^{-2} s^{-1} (Bruhn & Gerard 1996; Izquierdo et al., 2002). Seawater was changed every two days during the acclimation period. During the heat shock experiment this was done every day after exposure, to make sure individuals were not exposed to metabolites, as tidal flow would quickly wash them away.

Temperature tolerance of young sporophytes (5 replicates) was tested for a series of sequential 1 hour exposures to one of five temperature treatments; 22.5, 25, 27.5 or 30 °C. Unnaturally rapid warming was avoided by sequential transfer at each temperature, in a 30 min ramp, until the target temperature was reached. Exposure to the target temperature was for 1 h. Afterwards, individuals were directly transferred back to the control temperature (15 °C) to simulate the returning tide, and remained at the control temperature till a 24 h cycle was complete. This procedure was repeated for 4 cycles. Measurements were repeatedly performed on the same individual and each was daily exposed to the same target temperature.

2.3. Photosynthetic yield determination

Photosynthetic activity is considered to be one of the most heat sensitive cellular processes, both by damage to the oxygen-evolving complex in PS II, damage and rapid turnover of the D1 protein, and by impairment of recovery processes by reactive oxygen species. As such, in vivo, the efficiency of reaction center functioning (controlling electron flux for downstream processes) represents a balance between damage and repair (Allakhverdiev et al., 2008). Initial values of chlorophyll maximum quantum yield (Fv/Fm) were measured for each individual (5 replicates per treatment) under control conditions. All Fv/Fm measurements were made with a portable chlorophyll fluorometer (Junior-PAM, Walz, Germany). Individuals were dark incubated for 5 min, after which Fv/Fm measurements were made on two different areas, in the center of the blade of each individual. The mean of the two values was used in downstream analyses. Because small intrinsic differences in population- and/or location-specific Fv/Fm values can obscure subsequent statistical comparisons between species and/or populations, all Fv/Fm data were normalized as a proportion of the initial values (adjusted mean = 1). Initial Fv/Fm values were above 0.7 to make sure the conditions used were not stressful.

During each of 4 consecutive 24 h cycles, individuals were exposed to heat shock for 1 h at the target temperature, immediately after which Fv/Fm was measured. Individuals were then returned to the control temperature (15 °C) for recovery and Fv/Fm was measured again after 24 h to assess recovery. Controls remained at 15 °C throughout each cycle, but otherwise were manipulated in same way as the other treatments. The same individuals were used throughout the experiment and were always exposed to the same target temperature.