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COMMENTARY

Coastal upwelling areas as safe havens during climate warming

Seaweeds have long been recognized as 'ecosystem engineers' and carbon sinks in coastal marine ecosystems. However, recent ocean warming has had drastic ecophysiological impacts on seaweed assemblages and hence coastal community structure (Wernberg *et al.*, 2011, 2013). Seaweeds, particularly species that prefer lower water temperatures, are facing imminent threat and will experience strong population-size reductions at low-latitude range limits (Wernberg *et al.*, 2011, 2013). If they fail to acclimatize/adapt ecophysiologically to these new stressful conditions or fail to track more suitable habitats moving poleward, they will eventually become extinct (Wernberg *et al.*, 2011, 2013). Understanding how climate change affects seaweed distribution shifts may allow for the identification of potential refugia where these species and their associated biota can retreat to and persist; this, in turn, will offer pivotal conservation insights for sustaining biodiversity.

So, is there any chance for coastal temperate species to persist in global warming scenarios, even at their low-latitude range limits? Fortunately, the answer seems to be 'yes'. In a recent issue of *Journal of Biogeography*, Lourenço *et al.* (2016) found that the brown alga Fucus guiryi G.I. Zardi, K.R. Nicastro, E.S. Serrão & G.A. Pearson persists in several upwelling areas along the coasts of southwestern Iberia and northwestern Africa where sea surface temperatures (SST) have undergone significant warming during the last decades. These southern refugia have retained distinctive genetic pools, highlighting the fundamental potential of coastal upwelling systems to maintain regional or global marine biodiversity threatened by climate change. Interestingly, a study involving both phylogeography and ecological niche modelling has indicated that the southern upwelling centres of the Canary Current were stable refugia for another temperate brown alga (*Saccorhiza polyschides* (Lightfoot) Batters) during the warmer Mid-Holocene (Assis *et al.*, 2016).

Coastal upwelling regimes are located along continental margins where equatorial winds push surface waters offshore and replace them with deeper, cold, nutrient-rich waters, enabling higher primary production and colder SST than surrounding areas (Wang *et al.*, 2015). These current systems play a crucial role in structuring the abundance and richness of pelagic plankton, and hence coastal marine ecosystems and fisheries. It has been proposed that global climate change might intensify upwelling regimes (Wang *et al.*, 2015), allowing for the persistence of localized extensions of cold water embedded in warmer coastal waters for the years ahead and leading to more drastic gradients of oceanic conditions in these regions. However, these trends are not spatially homogeneous; if upwelling is expected to effectively strengthen along the poleward portions of these currents, it could diminish along equatorial coasts (e.g. along northwestern Africa for the Canary Current; Wang *et al.*, 2015). So, while some evidence suggests that these systems could be resilient to anthropogenic climate change, their fate remains uncertain due to the large number of physical and biogeochemical factors that influence ecosystem processes (Byrnes *et al.*, 2011; Wang *et al.*, 2015).

In spite of the clear importance of coastal upwelling systems as potential refugia for marine biota facing ocean warming, little attention has been paid to the diversity and dynamics of seaweeds in these areas. On one hand, Ormond & Banaimoon (1994) reported that along the coast of southern Yemen, the maximum growth of intertidal macroalgal assemblages followed the onset of elevated nutrient levels driven by intense southern Arabian coastal upwelling. On the other hand, Leliaert *et al.* (2000) described a drastic change in seaweed community composition around the Cape Peninsula of South Africa in relationship to oceanic conditions (i.e. the Atlantic side is dominated by the Benguela upwelling system while no upwelling occurs within False Bay). Such evidence indicates that coastal upwelling systems greatly influence the diversity and biogeographical patterns of coastal marine macroalgae.

The newly published work by Lourenço *et al.* (2016) has extended our understanding of how upwelling systems have acted as climatic refugia and how these systems have influenced the evolution and biodiversity of seaweeds. Comparing historical and recently collected data of algal presence and coverage along the North Atlantic, the authors were able to confirm that the range of *F. guiryi* is shrinking and that, south of 37°N, the species has disappeared except near upwelling centres that act as cold-water refugia. Moreover, information from nine microsatellite loci shows clear genetic uniqueness of the remaining southern populations, suggesting that these southernmost populations should potentially be targeted in future conservation and management plans. One could also wonder about the possible importance of the southernmost populations for the evolutionary potential of the species. Indeed, populations of genetic variants specifically encountered in the warmer areas of the range of *F. guiryi* could potentially be undergoing adaptive evolution to ocean warming conditions. However, even if upwelling centres show certain resilience to ocean warming (Wang *et al.*, 2015; Assis *et al.*, 2016; Lourenço *et al.*, 2016), one might ask how long they will act as refugia. Are these southern refugia sufficiently stable to allow remnant populations to adapt to new climatic conditions or even only to survive until conditions become favourable again – if ever? Lourenço *et al.* (2016) reported that relict populations of *F. guiryi* are small and sparse, and processes linked to the Allee effect (i.e. negative effects of decreasing population density on fitness) or genetic drift could greatly increase this species' vulnerability to extinction. Future studies of recruitment patterns in relict populations of *F. guiryi* would be interesting considering that

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Fucus is a perennial genus and some areas where it is found could be suitable for adult survival but not for successful reproduction; these areas could be mistaken for refugia. Moreover, some non-climatic factors have also been demonstrated to impose severe ecophysiological effects on the growth, reproduction and distribution of canopying-forming *Fucus* species (e.g. Vadas *et al.*, 1992). Knowledge of the effect of these non-climatic factors is highly relevant when developing effective management and conservation plans since they may further exacerbate the effect of oceanic warming on seaweed populations.

It is yet unknown whether the patterns of rapid population shrinkage and isolation at range limits reported by Lourenço *et al.* (2016) for *F. guiryi* can be generalized to other marine organisms facing the imminent threat of global warming. Sequential field surveys and genetic studies in other major coastal upwelling systems worldwide (i.e. the California Current System, the Benguela Current and the Peru–Humboldt Current) can undoubtedly provide more insights into the role of upwelling systems in shaping seaweed populations and communities. Assessing the environmental requirements for life cycle completion in populations along entire species ranges is a prerequisite to predicting possible shift in seaweed distributions. This is also critical for characterizing the underlying linear and/or nonlinear relationships between seaweed performance and key oceanic parameters (e.g. temperature, salinity or pH) that are expected to change steadily during the 21st century (Harley *et al.*, 2012). Finally, it is essential to gather historical and current distribution records for a large number of sympatric species in order to empirically identify coastal community changes under global warming scenarios.

Zi-Min Hu[1,2]* and Marie-Laure Guillemin[3,4]*

[1]*Key Laboratory of Experimental Marine Biology, Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, China,* [2]*Qingdao National Laboratory for Marine Science and Technology, Qingdao 266071, China,* [3]*Instituto de Ciencias Ambientales y Evolutivas, Facultad de Ciencias, Universidad Austral de Chile, Valdivia, Chile,* [4]*CNRS, Sorbonne Universités, UPMC University Paris VI, UMI 3614, Evolutionary Biology and Ecology of Algae, 29680 Roscoff, France*
**E-mails: huzimin9712@163.com; marielaure.guillemin@gmail.com*

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