Distributional shifts of canopy-forming seaweeds from the Atlantic coast of Southern Europe

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ORIGINAL PAPER

Distributional shifts of canopy-forming seaweeds from the Atlantic coast of Southern Europe

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Abstract

Canopy-forming seaweeds sustain critical ecosystem services in coastal habitats. Around the world, many of these seaweeds are suffering strong declines, mainly attributed to the progressive increase in sea surface temperature, in combination with other stressors due to current global changes. The southernmost part of the NE Atlantic is among those areas most affected by climate change. In this study, we estimated the distributional contractions of seven of the most conspicuous seaweeds from the Atlantic coasts of the Iberian Peninsula using an "Extent of Occurrence" methodology. Overall, during the last three decades, range shifts have been more pronounced east of the Cantabrian Sea than along the western coast of the Iberian Peninsula. In particular, regions with a semi-permanent summer upwelling seem to be critical to the persistence of brown seaweeds, fucoids and kelps. Range contractions of the cold-temperate fucoids were estimated to be ca. 21% and 45% for *Himanthalia elongata* and *Fucus serratus*, respectively; and for the kelps *Saccharina latissima* and *Laminaria hyperborea,* 6% and 14%, respectively. Range contractions for warm-temperate kelps were estimated to be ca. 13% and 10% for *Saccorhiza polyschides* and *L. ochroleuca*, respectively. Finally, a decline in the warm-temperate red algae *Gelidium corneum* occurred only in the easternmost area of the Cantabrian Sea (Basque Country), leading to a distributional contraction of 7%. We recommend conservation actions to better manage the remnant populations of these canopy-forming seaweeds, and their inclusion in national and regional catalogues of endangered species and on international Red Lists.

Keywords Kelp forests · Fucoids · Red algae · Climate change · Range contraction · Community replacement

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Introduction

Ecological systems are currently affected by a wide variety of impacts, as a result of the increases of human activity (Raudsepp-Hearne et al. 2010; Jorgenson and Clark 2011). Current rates of biodiversity loss are exceeding those of the historical past and show no indication of slowing (Ceballos et al. 2015). Global climate change, pollution, overexploitation, invasive species, and habitat fragmentation are the main drivers of the overall decline in biodiversity (Millennium Ecosystem Assessment 2005). Marine systems dominated by habitat-forming species (e.g., corals, sponges, oysters, seagrasses, kelps) are critical to ecosystem services (Palumbi et al. 2009; Laffoley and Baxter 2016). The previously mentioned threats affect their physiological and ecological performance, ultimately causing their decline (Walther et al. 2002; Hoegh-Guldberg and Bruno 2010; Smale and Wernberg 2013). Concurrently, community phase shifts may occur, because the dominant habitat-forming organisms are eliminated and/or replaced by a different group of species (Airoldi et al. 2008). This leads to consequences for associated biodiversity and trophic interactions (Hawkins et al. 2009; Wahl et al. 2015). Examples include temperate to tropical seagrasses (Waycott et al. 2009), mangroves (Polidoro et al. 2014; Fusi et al. 2015), corals (Pandolfi et al. 2003; Munday et al. 2008; Jones et al. 2014), and large canopy-forming seaweeds (Steneck and Johnson 2013; Wernberg et al. 2011, 2016).

Coastal systems dominated by canopy-forming seaweeds are one of the most ecologically and socio-economically important habitats in temperate waters (Steneck et al. 2002; Smale et al. 2013; Bennett et al. 2016). Through provisions of food, shelter and habitat to other species of flora and fauna, seaweeds provide a structural and trophic framework that supports a high diversity of associated organisms (Bustamante et al. 2017; Teagle et al. 2017). In addition, seaweeds provide many other ecosystem services, such as CO_2 sequestration, nutrient cycling, and shoreline protection (Duarte 2016; Krause-Jensen and Duarte 2016). A growing body of global evidence reveals a decline in seaweeds in different regions, mainly driven by increases in seawater temperature, along with a higher frequency and intensity of extreme climatic events (e.g., Wernberg et al. 2013, 2016; Fernández 2011; Tanaka et al. 2012; Duarte et al. 2013; Smale and Wernberg 2013; Krumhansl et al. 2016). These losses may have relevant consequences for local economies and biodiversity (Voerman et al. 2013; Vergés et al. 2016).

The Atlantic coast of Europe is a hotspot of warming, as sea surface temperatures have risen 0.3–0.8 °C per decade since the mid-20th century (OSPAR 2010; Lima and Wethey 2012; Smale et al. 2013). The southernmost region, the Iberian Peninsula, is among the areas most affected by climate change (Belkin 2009). The Iberian Peninsula has been traditionally divided into three biogeographic sub-regions. A "cool" region is located around W Portugal and NW Spain, characterized by seasonal, cold, nutrient-rich upwelling during the summer. The two "warmer" sub-regions include: the north of the Iberian Peninsula—the easternmost area of the Cantabrian Sea—and the south of the Iberian Peninsula—Algarve and the western end of the Strait of Gibraltar (OSPAR 2010). Differences in the summer temperature historically shaped the distribution of two different groups of seaweeds dominating the intertidal and subtidal zones (Gorostiaga et al. 2004; Bárbara et al. 2005; Araújo et al. 2009; Gallardo et al. 2016). On the one hand, cold- to warm-temperate brown seaweeds follow a W–E gradient (along the Cantabrian Sea) and a N–S gradient (from the Galician Rías to the Strait of Gibraltar) in terms of abundance. For most of these seaweeds, the Iberian Peninsula is their southernmost distributional limit, serving as refuge in the last glacial period (Hoarau et al. 2007; Maggs et al. 2008; Assis et al. 2017b). On the other

hand, red algae such as *Gelidium corneum* are characteristic of the northern, southwestern and, to a lesser extent, southern Atlantic coasts (Santos and Duarte 1991; Marqués et al. 1982; Gorostiaga et al. 2004).

In this study, we compiled published information, technical reports, and experts' knowledge on seven of the most conspicuous canopy-forming seaweeds from the Atlantic coasts of the Iberian Peninsula: the warm-temperate kelps *Laminaria ochroleuca* and *Saccorhiza polyschides*, the cold-temperate kelps and fucoids *L. hyperborea*, *Saccharina latissima*, *Himanthalia elongata* and *Fucus serratus*, and the warm-temperate red alga *Gelidium corneum.* Despite historical fluctuations in the distribution of these seaweeds (i.e., periods of expansion and retraction), a continuous decline was apparent since the late 1990s, mostly along the northern Iberian Peninsula. Local and regional studies have provided evidence of declining trends in the abundance of these canopy-forming seaweeds (e.g., Fernández 2011; Díez et al. 2012; Voerman et al. 2013; Araújo et al. 2016; Assis et al. 2016; Muguerza et al. 2017; Borja et al. 2018). At the same time, reduced recruitment and growth (e.g., Fernández 2011), and range contractions have been described (e.g., Duarte et al. 2013; Fernández 2016; Assis et al. 2016). Following the International Union for Conservation of Nature (IUCN) Red List criteria, which determines the relative risk of extinction of flora and fauna, our objective was to determine and quantify changes in the geographic range of the targeted species along the Atlantic coasts of the Iberian Peninsula. To accomplish this aim, we used the "Extent of Occurrence" (EOO) methodology (IUCN 2013). This work is expected to provide useful scientific recommendations for the conservation of canopy-forming seaweeds across the Atlantic Iberian Peninsula.

Materials and methods

We gathered information from the scientific literature, technical reports and the most recent knowledge from experts on the status, trends, and historical and present distribution on the Atlantic Iberian Peninsula, of the canopy-forming seaweeds: *F. serratus*, *H. elongata*, *S. latissima*, *L. hyperborea*, *L. ochroleuca, S. polyschides* and *G. corneum*. We also screened for information regarding major threats to these seaweeds. At the time of organizing the information, seven ecological regions were identified for the Iberian Peninsula, following Ramos et al. (2016) for the N and NW coasts, Tuya et al. (2012) for the W coasts, and Bermejo et al. (2015) for the S coasts. In the N Iberian Peninsula (from the French border to Ria de Vivero, 43°41.5′N, 7°35.9′W), two regions are distinguished: *Eastern* and *Western Cantabrian,* with Ria de Villaviciosa (43°32.4′N, 5° 23.2′W) as the border. In the NW Iberian Peninsula (from Ría de Vivero to the N Portuguese-Spanish border) two regions are distinguished: *Upper* and *Lower Rías,* separated by the Finisterre Cape (41°52.3′N, 8°51.7′W). On the W Iberian Peninsula (between N and S Portuguese-Spanish borders), two regions are differentiated: *Northern* and *Southern Portugal,* divided by the Nazaré Canyon (39° 35.9′N, 9° 4.6′O). In the south of the Iberian Peninsula, the region of the *Strait of Gibraltar,* from Punta Camarinal (36°4.7′N, 5°47.8′W) to Gibraltar (36º4′N, 5°20.7′W) was considered.

Estimation of range shifts

We assembled a GIS database using ArcView (v.10.2.1.) to include all presence records from different databases (Global Biodiversity Information Facility, GBIF; Ocean

Table 1 Survival temperature interval (STI) and threats over seaweeds

Species	STI (°C)	Threats	References
Species with intertidal and subtidal distribution (km²)			
Warm-temperate kelps			
Laminaria ochroleuca	15–23	Seawater temperature warming trends Summer periods more than 30 consecutive days of seawater temperature > 20 °C Heat waves	STI: a, b, d Analysed literature: 2–10, 12, 15, 16, 18, 19, 22–31, 34, 37, 39, 42, 43, 46 Threats: 21, 28, 30, 35, 38, 42, 43, 44, 48
Saccorhiza polyschides	5–23	Grazing by fish	STI: a Analysed literature: 2–10, 12, 14–16, 18, 22–30, 34, 39, 42, 43, 45, 46 Threats: 21, 28, 30, 35, 38, 42, 43, 44, 45, 48
Cold-temperate kelps			
Laminaria hyperborea	5–<21 °C	Seawater temperature warming trends Grazing by fish	STI: a, b Analysed literature: 3–8, 10, 18, 20, 22, 27, 28, 35, 42–44, 46 Threats: 21, 20, 28, 35, 43, 44, 46
Saccharina latissima	10–<21		STI: a, b Analysed literature: 4, 6-8, 10, 18, 20, 24, 25, 27, 28, 35, 43, 44, 46 Threats: 21, 20, 28, 43, 44
Warm-temperate red seaweeds			
Gelidium corneum	13–21	Seawater temperature warming trends Summer increase in solar radiation Summer decrease in nutrient availability Winter decrease in solar radiation Intensification in the frequency of swells	Analysed literature: 2, 4, 12, 16, 17, 18, 20, 27, 29-31, 34, 36, 40, 41, 47, 48 Threats: 29, 30, 36, 41, 48,49

Table 1 continued

Species	STI (°C)	Threats	References
Species with intertidal distribution: fucoids (km)			
Himanthalia elongata	8–18	Seawater temperature warming trends	STI: d, e
Fucus serratus	0–<25	Increase in air temperature	Analysed literature: 1,3,4,7, 8, 11, 13, 18, 20, 23, 25, 26, 27, 32, 37, 44
		Increase in solar radiation (*F. serratus*)	Threats: 20, 30, 32, 33, 37, 44

STI: a. van den Hoeck (1982), b. tom Dieck (1993); c. Lüning (1990); d. Izquierdo et al. (2002); e. Martínez et al. (2015a)

1. Fischer-Piette (1955a, b); 2. Seoane-Camba (1965); 3. Fischer-Piette and Ginsburg-Ardré (1963); 4. Ardré (1971); 5. Gili et al. (1979); 6. Anadón and Niell (1981); 7. Fernández and Niell (1981); 8. Anadón (1983); 9. Borja and Gorostiaga (1990); 10. McNeill (1992); 11. Arrontes (1993); 12. Gorostiaga et al. (1998); 13. Arrontes (2002); 14. Gorostiaga et al. (2002–2005), unpublished; 15. Gorostiaga et al. (2003–2005), unpublished; 16. Borja et al. (2004); 17. Gorostiaga et al. (2004); 18. Bárbara et al. (2005); 19. Arroyo et al. (2006); 20. Lima et al. (2007); 21. Bode (2008); 22. Fernández and Anadón (2008); 23. Anadón et al. (2009); 24. Assis et al. (2009); 25. Araújo et al. (2009); 26. Rico et al. (2009); 27. Rodríguez and Moliner (2010); 28. Fernández (2011); 29. Bermejo et al. (2012); 30. Díez et al. (2012); 31. Guinda et al. (2012); 32. Lamela-Silvarrey et al. (2012); 33. Martínez et al. (2012); 34. Pérez Llorens et al. (2012); 35. Tuya et al. (2012); 36. Borja et al. (2013); 37. Duarte et al. (2013); 38. Voerman et al. (2013); 39. Gorostiaga et al. (2013), unpublished; 40. IHC (2014), unpublished; 41. Quintano et al. (2015); 42. Pinho et al. (2016); 43. Araujo et al. (2016); 44. Piñeiro-Corbeira et al. (2016); 45. Assis et al. (2017a, b); 46. Franco et al. (2017); 47. IHC (2017), unpublished; 48. Muguerza et al. (2017); 49. Borja et al. (2018)

Fig. 1 Extent of Occurrence (EOO) of warm-temperate kelps with an intertidal and subtidal distribution ▶ (*Laminaria ochroleuca* and *Saccorhiza polyschides*). Ecological regions correspond to those described by Ramos et al. (2016), Tuya et al. (2012) and Bermejo et al. (2012) (see "Materials and methods"). Numbered lines correspond to the limits of ecological units. *FR–SP* France–Spain border, *RVi* Ría Villaviciosa, *RV* Ria de Viveiro, *FC* Finisterre Cape, *SP–PT* Spain–Portugal border, *NC* Nazaré Canyon, *PT–SP* Portugal–Spain border, *PC* Punta Camarinal, *Gib* Gibraltar. The outer coastline represents kelp distribution during *Period 1* (1980's–1990's), dark polygons correspond to estimated EOO. The inner coastline corresponds to *Period 2* (2013–2016), dark polygons correspond to estimated EOO; dashed lines indicate areas where the kelps have not been found; light polygons correspond to areas where sparse isolated individuals have been found in the deep subtidal zone

Biogeographic Information System, iOBIS), and herbarium collections from the Iberian Peninsula (BCN-Phycophyta, BIO- Cryp, FCO, HGI-A, MA-Algae, MACB, MAF-Algae, MGC-Phyc., MUB, PO, SANT, UALG, and VAL; herbarium abbreviations follow Thiers (2017). The geographic position of each record was checked for consistency to avoid redundancies and incongruences from the different data sources. Those presences erroneously geo-referenced, on land or far from the coastline, were omitted or corrected with the aid of experts. To estimate species' distributional shifts, we grouped the available information on presence records of each seaweed into two periods: during the 1980's and 1990's (hereafter, *Period 1*) and the present time, i.e., between 2013 and 2016 (hereafter, *Period 2*). We then calculated the differences in the "Extent of Occurrence" (EOO; IUCN 2013) during the two periods. We did not consider sites where species were observed as sparse individuals. The EOO is defined as the smallest area that can be drawn to include all the known, inferred or projected presence sites of a species (IUCN 2013). This estimation may exclude geographic discontinuities or disjunctions within the overall distribution of the species (e.g., large areas of unsuitable habitat). EOO has seldom been used for seaweeds. Thus, we adapted this parameter using two distinct methodologies for subtidal and intertidal species. For the species present in the lower intertidal and subtidal zones, EOO was delimited using the minimum convex polygon method, or convex hull (IUCN 2013). We built the convex hulls using the Minimum Bounding Geometry tool of ArcGIS, from 1:25,000 maps. The polygons were corrected, such that areas of unsuitable habitats (i.e., areas of sand and muddy bottoms) were discarded. This was implemented from a layer of substrate type (EMODnet Seabed Habitats, Populus et al. 2017). Because of the distribution in depth of the species, polygons were clipped with the bathymetric layer (General Bathymetric Chart of the Oceans, 30 arc-sec interval grid). For *Laminaria* spp., a maximum depth of 25 m was used (Gili et al. 1979; Arroyo et al. 2006; Guinda et al. 2012); in the case of *S. latissima*, *S. polyschides* and *G. corneum*, layers were cut to a maximum of 20 m depth (Borja and Gorostiaga 1990; Gorostiaga et al. 1998; Borja et al. 2004; Fernández 2011). Distributional shifts were calculated by comparing the measured area (km^2) of the polygons between *Period 1* and *Period 2*, which provided the percentage of EOO loss for each species.

The intertidal species *H. elongata* and *F. serratus* have a linear distribution along rocky fringes, normally < 1 km in width. We used the linestring of the coastline from 1:25,000 maps, but exclusively including rocky shores based on digital images. An exception was made in the case of *F. serratus* in NW Spain (Galician Rías) and the *Northern Portugal* region, because the distribution of this species is restricted to a few localities (Duarte et al. 2013, 2015). In this case, the distribution was estimated with several independent linear transects (1 km width) parallel to the coast. We estimated distributional contractions by comparing the length (measured in km) of the linestring of the coastline covered by the species during *Period 1* and *Period 2*, and estimating the percentage lost.
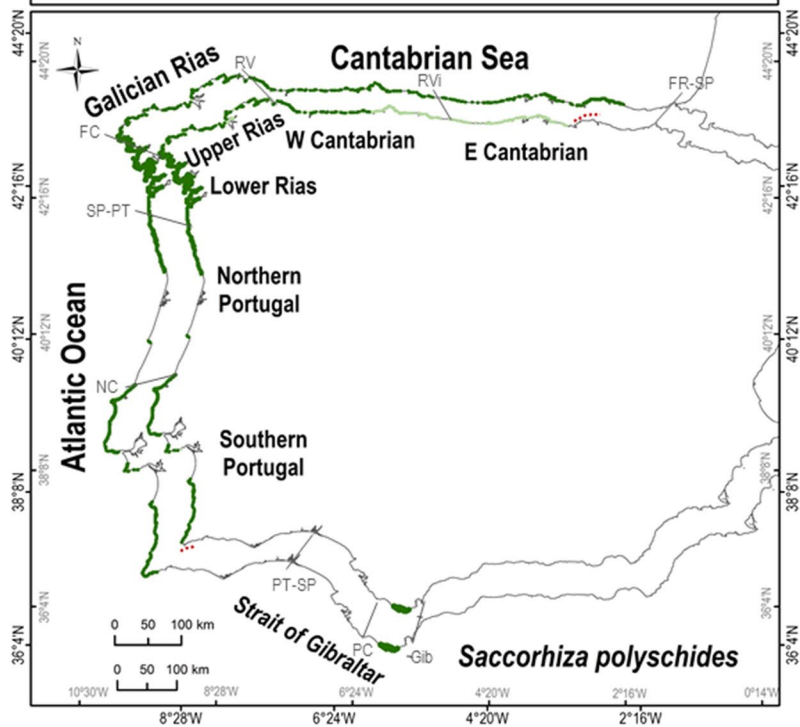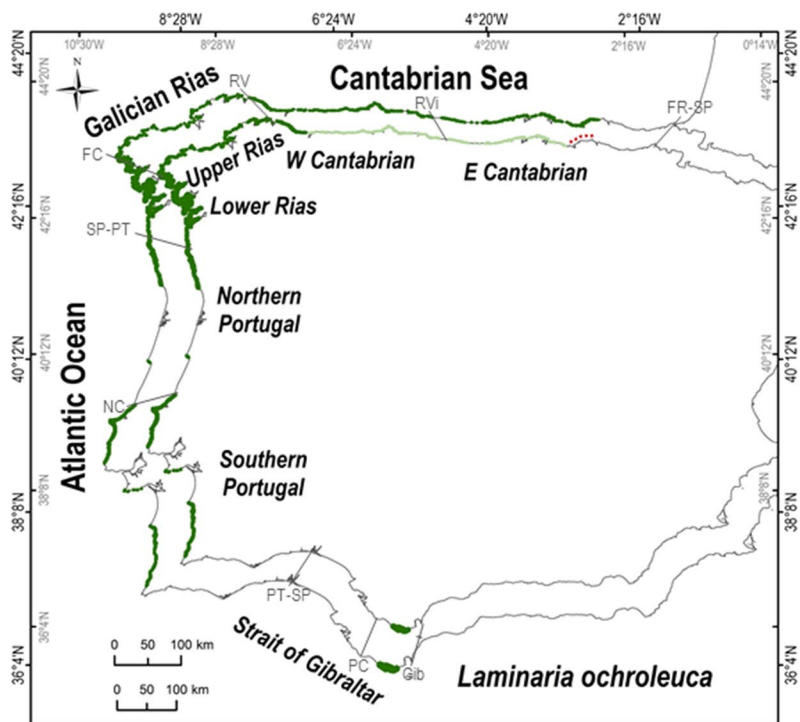
Table 2 Estimated "Extent of Occurrence" (EOO), distributional shifts and contraction rates for the studied seaweeds. *Period 1* correspond to EOO between the 1980's and 1990's and *Period 2* between 2013 and 2016. N/A, not applicable

Species	EOO period 1	EOO period 2	N shift	W shift	Overall shift	Distributional contraction (%)
Species with intertidal and subtidal distribution (km^2)						
Warm-temperate kelps						
Laminaria ochroleuca	1559	1415	N/A	144	144	10
Saccorhiza poly-schides	1350	1178	22	150	172	13
Cold-temperate kelps						
Laminaria hyperborea	1379	1189	72	118	190	14
Saccharina latissima	787	736	21	30	51	6
Warm-temperate red seaweeds						
Gelidium corneum	1370	1280	N/A	90	90	7
Species with intertidal distribution: fucoids (km)						
Himanthalia elongata	978	769	33	176	209	21
Fucus serratus	197	109	1	87	88	45

Results

A total of 49 published studies and technical reports provided information on the distribution of the targeted seaweeds at local and regional scales (Table 1). A total of 21 studies reported declines in the targeted seaweeds associated with several threats. Global warming was regarded as the most relevant stressor. However, other factors were also reported as relevant, such as irradiance and intensification in the frequency of swells, and non-climatic factors such as fish grazing.

Range shifts

Seaweeds with intertidal and subtidal distributions

For the warm-temperate kelps *Laminaria ochroleuca* and *Saccorhiza polyschides*, a total of 212 and 106 occurrences were obtained, respectively. Both kelps were distributed from the *Eastern Cantabrian* to the *Strait of Gibraltar* during *Period 1* (Fig. 1). Both kelps were commonly found forming mixed forests. Information on the decline of *L. ochroleuca* from *Period 1* to *Period 2* was found for the *Eastern* and *Western Cantabrian*. Changes in the geographical range of *L. ochroleuca* have been assessed using quantitative data from *Eastern Cantabrian* and *Northern Portugal*. In the case of *L. ochroleuca*, in *Period 1*, according to quantitative local-scale studies, dense kelps forests (50–75% cover) were observed in the intertidal and subtidal zones. In *Period 2*, forests of *L. ochroleuca* were not observed in the previously mentioned regions; sparse individuals of small size were largely found inhabiting the subtidal zone (Fig. 1). This resulted in an estimated EOO decrease of 10% (Fig. 1, Table 2) from *Period 1* to *Period 2* (i.e., in the last ca. 30 years). Although the

obtained information did not allow the detection of a decreasing trend in the distribution of this kelp in *Southern Portugal*, it should be noted that expert knowledge suggests local declining trends.

We found information on the decline of *S. polyschides* through *Period 1* to *Period 2* for the *Eastern* and *Western Cantabrian* and *Southern Portugal*. In *Period 1* and according to quantitative local-scale studies, dense kelp forests (85–100% cover) were observed in the intertidal and subtidal zones of those these regions. Through *Period 1* to *Period 2*, a continuous decline in population density was observed in the *Eastern Cantabrian*, where the kelp has not been found to date (Fig. 1). In the *Western Cantabrian* and *Southern Portugal*, fluctuations in the presence and abundance of this kelp have been observed in both periods. During *Period 2*, this kelp was not observed in the southernmost tip of *Southern Portugal* (Fig. 1). This resulted in an estimated EOO decrease of 13% (Fig. 1, Table 2) in the last ca. 30 years.

In the case of the cold-temperate kelps *Laminaria hyperborea* and *Saccharina latissima*, a total of 74 and 144 occurrence records were obtained, respectively. In *Period 1*, both kelps were distributed from the *Western Cantabrian* to *Northern Portugal*. During *Period 1*, *L. hyperborea* was commonly found intermixed with *L. ochroleuca* and *S. polyschides*. The presence of *S. latissima* was rare and distributed from the westernmost end of *Western Cantabrian* to the upper tip of *Northern Portugal*. Qualitative information from local-scale studies and experts' knowledge showed declining trends of both kelps from the *Western Cantabrian* to *Northern Portugal* (Fig. 2). In *Period 2*, only some sparse subtidal individuals of *L. hyperborea* and *S. latissima* were observed in both regions. Thus, in *Period 2*, the distribution of both kelps was limited to the *Upper* and *Lower Rías* and, to a lesser extent, the upper tip of *Northern Portugal*. This led to EOO decreases of 14% and 6%, respectively, for *L. hyperborea* and *S. latissima* (Fig. 2, Table 2) in the last ca. 30 years.

For *G. corneum*, a total of 96 occurrences were recorded. In *Period 1*, this seaweed was distributed all along the Atlantic coast of the Iberian Peninsula, from the *Eastern Cantabrian* to the *Strait of Gibraltar*. Dense beds of the species were mainly distributed in the *Western* and *Eastern Cantabrian*, *Southern Portugal* and the *Strait of Gibraltar*. Changes in the distributional range of *G. corneum* have been assessed using quantitative data from *Eastern Cantabrian*. Published literature, technical reports and experts' knowledge showed a continuous decline in *G. corneum* biomass (up to ~80%) and coverage (up to ~60%) since the 1990's-2000. However, some studies have suggested an increase in abundance in the *Western Cantabrian* and the westernmost part of the *Eastern Cantabrian*. Overall, the estimated EOO reduction for *G. corneum* was 7% (Fig. 3, Table 2) in the last ca. 30 years.

Seaweeds with intertidal distribution

A total of 87 and 44 occurrences were found for *H. elongata* and *F. serratus*, respectively. During *Period 1*, the distribution of both fucoids covered the lower intertidal zone from the *Western Cantabrian* to *Northern Portugal*. According to information from studies and surveys, both species have disappeared, since 2000, from numerous localities (Fig. 4) of the *Western Cantabrian* and *Northern Portugal*. Only *F. serratus* remains in a few localities of the *Western Cantabrian*, mostly as sparse individuals of depauperated conservation status, i.e., "dwarf-morphs". Estimated EOO reductions were 21% and 45% for *H. elongata* and *F. serratus*, respectively (Fig. 4, Table 2) in the last three decades. The current distribution of both fucoids is restricted to the NW corner of the Iberian Peninsula (*Upper* and *Lower Rías* and *Northern Portugal*), where ongoing declines have been recently reported.

Fig. 2 Extent of Occurrence (EOO) for cold-temperate kelps with an intertidal and subtidal distribution ▶
(*Laminaria hyperborea* and *Saccharina latissima*). Ecological regions correspond to those described by
Ramos et al. (2016) and Tuya et al. (2012) (see "Materials and methods"). Numbered lines correspond
to the limits of the ecological units. *RVi* Ría Villaviciosa, *RV* Ria de Viveiro, *FC* Finisterre Cape, *SP–PT*
Spain–Portugal border, *NC* Nazaré Canyon. The outer coastline represents the kelp distribution during
Period 1 (1980's–1990's), dark polygons correspond to estimated EOO. The inner coastline corresponds to
Period 2 (2013–2016), dark polygons correspond to estimated EOO; dashed lines indicate areas where the
kelps have not been found; light polygons correspond to areas where sparse isolated individuals have been
found in the deep subtidal zone

Discussion

In this study, we compiled the most recent information on the local and regional decline of
seven of the most conspicuous cold- and warm-temperate canopy-forming seaweeds from
the Atlantic coasts of the Iberian Peninsula. By estimating the "Extent of Occurrence"
(EOO, IUCN 2013), we quantified their range contractions over the last three decades.

Several studies point towards the continuous increase in seawater temperature as the
most relevant threat to these seaweeds (this study, Table 1). Seaweeds are temperature-
dependent organisms for which growth and photosynthesis are reduced when temperatures
differ from the optimum (Breeman 1988; Lüning 1990). The distribution of these seaweeds
on the Atlantic coast of the Iberian Peninsula has historically been associated with the
August oceanic isotherm of 20 °C (Lüning 1990). Since the 1980's, the Atlantic coastal
waters of the Iberian Peninsula have experienced a significant warming. The greatest sea-
water temperature increases have been observed during spring, summer and early autumn
and, subsequently, the warm season is lengthening (Lima and Wethey 2012; Costoya et al.
2015; Piñeiro-Corbeira et al. 2016). Overall the range shift in the brown seaweeds was
estimated to be higher westward along the Cantabrian Sea, than northward along the W
Iberian Peninsula. This may be explained by the fact that the longitudinal increase in sea-
water temperature in the Atlantic Iberian Peninsula has been twice as high as the latitudi-
nal increase (Gómez-Gesteira et al. 2008). Seawater temperature increases have been more
pronounced towards the eastern Cantabrian Sea, achieving an increase of ca. 0.26 °C per
decade (Goikoetxea et al. 2009). In all other regions, seawater temperature increases have
been ca. 0.15 °C (Gómez-Gesteira et al. 2011; Piñeiro-Corbeira et al. 2016; Goela et al.
2016) due to the cooling effects of periodically upwelling events in near-shore waters. In
addition to ongoing warming, periods of > 30 consecutive summer days of seawater tem-
peratures > 20 °C, i.e., the maximum survival threshold for most species (Table 1), have
been detected since 2000 (Fernández 2011; Díez et al. 2012; Assis et al. 2017a). In turn,
summer heat waves have also been documented. For example, in 1997, 2003 and 2006, sea-
water temperature reached > 25 °C in the *Eastern Cantabrian* (Díez et al. 2012). In 2003
and 2006, seawater temperature reached maximum values of ~ 23 °C in the *Western Canta-
brian* (Voerman et al. 2013). Particularly for *Laminaria ochroleuca* and *Saccorhiza poly-
schides* this has been indicated as a key reason for the observed range shifts in the *West-
ern* and *Eastern Cantabrian,* respectively (Fernández 2011; Díez et al. 2012; Muguerza
et al. 2017; this study, Table 1). Similarly, this may explain the shifts of the other kelps,
as experiments demonstrate for *Saccharina latissima* (Simonson et al. 2015). Increases in
seawater temperature above species' temperature thresholds, during prolonged periods,
cause severe damage to cellular structures, limiting tissue growth (Martínez et al. 2012;
Simonson et al. 2015). Thus, photosynthesis, growth and individual survival are negatively
affected (Flukes et al. 2015). Individual and populations resilience are reduced and, there-
fore, species are more vulnerable to other stressors (Whal et al. 2015). On the other hand,

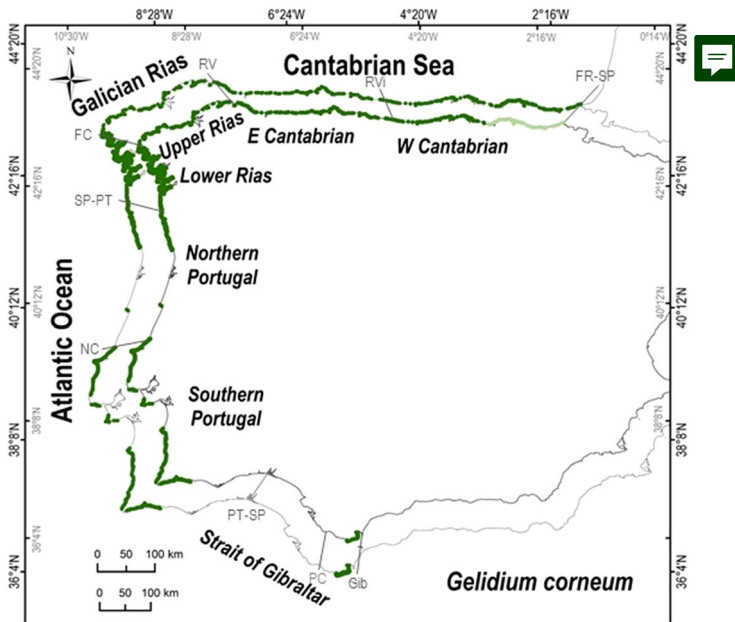*Laminaria hyperborea*

Saccharina latissima
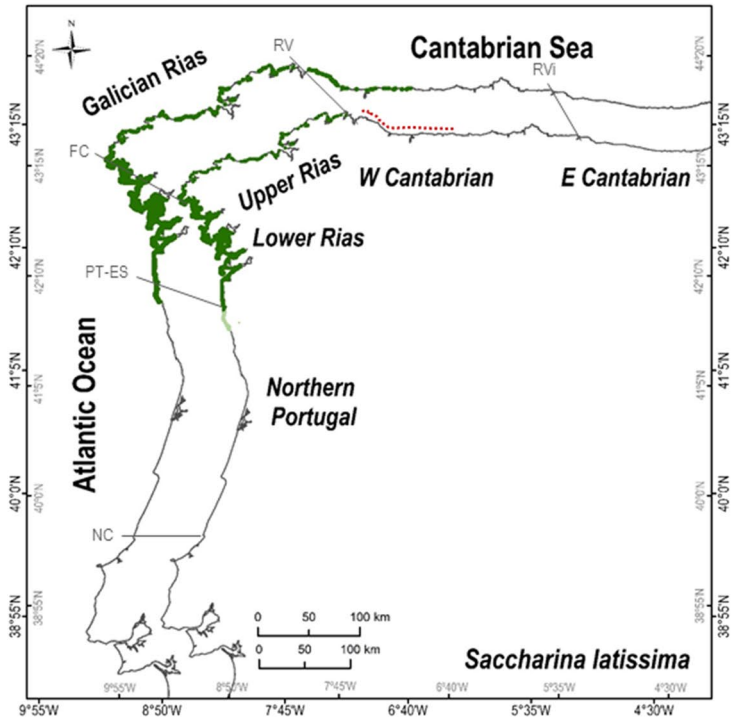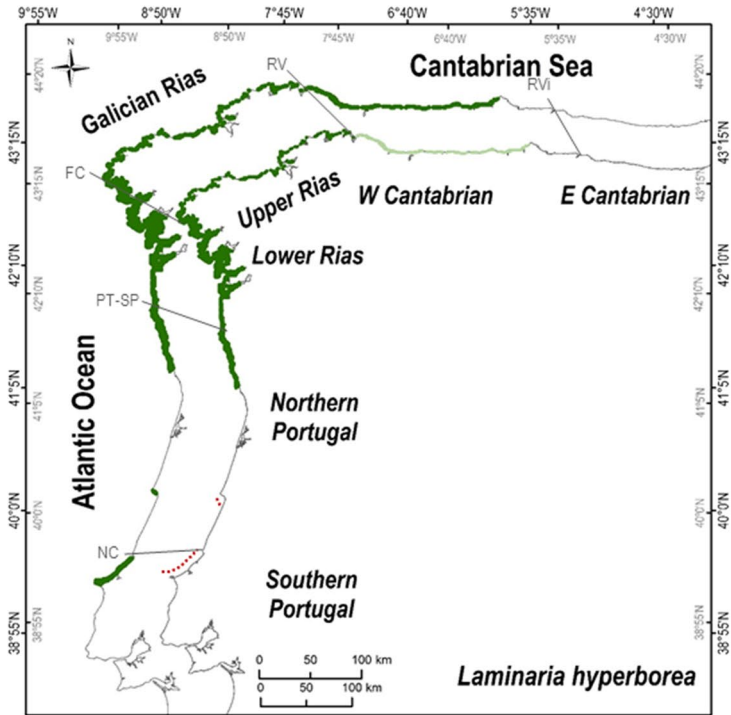
Fig. 3 Extent of Occurrence (EOO) for the warm-temperate red algae *Gelidium corneum*. Ecological regions correspond to those described by Ramos et al. (2016), Tuya et al. (2012) and Bermejo et al. (2012) (see "Materials and methods"). Numbered lines correspond to the limits of the ecological units. *RVi* Ría Villaviciosa, *RV* Ria de Viveiro, *FC* Finisterre Cape, *SP–PT* Spain–Portugal border, *NC* Nazaré Canyon. The outer coastline represents the algal distribution during *Period 1* (1980's–1990's), dark polygons correspond to estimated EOO. The inner coastline corresponds to *Period 2* (2013–2016), dark polygons correspond to estimated EOO; light polygons correspond to areas where a sharp decline in *G. corneum* meadows was observed

while *S. polyschides* has almost disappeared from the *Eastern Cantabrian*, extreme fluctuations (periods of extinction followed by recolonization) have been observed in the *Western Cantabrian* and *Southern Portugal* (Assis et al. 2017a; this study). These fluctuations have been associated with the seasonal effect of winter temperatures on microscopic stages and nutrient availability during spring, i.e., the sporophyte growth phase (Fernández 2011; Assis et al. 2017a). However, if current warming conditions persist, projections through the next three decades predict the extinction of this kelp in these regions (Assis et al. 2017a).

Because of the current warming conditions, the current distribution of the targeted brown seaweeds is restricted to the influence of cold-water nutrient rich upwelling (Bermejo et al. 2012; Ramos et al. 2016; Lourenço et al. 2016; this study, Table 1). Cold-temperate fucoids and kelps find refuge along the NW corner of the Iberian Peninsula (*Upper* and *Lower Rías,* and *Northern Portugal*). Warm-temperate kelps are not only found along the NW corner of the Iberian Peninsula, but also throughout *Southern Portugal* and *Strait of Gibraltar*. However, indications of an ongoing decline have been observed, particularly in the intertidal zone of the *Upper* and *Lower Rías* (Piñeiro-Corbeira et al. 2016), raising uncertainty on the potential role of these regions as refuges for these species in the near future (Martínez et al. 2015b).

Along the Atlantic European coasts, other studies have shown declining trends of the targeted canopy-forming seaweeds, mainly driven by global warming (reviewed by

Araújo et al. 2016). The cold-temperate brown seaweeds of our study are distributed up to the Arctic region. In the English Channel, declines in abundances of *L. hyperborea*, driven by warmer winter temperatures, were observed (Yesson et al. 2015; Assis et al. 2016). In Scotland, the Irish and the North Seas, Skagerrak and Norway, *L. hyperborea* has been documented to be stable, whereas *F. serratus* has increased in abundance (Yesson et al. 2015; Araújo et al. 2016). Even *S. latissima* has increased after a significant reduction driven by overgrazing by sea urchins (Norderhaug et al. 2015; Araújo et al. 2016). The distribution of the warm-temperate kelps, *L. ochroleuca* and *S. polyschides*, has extended to the British Isles and mid-Norway, while decreasing in northern France (Smale et al. 2015; Yesson et al. 2015; Araújo et al. 2016) due to warmer summer temperatures. Therefore, all of this evidence suggests that the distributional limit of the targeted brown seaweeds is shifting poleward.

The decline in canopy-forming seaweeds, driven by increases in seawater temperature, has been described in other regions worldwide. In the central Atlantic coast of Nova Scotia, 85–99% of the biomass of *S. latissima* and *L. digitata* was lost over the last three decades, leading to a regime shift from kelps to turf-dominated rocky reefs and invasive seaweeds (Filbee-Dexter et al. 2016). On the SW coast of Japan, Tanaka et al. (2012) reported that kelp forests dominated by *Ecklonia* spp. have mostly disappeared over an area of ca. 700 km. Similarly, these authors showed that temperate *Sargassum* spp. have been replaced by the tropical species *Sargassum ilicifolium*. On the western temperate coast of Australia, the gradual increase in seawater temperature over the last three decades, in combination with extreme marine heat waves (Wernberg et al. 2013), has facilitated a shift toward communities dominated by turfs, invertebrates and corals of subtropical affinity (Wernberg et al. 2013, 2016).

Other climatic and non-climatic factors may also threaten the presence of the targeted seaweeds. The presence of cold-temperate seaweeds along *Northern Portugal* has been associated with cold-water upwelling (Lima et al. 2007). The magnitude and frequency of the summer upwelling has been observed to be weakened (Lemos and Pires 2004) due to a decrease in favorable winds (Sydeman et al. 2014). Because of upwelling instability, not only may water temperature be warmer, but the period of summer stratification also increases, reducing the availability of nutrients, which are also important for kelp performance (Fram et al. 2008; Franco et al. 2018). The intertidal fucoids, *F. serratus* and *H. elongata*, are probably also influenced by climatic factors related to emersion times (Viejo et al. 2011; Duarte et al. 2013), e.g., increased air temperatures (Helmuth et al. 2002) and irradiance (Martínez et al. 2012; Sanchez-Lorenzo et al. 2013). On the northern coast of the Iberian Peninsula, an average annual increase of ca. 2.3 W m^{-2} per decade, from 1985 to 2010, has been reported (Sanchez-Lorenzo et al. 2013). Increased solar irradiance in *F. serratus* has been associated with photosynthetic inhibition and damage (Martínez et al. 2012). In the easternmost area of the *Eastern Cantabrian* (Basque Country), increasing levels of irradiance during summer, in combination with seawater temperature increases, and decreases in solar irradiance during winter, have gradually threatened the intertidal and subtidal *Gelidium corneum* populations (Díez et al. 2012; Muguerza et al. 2017; Quintano et al. 2015; Borja et al. 2018). Moreover, storms are becoming more frequent and intense, and increased wave energy has had a strong dislodging effect on *G. corneum* (Borja et al. 2013, 2018). Seaweeds are likewise affected by local stressors such as water quality, invasive species, harvesting, trampling and habitat modification (Wahl et al. 2015; Mineur et al. 2015). However, on the Atlantic coasts of the Iberian Peninsula, the mid- and long-term effects of these stressors are less studied than other variables

regularly monitored at global and regional scales (e.g., seawater temperature, nutrients, irradiance, wave intensity). For example, seaweed harvesting increased in NW Iberia in recent years, particularly for edible species used as human food (e.g., *L. ochroleuca*, *L. hyperborea*, *S. polyschides*, *H. elongata, S. latissima*). However, the effects of harvesting have not been properly assessed (García-Tasende and Peteiro 2015). It is recommended that studies on the effects of exploitation on the targeted seaweeds are carried out. The resilience of the populations under current conditions of global must be also considered at the time of designing exploitation plans. In addition, warming contributes to accelerating population growth and grazing activities of mesograzers (Vergés et al. 2016). Several studies have demonstrated that kelps are intensely consumed not only by native fish, but also by tropical species moving to temperate areas because of the warming of the oceans (Tuya et al. 2012; Brodie et al. 2014; Franco et al. 2017; this study, Table 1). On the NE Atlantic European coasts, the percentage of introduced seaweed species account for around 20% of the worldwide total (Williams and Smith 2007); for example, the Galician Rías is considered an outstanding European Atlantic hotspot of introduced marine species (Bárbara et al. 2008). Non-native species can affect native ones, including competition for available resources (substratum, nutrients, solar radiation). Climate-driven changes may affect the dispersion of non-native species because of the variation in the currents system. Also, competitive interactions may occur considering the onset of new thermal conditions and availability empty ecological niches (Davidson et al. 2015).

On the Atlantic coasts of the Iberian Peninsula, the consequences of the loss of canopy-forming seaweeds may be relevant to associated assemblages, because their structural and functional role cannot be easily fulfilled by other species (Crowe et al. 2013). Studies of community replacement on these coasts reported, in the subtidal zone of the *Eastern Cantabrian* (Díez et al. 2012), an increase in less conspicuous seaweeds, such as coralline algae (e.g., *Lithophyllum incrustans* and *Ellisolandia elongata*), warm-water filamentous species (e.g., *Gayliella flaccida* and *Aglaothamnion tenuissimum*), and introduced seaweed species (e.g., *Asparagopsis armata, Bonnemaisonia hamifera, Sargassum muticum* and *Codium fragile*). Introduced species, such as *A. armata*, have also been observed to spread in the subtidal zone of previously kelp-dominated areas of the *Western Cantabrian*, together with other warm-temperate species (e.g., *Gelidium corneum*, *Jania squamata* and *Dictyota dichotoma*) (Voerman et al. 2013). In the intertidal zone, an increase in opportunistic species (e.g., *Ulva* and *Ceramium* spp.) (Duarte et al. 2015) has been observed. Because large macroalgae regulate key functions, the loss of canopy-forming seaweeds is expected to lead to a simplification of the food-web complexity and length (Graham 2004; Airoldi et al. 2008; Byrnes et al. 2011). This occurred in the intertidal assemblages dominated by *F. serratus* in the *Western Cantabrian* region (Duarte et al. 2015), where this fucoid was replaced by ephemeral and turf-forming species, leading to a decline in associated diversity and food-web complexity.

Himanthalia elongata

Fucus serratus
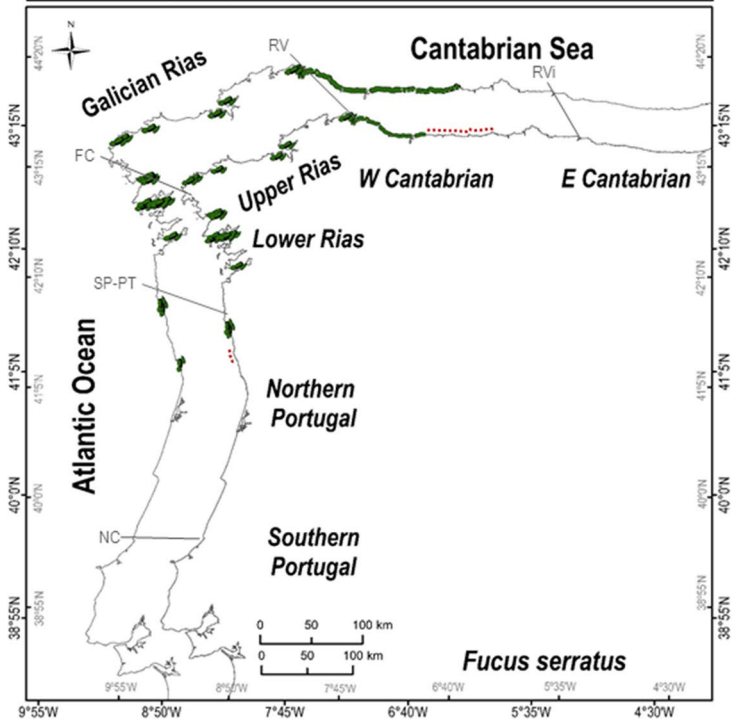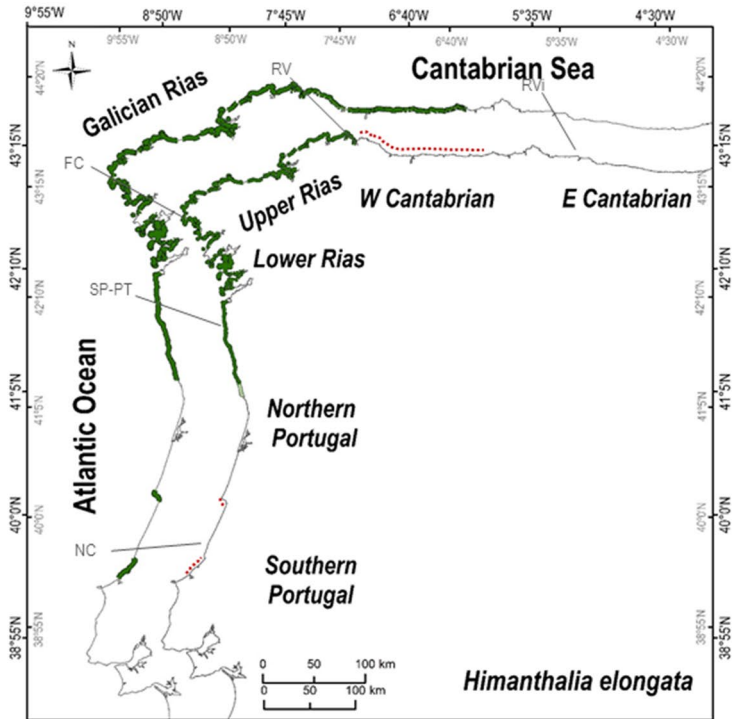
Recommendations for management and conservation

In this study, we quantified the distributional shifts of seven of the most conspicuous canopy-forming seaweeds from the Iberian Peninsula. Given their importance as habitat-forming species, or ecosystem engineers, conservation actions must be established to better manage remnant populations. We have summarized their status and trends, showing a major decline in kelp abundance with respect to their entire distributional range within the NE Atlantic. An overall IUCN Red List assessment, considering the European coasts, is highly recommended. In the case of the fucoids, we propose adapting the standard methodology used by the IUCN guidelines, which suggests measuring EOO, in the case of linear habitats, through 2×2 km grids (IUCN 2013). Nonetheless, at least regarding the distribution of the targeted fucoids on the Atlantic coast of the Iberian Peninsula, the use of a system based on areas would not be realistic and would lead to bias and overestimations. Thus, we recommend that thresholds should be adapted for coastal linear habitats.

Scientific knowledge on the dynamics of communities dominated by seaweeds has potential applications to the better management of coastal ecosystems. The management and conservation of the targeted seaweeds should involve improved monitoring of critical areas, such as those regions where the species are currently distributed in the NW Iberian Peninsula. The reduction of local threats (e.g., invasive species, overexploitation) should be examined and considered at the time of elaborating management plans. In-situ studies to evaluate the potential success of transplantation methodologies and to assess if these strategies are cost-effective to boost the size and long-term viability of wild populations are highly recommended, together with ex situ conservations methods (e.g., seed banks, and cultures). Our study indicates the paramount importance of better implement of marine policies, such the Marine Strategy Framework Directive (Directive 2008/56/EU) on the sub-region *Bay of Biscay* and *Iberian Peninsula*, according to, at least, three of the established descriptors (Commission Decision (EU) 2017/848): 1—biodiversity is maintained; 4—elements of food webs ensure long-term abundance and reproduction; 6—the sea floor integrity ensures functioning of the ecosystems.

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