

Thermal stress resistance of the brown alga *Fucus serratus* along the North-Atlantic coast: Acclimatization potential to climate change



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ABSTRACT

Seaweed-dominated communities are predicted to disappear south of 45° latitude on North-Atlantic rocky shores by 2200 because of climate change. The extent of predicted habitat loss, however, could be mitigated if the seaweeds' physiology is sufficiently plastic to rapidly acclimatize to the warmer temperatures. The main objectives of this study were to identify whether the thermal tolerance of the canopy-forming seaweed *Fucus serratus* is population-specific and where temperatures are likely to exceed its tolerance limits in the next 200 years. We measured the stress response of seaweed samples from four populations (Norway, Denmark, Brittany and Spain) to common-garden heat stress (20 °C–36 °C) in both photosynthetic performance and transcriptomic upregulation of heat shock protein genes. The two stress indicators did not correlate and likely measured different cellular components of the stress response, but both indicators revealed population-specific differences, suggesting ecotypic differentiation. Our results confirmed that thermal extremes will regularly reach physiologically stressful levels in Brittany (France) and further south by the end of the 22nd century. Although heat stress resilience in photosynthetic performance was higher at the species' southern distributional edge in Spain, the *hsp* expression pattern suggested that this edge-population experienced reduced fitness and limited responsiveness to further stressors. Thus, *F. serratus* may be unable to mitigate its predicted northward shift and may be at high risk to lose its center of genetic diversity and adaptability in Brittany (France). As it is an important intertidal key species, the disappearance of this seaweed will likely trigger major ecological changes in the entire associated ecosystem.

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1. Introduction

1.1. Increasing thermal stress along North-Atlantic intertidal shores

Heat waves have become more frequent and extreme throughout the 20th century and are predicted to increase in the 21st century (Easterling et al., 2000; Meehl et al., 2007). On a global scale, species are responding to thermal stress with phenological changes and distributional range shifts that often involve local extinction (Hickling et al., 2006; Walther et al., 2002). The response of marine rocky intertidal species is often considered an early warning signal of climate change (Pearson et al., 2009) since they generally live close to their upper thermal tolerance limits and have low potential to respond to further rising temperatures (Somero, 2010; Tomanek, 2010). Intertidal species along North-Atlantic shores will experience up to 4 °C warmer water temperatures by the end of the 21st century (Müller et al., 2009) and a 5 to 10 times higher frequency of heat waves within the next

40 years (Barriopedro et al., 2011; Schär et al., 2004). In order to better understand the impact of increasing numbers of heat waves upon rocky intertidal shores, it is important to investigate the acclimatization potential of foundational key species (*sensu* Dayton, 1972) that play a pivotal role for the structure of the intertidal rocky-shore community.

1.2. An intertidal key species under thermal stress

The brown seaweed *Fucus serratus* provides habitat and food for a highly diverse community of species (Fredriksen et al., 2005), thus playing a key role in the Northeast-Atlantic rocky intertidal where it inhabits rocky shores from northern Portugal to northern Norway (Lüning et al., 1990). On the Northwest-Atlantic coast, *F. serratus* was introduced to Nova Scotia (Canada) 100–150 years ago (Brawley et al., 2009). A recent study predicted that *F. serratus*, together with two other macroalgal key species (*Fucus vesiculosus* and *Ascophyllum nodosum*), will disappear by 2200 from North-Atlantic shores south of 45° latitude under projected climate change (Jueterbock et al., 2013).

While the North-Iberian Peninsula is one of three putative glacial refugia where *F. serratus* survived the Last Glacial Maximum

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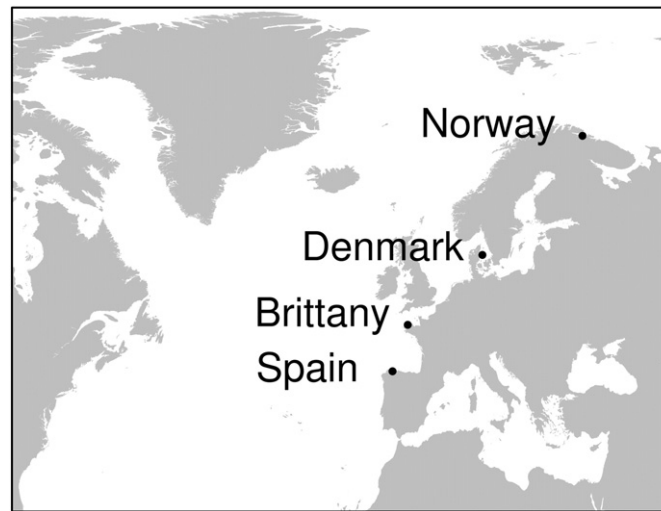


Fig. 1. Sampling sites where >30 individuals/site were collected in May/June 2011. See Supplementary material S8 for precisely mapped locations.

(18–20 kya) (Hoarau et al., 2007), its within-population genetic diversity eroded during thermally induced cycles of range contractions and expansions (Coyer et al., 2003). This may impede phenotypic plasticity and adaptive evolvability (Bijlsma and Loeschcke, 2012) and thus could explain maladaptation to warm thermal stress in northern Portugal (Pearson et al., 2009) and inhibition of growth, physiological performance (Martínez et al., 2012) and reproductive capacity (Arrontes, 1993; Viejo et al., 2011) by extreme summer temperatures in northern Spain.

In contrast, the other two refugia, Southwest-Ireland and Brittany, are hot-spots of genetic diversity (Coyer et al., 2003; Hoarau et al., 2007) and thus may be more resilient to climate change (Ehlers et al., 2008). Moreover, the low dispersal potential and small-scale genetic differentiation of *F. serratus* (Coyer et al., 2003) might favor local thermal adaptation (Hampe and Petit, 2005). Thermal acclimatization and local thermal adaptation are crucial factors to assess a species' extinction risk under climate change but the geographical patterns of these factors along the distributional range of *F. serratus* are presently unknown.

1.3. Physiological acclimatization to thermal extremes

A universal strategy of molecular acclimatization to stressful temperatures is the heat shock response (HSR), which involves the transcriptional up-regulation of heat shock proteins (HSPs). HSPs act as molecular chaperones and protect the organism from inappropriate interactions of denatured or aggregated non-native proteins (Feder and Hofmann, 1999). Some HSP forms can be used as universal stress biomarkers since their genes are highly conserved among widely disparate species and their expression level is induced by different forms of environmental stress (Feder and Hofmann, 1999). The response is, however, limited by the corresponding energetic costs and cytotoxic effects it involves (reviewed in (Feder and Hofmann, 1999; Sørensen and Loeschcke, 2007)).

Photosynthetic performance is another sensitive indicator of thermo tolerance in photosynthetic organisms, as photosynthesis is specifically sensitive to heat stress (Berry and Bjorkman, 1980). Photosystem II (PS II) was shown to be affected first, with warm temperatures negatively influencing carbon metabolism and electron transport in the photosynthetic apparatus (Berry and Bjorkman, 1980).

1.4. Objectives

The main aim of this study was to identify whether the acclimation potential of *F. serratus* could mitigate its predicted extinction from

shores south of 45° N under climate change scenarios. More specifically, we addressed three questions:

1. Is photosynthetic performance and *hsp* expression of *F. serratus* under acute heat stress population-specific, thus indicating local adaptation?
2. How is individual variation in *hsp* gene expression correlated with photosynthetic performance?
3. Where will temperatures rise over the next 200 years beyond the thermal tolerance limits of *F. serratus* and thus threaten it with extinction?

2. Materials and methods

2.1. Common garden heat stress experiments

We collected ≥ 30 adult individuals of *F. serratus* from four locations covering the species' latitudinal range of distribution (see Fig. 1 and mapped sampling sites in Supplementary material S8) during a span of four weeks in May/June 2011: 1) Kirkenes, Norway (69° 47' 24.36" N, 30° 47' 26.94" E), 2) Blushøj, Denmark (56° 10' 1.56" N, 10° 43' 57.98" E), 3) Roscoff, Brittany (48° 42' 46.71" N, 4° 1' 18.62" W), and 4) La Coruña, Spain (43° 21' 59.14" N, 8° 23' 17.51" W). The individuals were transported to the wet lab facilities of the University of Nordland in Mørkvedbukta (Bodø, Norway), placed in two aquaria (1 m × 1 m × 0.5 m, Norwegian and Danish samples in one, Brittany and Spanish samples in the other) within 1–2 days after collection, and then acclimated for >4 weeks to ca. 9 °C running natural seawater (both aquaria connected with the same water flow-through), a 16:8 h L:D cycle, and 40–70 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (OSRAM Fluora, 150 W). Common-garden heat stress experiments were conducted from July to December 2012, consisting of 4 apical tips (ca. 5 cm) cut from each of 6–10 individuals in each population. Three of the 4 tips were transferred to aquaria for 1 h in which water temperature was increased.

We applied 5 stress temperatures in 5 independent experiments with longer acclimation times for the experiments that were carried out later in the year: 1) 20 °C stress after 8 weeks of acclimation, 2) 24 °C stress after 7 weeks of acclimation, 3) 28 °C stress after 23 weeks of acclimation, 4) 32 °C stress after 7 weeks of acclimation, and 5) 36 °C stress after 8 weeks of acclimation. Temperatures ≥ 24 °C exceed the maximum *in situ* water temperatures experienced by *F. serratus*, even at its southern distribution limit (Martínez et al., 2012; Pearson et al., 2009), but *Fucus* canopy-temperatures can exceed 30 °C during summer in North-Portugal (Pearson et al., 2009). With the selected stress temperature range (20 °C–36 °C), we aimed for a forced response

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