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European seaweeds under pressure: Consequences for communities and ecosystem functioning

Frédéric Mineur [a,b,*], Francisco Arenas [c], Jorge Assis [d], Andrew J. Davies [e], Aschwin H. Engelen [d], Francisco Fernandes [d], Erik-jan Malta [f], Thierry Thibaut [g], Tu Van Nguyen [a], Fátima Vaz-Pinto [c], Sofie Vranken [a], Ester A. Serrão [d], Olivier De Clerck [a]

[a] Phycology Research Group, Biology Department, Ghent University, Belgium
[b] School of Biological Sciences, Queen's University of Belfast, UK
[c] Interdisciplinary Centre of Marine and Environmental Research (CIIMAR), Porto, Portugal
[d] Centre of Marine Sciences (CCMAR), University of the Algarve, Faro, Portugal
[e] School of Ocean Sciences, Bangor University, Menai Bridge, UK
[f] Instituto de Investigación y Formación Agraria y Pesquera (IFAPA), Centro Agua del Pino, Cartaya, Spain
[g] Aix-Marseille University, Mediterranean Institute of Oceanography (MIO), CNRS/INSU, IRD, UM 110, Campus of Luminy, Marseille, France

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ABSTRACT

Seaweed assemblages represent the dominant autotrophic biomass in many coastal environments, playing a central structural and functional role in several ecosystems. In Europe, seaweed assemblages are highly diverse systems. The combined seaweed flora of different European regions hold around 1550 species (belonging to nearly 500 genera), with new species continuously uncovered, thanks to the emergence of molecular tools. In this manuscript we review the effects of global and local stressors on European seaweeds, their communities, and ecosystem functioning. Following a brief review on the present knowledge on European seaweed diversity and distribution, and the role of seaweed communities in biodiversity and ecosystem functioning, we discuss the effects of biotic homogenization (invasive species) and global climate change (shifts in bioclimatic zones and ocean acidification) on the distribution of individual species and their effect on the structure and functioning of seaweed communities. The arrival of new introduced species (that already account for 5–10% of the European seaweeds) and the regional extirpation of native species resulting from oceans' climate change are creating new diversity scenarios with undetermined functional consequences. Anthropogenic local stressors create additional disruption often altering dramatically assemblage's structure. Hence, we discuss ecosystem level effects of such stressors like harvesting, trampling, habitat modification, overgrazing and eutrophication that impact coastal communities at local scales. Last, we conclude by highlighting significant knowledge gaps that need to be addressed to anticipate the combined effects of global and local stressors on seaweed communities. With physical and biological changes occurring at unexpected pace, marine phycologists should now integrate and join their research efforts to be able to contribute efficiently for the conservation and management of coastal systems.

1. Introduction

Coastlines harbor some of the most ecologically and socio-economically significant ecosystems on the planet (Harley et al., 2006). Marine habitats from the intertidal zone to the continental shelf are estimated to provide over €10 trillion worth of ecosystem goods and services per year, amounting to approximately 43% of the global total (Costanza et al., 1997). In such coastal systems, particularly on rocky shores, seaweeds are the dominant autotrophic biomass, playing a central structural and functional role in several habitats ranging from turfs to kelp forests. Along the Atlantic European coastlines, seaweed biomass is dominated by brown perrenial algae (Phaeophyceae) belonging to the orders Tilopteridales, Laminariales (kelps), and Fucales (wracks). Kelps are usually found in the subtidal and lower intertidal, and have been described as the "trees" of the oceans (Dayton, 1985). Most Fucales, communally referred to as wracks, are found in the intertidal zone, and although they are usually smaller than kelps (e.g. *Fucus* spp., *Ascophyllum nodosum*, *Pelvetia canaliculata*), they can also form large subtidal forests (namely *Cystoseira* spp.) (Fig. 1). The understorey habitat is made up of turf-forming species that can include a wide range of red (Rhodophyta), green (Ulvophyceae) and other brown seaweeds. Mediterranean shorelines are often characterized by turf forming algal communities, but canopies formed by a

* Corresponding author at: School of Biological Sciences, Queen's University of Belfast, UK.
E-mail address: f.mineur@qub.ac.uk (F. Mineur).

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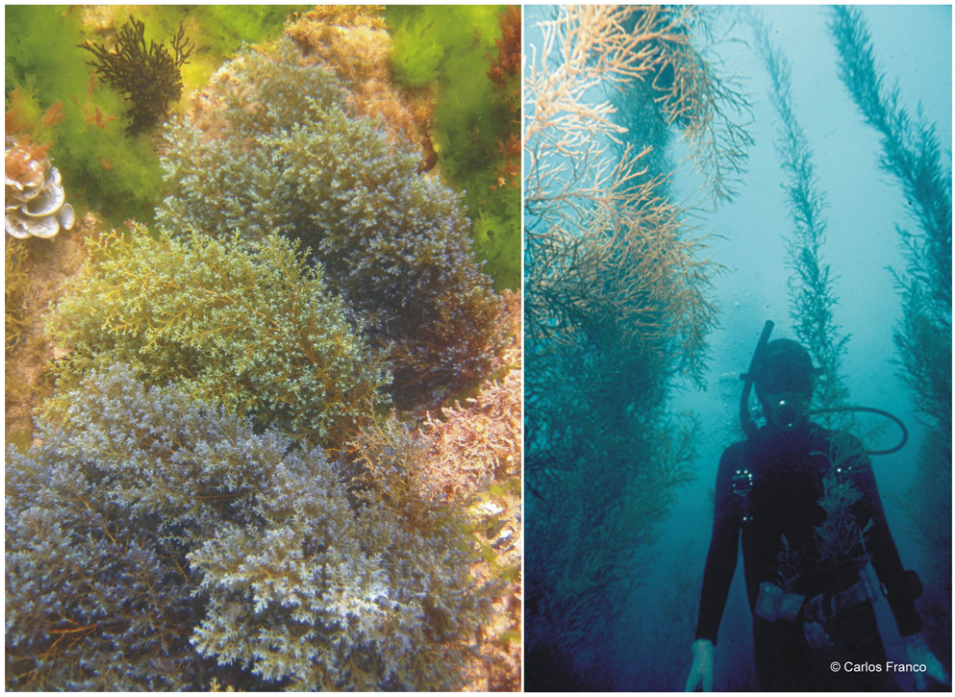

Fig. 1. *Cystoseira* spp. canopies. Left: *Cystoseira tamariscifolia* forming a low 'bushy' canopy (Almograve, Portugal; photo AHE), right: *Cystoseira usneoides* (Arrábida, Portugal; photo courtesy of Carlos Franco).

range of *Cystoseira* species can dominate the littoral fringe to the lower sublittoral zone (e.g. Ballesteros, 1990; Feldmann, 1937; Giaccone et al., 1994). These different communities are important for coastal ecosystems as they can support high biodiversity through structuring complex habitats for associated species, that range from vertebrate predators (Araujo et al., 2013; Steneck et al., 2002) to infaunal communities (Thrush et al., 2011). Seaweeds are widely recognized as autogenic "ecosystem engineers" (Jones et al., 1994) or "foundation species" (Dayton, 1975). Changes in the composition of seaweed communities, either through habitat loss or climate change, will resonate through entire coastal ecosystems.

Anthropogenic activities on coastal areas, such as fishing, tourism, maritime traffic, or exploitation of natural resources, create increasing anthropogenic stress. One third of the world's population live in coastal areas that account for approximately 4% of Earth's total land area (UNEP, 2006). Europe in particular has a densely populated coastline, which is highly impacted by human activities (EEA, 2006). Marine ecosystems surrounding Europe are among the most threatened by human impacts (Halpern et al., 2008). The most important direct drivers of change in coastal ecosystems, and marine biodiversity loss in particular, are believed to be habitat destruction, overexploitation of resources (e.g. fisheries), pollution, increases in sedimentation, climate change, and invasive species (Claudet and Fraschetti, 2010; Munday et al., 2013; Walker and Kendrick, 1998). Changes in the average and extreme values of air and sea surface temperatures, due to increasing greenhouse gases in the atmosphere, have a pronounced impact on marine organisms and ultimately on the composition of coastal communities (Wernberg et al., 2011a,b). Species that become invasive also impact ecosystems, and are second only to habitat loss as a cause of species endangerment and extinction (Wilcove et al., 1998). European coasts, with nearly a thousand recorded marine alien species (Daisie, 2014; Galil et al. 2014), are highly exposed to that threat.

Seaweeds are affected by both global and local stressors (sensu Brown et al., 2013) (Fig. 2). Global stressors result from human activities or natural fluctuations, that occur on a worldwide level. Although they will have local impacts, they cannot be halted by local action. Earth's orbital eccentricity has an impact on global temperature over periods of thousands of years (Hays et al., 1976). On a shorter (and contemporary) scale (i.e. since the industrial revolution), global warming is mostly triggered by greenhouse gas emissions (mostly originating from human activities), which are also leading to ocean acidification. Disruption of weather patterns due to global warming will also have an impact on coastal areas with more frequent and stronger storm events. These stressors, that have complex interactions, are gathered here under the umbrella of "climate change", in which we also included ocean acidification. The other major global stressor is a process called "biotic homogenization" (McKinney and Lockwood, 1999), that results from human-mediated transport and introduction of living organisms outside their native range, with biological invasions as local impacts. Some local stressors on seaweeds may be direct and evident, such as seaweed harvesting and trampling. Others, such as eutrophication, overgrazing or habitat modification can have either direct or indirect consequences and origins. For instance, eutrophication may have a remote (although local) origin and will trigger a cascade of consequences on coastal ecosystems. Overgrazing is a consequence of changes in the abundance of herbivores and their predators (top-down controls). Habitat modification can also lead to complex consequences, such as increased sedimentation that will ultimately disturb seaweed communities.

This manuscript reviews the effects of the abovementioned stressors on seaweed diversity, their communities and the functioning of the ecosystems that they sustain. This review is mostly focused on the marine biogeographical provinces surrounding Europe, considering both global and local stressors to give an overview of the current knowledge of seaweed diversity of European coastlines and how they are affected by human activities.

2. Seaweed diversity in Europe

Accurate estimates of the diversity and distribution of species are essential to understand how communities and ecosystems respond to environmental change and to be able to forecast those changes that will influence ecosystem services on which humans depend. Information on macroalgal diversity and taxonomy is primarily available through