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Invasion of the Reds? Long-term shifts on intertidal seaweed at distribution limits

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Abstract in English

The effects of climate change on biodiversity are well documented on the Portuguese intertidal marine flora. However, heatwaves and extreme events have been increasing in frequency and intensity since the last assessment. The present study aims to update the Portuguese intertidal macroalgae database and see how it changed since 2003 and its baseline in the 1960s. To achieve this objective, we assessed the relative abundance and sampled, for subsequent taxonomical identification, in October 2020, and in late May and late June 2021 in the north (Ancora, Montedor, and Viana do Castelo) and in the south (Carrapateira, Sagres, and Lagos) of Portugal, which coincides with the rear-edge distributions of many cold and warm-water species. In the sampling campaigns, we identified 184 different taxa and determined their relative abundance. From 2003, we observed a 62% and 72% decrease in Northern and Southern species, respectively, while the Cosmopolitan species dominated. Also, from the 13 cold-water species not detected in the sampling campaigns, *Himanthalia elongata, Laminaria hyperborea*, and *Saccharina latissima* can be highlighted since, for instance, these provide an abundant quantity of biomass, diversity, and coastal protection. Last, the novel presence of the invasive *Rugulopteryx okamurae* in the intertidal, in Lagos 2021, meant a 57% decrease in the macroalgae species richness. These flora changes may be related to climate change as it negatively impacts the survival of seaweeds. Further research is needed to see how the rest of the Portuguese intertidal flora is facing climate change and which effects can cause. In addition, monitoring of *R. okamurae* is imperative as it negatively transforms the seascape.

Abstract in Portuguese

Os efeitos das alterações climáticas na flora marinha intertidal portuguesa estão bem documentados. No entanto, as ondas de calor (ar e água do mar) e eventos extremos (tempestades energéticas incluindo forte ação das ondas e eventos de refrescamento) têm vindo a aumentar em frequência e intensidade desde a última avaliação no início dos anos 2000. O presente estudo visa atualizar a base de dados portuguesa de macroalgas intertidais e ver como mudou a biodiversidade desde os anos 1960, 2000 até o presente, especialmente, em pontos geográficos que representam limites de distribuição de muitas espécies de águas frias e quentes.

Para o conseguir, primeiro avaliamos a abundância relativa e fizeram amostragens em diversos pontos da costa portuguesa na temporada das marés vivas, em Outubro de 2020 e no final de Maio e Junho de 2021. Os locais amostrados foram três no norte de Portugal (Ancora, Montedor, e Viana do Castelo) e três no Sul (Carrapateira, Sagres e Lagos). Em detalhe, as amostragens foram feitas no intertidal inferior, médio e superior e as amostras foram separadas pelos distintos habitats considerados: emerso e submerso e ao sol ou sombra, o que ajudou a identificação de algumas espécies. A abundância relativa das espécies foi avaliada tomando notas e vídeos antes de começar a recolher as algas marinhas e depois, após a amostragem, se atribuiu a cada espécie um valor de abundância de 0 a 4, seguindo uma escala DAFOR modificada: 4 - Dominante, 3 - Frequente, 2 - Observada, 1 - Rara, e 0 – ausente. Este formato foi utilizado previamente em anteriores estudos. Depois, as amostras recolhidas foram armazenadas em forma de herbário ou em solução KEW (contendo formol), para posterior inspeção, e identificadas com a ajuda de guias visuais e chaves taxonómicas das algas marinhas da zona. Para confirmar as identificações das espécies, fotografias foram tiradas através do microscópio e da lupa disponíveis.

Uma lista de controlo com 184 taxas diferentes foi obtida das campanhas de amostragem, das quais 121 foram classificadas no phylum Rhodophyta, 39 Ochrophyta, e 22 Chlorophyta. Os dados de abundância relativa permitiram detetar não só mudanças sazonais, mas também tendências a longo prazo, por exemplo, espécies de água fria que eram dominantes num período, e agora raras, e que provavelmente num futuro próximo desapareçam devido ao aquecimento global (caso da *Saccharina latissima*), mesmo que isto não tenha sido incluído no estudo. Em relação com às alterações sazonais, encontramos alterações na abundância relativa de espécies

como *Pterocladiella capillacea*, *Gymnogongrus crenulatus*, e *Saccorhiza polyschides*, que eram mais abundantes em Outubro de 2020 do que em Junho de 2021. Além disso, a amostragem de Junho de 2021 foi especificamente útil para detetar espécies sazonais tais como *Desmarestia ligulata*, *Undaria pinnatifida*, e a nova *Rugulopteryx okamurae*. Este estudo também relata a nova presença de *Plocamium lyngbyanum* que foi detectada em 2020 no sul de Portugal. Estas novas espécies são crípticas, e semelhantes às nativas *Dictyota dichotoma* e *P. cartilagineum.*

Uma vez obtida a lista de controlo das campanhas de amostragem, a riqueza relativa e absoluta de 217 taxa foi comparada entre os anos 60 e 2003 a 2020 e 2021. As espécies foram classificadas em quatro grupos provenientes de diferentes províncias: Cosmopolitas, Lusitanias, do Norte, e do Sul. Os resultados indicaram que a riqueza relativa dos principais grupos aumentou geralmente no caso do grupo Cosmopolita, especialmente em Ancora e Montedor. Os grupos Lusitania e do Sul mantiveram aproximadamente a sua riqueza relativa a partir dos anos 60, embora esta última estivesse mais presente em 2003. Além disso, não foram encontradas espécies do Norte nos sítios do Sul de Portugal. Em relação ao número absoluto de espécies, em geral, o número aumentou ligeiramente desde os anos 60, mas diminuiu em 2021, semelhante ao caso das espécies lusitanas.

As espécies do Norte passaram de ser 20-21 espécies dos anos 60/2003 para 7-8 espécies em 2020/2021. Esta diminuição representou o desaparecimento de 62% das espécies do Norte em menos de 20 anos. No caso das espécies de águas frias, 13 espécies foram detetadas não encontradas nas campanhas de amostragem dos anos 60 e 2003. Por exemplo, as conspícuas *Chorda filum*, *Desmarestia aculeata*, *Himanthalia elongata*, *Laminaria hyperborea*, *Saccharina latissima*, e *Palmaria palmata*. Estas espécies fornecem uma quantidade abundante de biomassa, diversidade, e proteção costeira. Em contraste com *Gelidium corneum* que aumentou em abundância que parece que não vai a desaparecer.

No caso das espécies do Sul, estas também diminuíram, passando de 20-36 espécies para 12-10 espécies, representando uma diminuição de 52-72% desde os anos 60 e 2003 até ao presente, respetivamente. As espécies Cosmopolita dominaram em número absoluto e relativo em todos os locais. Este facto indica que a flora se inclina para a simplificação e acabará, se não já, por ser composta por espécies cosmopolitas não nativas. Especialmente, em finais de Junho de 2021 em Lagos, a espécie *R. okamurae* foi encontrada. Esta espécie mostrou-se extremamente dominante, formando uma manta castanha submersa no sublitoral superior e no intertidal. Em 2020, foram encontradas 77 espécies e em 2021, apenas 33 espécies foram encontradas, o que significa uma diminuição de 57% das espécies, provavelmente associado ao aumento de *R. okamurae.* Nas poças do intertidal grandes espécies como *Sargassum flavifolium* e *Gongolaria montagnei* foram encontradas em Outubro de 2020, mas não em Junho de 2021.

Para concluir, embora este estudo seja uma abordagem taxonómica, encontramos indicações dos possíveis impactos da mudança climática na biodiversidade marinha, já que especialmente os eventos extremos, tais como ondas de calor e fortes tempestades podem afetar negativamente a sobrevivência das algas marinhas. É necessária mais investigação para avaliar a resposta do resto da flora intertidal portuguesa às alterações climáticas, pois este estudo abrange apenas os locais anteriormente estudados do Norte e do Sul e precisaria de mais locais amostrados para determinar as mudanças de distribuição destas algas marinhas. Por outro lado, é preciso continuar a estudar as espécies invasoras não nativas e os seus possíveis efeitos negativos na comunidade nativa. No caso das algas marinhas, a monitorização de *R. okamurae* é imperativa, uma vez que transforma a paisagem marítima.

Introduction

With the increasing rate of climate change, the sea surface temperature (SST) of the CCUS (Canary Current Upwelling System) is warming faster than the global average (Barton et al., 2013) and cooling less (Meneghesso, 2019). The upwelling of the Portuguese coast is not constant all year round, and the increase or decrease of the intensity can last decades (Leitão et al., 2019). The warming of this region was detected by Lima et al. (2007) and Berecibar (2011), among others, which is known to cause a change in the functional groups of the ecosystem as the larger brown seaweeds disappear due to thermal stress (Meneghesso, 2019). Moreover, the distribution ranges of large cold-water species in the north-west Iberia are contracting, and smaller warmer-water species are replacing them (e.g., Díez et al., 2012; Fernández, 2016; Piñeiro-Corbeira et al., 2016).

The large canopy-forming species (hereafter called *canopies*, e.g., *Himanthalia elongata*, *Laminaria spp.*, *Fucus spp.*), and sub-canopies (e.g., *Chondrus crispus*, *Mastocarpus stellatus, Bifurcaria bifurcata*) decreased in relative abundance, while the turfs (e.g., *Halopteris scoparia*, *Corallina spp.*, *Ceramium spp.*) and the encrusting (e.g., *Lithophyllum incrustans*, *Codium adhaerens*) groups have increased in the last 15 years (Meneghesso, 2019).

Besides the SST, the air temperature also affects the intertidal seaweeds' survival (Ramos et al., 2020). When exposed to consecutive heatwaves during emersion phases, the air temperature has a cumulative effect on physiological performance and mortality (Román et al., 2020). Air temperature is also experimenting heatwaves (HW) from the Sahara, with an increase of extreme summers in the last decades (Sousa et al., 2020), which can impact seasonality by decreasing the resistance to unwanted epiphytes, therefore jeopardizing the survival of individuals (Wahl et al., 2020). In addition to this, the Northern Atlantic Oscillation (NAO), together with European Blocking, can contribute to the intensity and persistency of heatwaves (Li et al., 2020).

Marine heatwaves (MHWs) are prolonged periods of atypically high SST (Hobday et al., 2016), and their impacts have been widely studied (reviewed in Oliver et al., 2021). From 1925 to 2016, the global MHWs average increased 34% in frequency and 17% in duration, increasing the total number of annual MHW days to 54% (Oliver et al., 2018). The main effects of this phenomena on seaweeds are the decrease in the abundance of canopies and an increase in turfs, even with the local extinction of some canopy species (reviewed in Straub et al., 2019). Also, the MHWs are known to impact other critical primary producers such as seagrasses (Arias-Ortiz et al., 2018).

The compromised CCUS (Meneghesso, 2019) together with the increasing frequency and intensity of MHWs (Oliver et al., 2018) and HWs (Sousa et al., 2020) affect the performance of seaweeds, having an impact on the seaweed communities and their ecological function (Román et al., 2020). Changes in biodiversity and ecosystem functioning were detected in the last decades, for instance in the north of Spain and in the north-eastern Atlantic (e.g.: Muguerza et al., 2017; Meneghesso, 2019), but recent work on the Portuguese Iberian coast needs updating.

Different methods have been used to detect these changes in the seaweed ecosystem, such as focusing on genetic information of one species over an extensive range to tell historical range dynamics (e.g., Neiva et al., 2012, 2014; Assis et al., 2017). Others, used taxonomical identification to focus on a group of species to assess the general effect of climate change (e.g., Gallon et al., 2014; Lima et al., 2007; Piñeiro-Corbeira et al., 2016), or focus on all the species possible to infer adaptive responses of the ecosystem (e.g., Berecibar, 2011; Wernberg et al., 2011, 2016). One example is Wernberg et al., (2011), where they consulted herbariums of Australia from the 1940s to early 2000s, besides monitoring, to show the range shifts poleward and how 25% of the species might face extinction under future warming temperatures. Lima et al., (2007) measured the range shifts of the extensive Portuguese intertidal flora and found a net poleward shift only for the warm-water species. Past studies focused on the changes in distribution (e.g., Berecibar, 2011; Lima et al., 2007; Wernberg et al., 2011) and on the difference in the ecological role of seaweeds in the ecosystem (Meneghesso, 2019; reviewed in Straub et al., 2019). Furthermore, using as many species as possible allow a proper assessment of ecosystem's resilience and services (Straub et al., 2019).

The present study takes place after the recent heatwaves (Sousa et al., 2020), which may show novel changes in the biodiversity across the continental Portuguese coast. The aim is to see how the seaweed communities at distribution limits have been affected since the 1960s (Ardré, 1970, 1971) and 2003 (Berecibar, 2011) using a taxonomical approach.

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Invasion of the Reds? Long-term shifts on intertidal seaweed at distribution limits

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Keywords: distribution limits, biodiversity, climate change, Portugal, seaweed

Abstract

The effects of climate change on biodiversity are well documented on the Portuguese intertidal marine flora. However, heatwaves and extreme events have been increasing in frequency and intensity since the last assessment. The present study aims to update the Portuguese intertidal macroalgae database and see how it changed since 2003 and its baseline in the 1960s. To achieve this objective, we assessed the relative abundance and sampled, for subsequent taxonomical identification, in October 2020, and in late May and late June 2021 in the north (Ancora, Montedor, and Viana do Castelo) and in the south (Carrapateira, Sagres, and Lagos) of Portugal, which coincides with the rear-edge distributions of many cold and warm-water species. In the sampling campaigns, we identified 184 different taxa and determined their relative abundance. From 2003, we observed a 62% and 72% decrease in Northern and Southern species, respectively, while the Cosmopolitan species dominated. Also, from the 13 cold-water species not detected in the sampling campaigns, *Himanthalia elongata, Laminaria hyperborea*, and *Saccharina latissima* can be highlighted since, for instance, these provide an abundant quantity of biomass, diversity, and coastal protection. Last, the novel presence of the invasive *Rugulopteryx okamurae* in the intertidal, in Lagos 2021, meant a 57% decrease in the macroalgae species richness. These flora changes may be related to climate change it negatively impacts the survival of seaweeds. Further research is needed to see how the rest of the Portuguese intertidal flora is facing climate change and which effects can cause. In addition, monitoring of *R. okamurae* is imperative as it negatively transforms the seascape.

Introduction

Seaweeds are important primary producers that provide many ecosystem functions and services such as habitat and food for other organisms (compiled in Hurd et al., 2014), including many utilities for human use (Gaspar et al., 2019). However, extreme seawater temperatures threaten seaweeds (Piñeiro-Corbeira et al., 2018), but when found in the intertidal, these are also affected by high air temperatures (e.g., Ramos et al., 2020b; Román et al., 2020), strong wave action (e.g., Pereira et al., 2017; Piñeiro-Corbeira et al., 2016), and freshening events (e.g., Kinnby et al., 2021; McKnight et al., 2021). Climate change can simplify the seaweed community modifying the functioning and the services these organisms can provide (Muguerza et al., 2017). These transformations can have profound ecological and socioeconomic implications (Wernberg et al., 2016).

The world is already seeing a faster and more acute climate change (IPCC, 2021). This human-induced climate change represents global warming in the form of severe storms (Stojanovic et al., 2021), and longer and more frequent heatwaves (Sousa et al., 2020). In the marine system, the upwelling currents are cooling less (Meneghesso, 2019) and the Canary upwelling system is warming even faster than the average (Barton et al., 2013). The Marine Heat Waves (MHWs) have been widely studied (reviewed in Oliver et al., 2021), and these are disrupting the ecological goods and services for the upcoming decades (Smale et al., 2019).

With climate change, the natural seasonal fluctuations are more aggravated and affect the intertidal community (Wahl et al., 2020). For example, the main effects of MHWs on seaweeds are the downgrading ecosystem structure with cases of local extinction of some canopy species (reviewed in Straub et al., 2019). Due to warming, in Australia, the seaweed communities have shifted poleward, and with given future warming, about 25% of the species might face extinction (Wernberg et al., 2011). Moreover, marine species shift poleward six times faster than terrestrial species (Lenoir et al., 2020). Predictions expect significant contractions of large habitat-forming seaweeds (Martínez et al., 2018) even though the relative abundance has decreased over the last two decades in the NE Atlantic (Meneghesso, 2019). As the habitat-forming seaweed group is a valuable CO2 sink (Wilmers et al., 2012) this process could have more negative implications than initially thought.

Moreover, extreme fluctuations due to climate change might benefit non-native over the native species and be worse than just global warming (McKnight et al., 2021). Another importance of doing such a study is the skewed perception of the ecosystems due to global warming and biological invasions. This phenomenon is called the shifting baseline syndrome (SBS), when the present state of the ecosystem is thought to be the normal and unchanged (Soga & Gaston, 2018). Assessing the variations during decades and reevaluating the study of species as the primary ecosystem factor could revert SBS (Gravina et al., 2020).

In Portugal, the upwelling is not constant all year round, and the increase or decrease of the intensity can last decades (Leitão et al., 2019). The upwelling makes this zone the range-edge distribution of the cold-water species and the warm-water species, coinciding with the southern and northern range of these, respectively (Ardré, 1971; Hoek, 1975). With all mentioned above, this zone is seeing significant distributional changes (Berecibar, 2011; Lima et al., 2007; Piñeiro-Corbeira et al., 2016) and extreme climate events lately (Oliveira et al., 2020; Stojanovic et al., 2021). Furthermore, researchers predicted large brown seaweeds' distributions to shift poleward and even become locally extinct in Portugal (Assis et al., 2016 & 2017). However, recent reviews and studies (e.g., Casado-Amezúa et al., 2019; Straub et al., 2016) use the research of Lima et al. (2007) as an indicator of the state of the Portuguese flora. With this said, it is necessary to update the Portuguese database as many extreme events have happened since 2006.

The seaweed resources are of great value (Gaspar et al., 2019) and having an updated list of the species is of great importance. Moreover, a recent in-depth study of the complete macroalgae diversity of the intertidal is needed. In this study, we reevaluated the species richness and relative abundance of the sites sampled in the late 50s and early 60s (Ardré, 1970, 1971) and in 2003 (Berecibar, 2011) to understand better and manage our changing ecosystems. We expect the northern species, cold-water species, to decrease in richness and abundance while the southern species, warm-water species, to increase. Also, we expect to see more non-indigenous species since these are increasing with globalization (Chainho et al., 2015).

Materials and methods

Study area and sampling sites

The study area is in Portugal, three sites in the North: Ancora (41°47'48.3"N 8°52'27.4"W), Montedor (41°44'40.3"N 8°52'41.1"W), and Viana do Castelo (41°41'45.6"N 8°51'07.6"W); and three sites in the South: Carrapateira (37°11'55.1"N 8°54'21.9"W), Sagres - Praia da Ingrina (37°02'44.8"N 8°52'40.8"W), and Lagos - Dona Ana (37°05'22.5"N 8°40'07.7"W), see *Figure 1*.

Data collection

Sampling

The sampling was performed during spring tides in October 2020 and in late May and late June 2021. The locations sampled coincide with the ones sampled by Ardré in the 1960s (Ardré, 1970, 1971), and by Berecibar in 2003 (Berecibar, 2011). The seaweeds were collected in the intertidal, distinguishing between lower, middle, and upper intertidal zones. Within each zone, all the specific habitat combinations were sampled between shade or sunlight and emersed or submerged (rocky pools). When the samples were collected, most were pressed and stored in the form of Herbarium, and the small and sensitive individuals were stored in KEW solution (40% seawater, 40% ethanol (70%), 10% glycerine, and 10% formalin) for better preservation, and future inspection.

Identification

Individuals were inspected using a magnifying glass (Leica M165C, Leica Microsystems, Germany*)* and microscope (Aixoskop 2, Oberkochen, Germany*)* and identified to the lowest taxonomic level. For this purpose, the visual guides (Bárbara, 2012, 2014; Brodie et al., 2007; Pérez Lloréns et al., 2012; Rodriguez-Prieto et al., 2013), taxonomic books (e.g.: Maggs & Hommersand, 1993) and articles (Díaz-Tapia & Bárbara, 2013, 2014), of the macroalgae of the zone were used. The nomenclature was updated with the Algaebase database (Guiry & Guiry, 2021).

To handle preserved samples, the Herbarium individuals were rehydrated with a mix of water and a drop of soap, and the individuals from the KEW solution were rinsed with seawater and left overnight in the fume hood for the sample to evaporate formaline.

Relative abundance

During sampling, the relative abundance of the macroalgae species was assessed by noting the species presence and relative abundance. A modified version of the DAFOR scale was used, where 4 = Dominant, 3 = Abundant, 2 = Frequent, 1 = Rare (as in Ardré, 1971 and Berecibar, 2011).

Data analysis

With the aim of comparing historical data, the data from the studies of Ardré (1971) and Berecibar (2011) were used. Berecibar's (2011) geographical distribution classification of each species, based on the phytogeography provinces was followed here: *Cosmopolitan*, found in all temperate oceans; *Lusitanian*, found from the colder northern European to the southern flora of the Mediterranean Sea, Macaronesia, and North Africa, as defined; *Northern*, usually found in colder waters of northern Europe; and *Southern*, distribution limited by the tolerance of the highest temperature as in Hoek (1975). For this analysis, 217 taxa were used where 118 sp. and 5 spp. belong to Cosmopolitan, 38 sp. to Lusitanian, 23 sp. to Northern, and 38 sp. to Southern phytogeography provinces. The doubted taxa were either simplified to genus or not included in the comparison. The seaweed was separated by province group, location, and year. Then, for the comparison, only the presences were used per group divided by the site's total and year, resulting in a proportion. The proportion allowed us to compare how the different seaweed groups varied in the sites and the four different periods: late 1950s-early 1960s (Ardré, 1971), 2003 (Berecibar, 2011), 2020, and 2021 (this study).

Moreover, to see if and how the different seaweed groups vary in these periods, absolute numbers of species present were used. However, it must be taken into account that the sampling and identification efforts were different, due to different observers. The seasonal differences were assessed by comparing the localities sampled in October 2020 and June 2021. In the case of Lagos, where in June 2021 an invasion by large quantities of *Rugulopteryx okamurae* was observed, the overall species richness of October 2020 and June 2021 were compared to test the effects of the invasion.

Results

In the sampling campaigns performed for this study, 1.270 individuals were pressed and identified, of which 184 different taxa were identified and quantified. Of these, 170 were identified to species level (114 Rhodophyta, 37 Ochrophyta, and 19 Chlorophyta), 12 to genus level (7 Rhodophyta, 2 Ochrophyta, and 3 Chlorophyta), and two taxa are stages that have a different name than the species (only Rhodophyta). Furthermore, the new additions to the Portuguese flora *Plocamium lyngbyanum* (main characteristics shown in Figure 1), found once in Carrapateira in 2020, and *R. okamurae* (main characteristics shown in Figure 2), found dominating in Lagos in 2021, are both cryptic to native species *P. cartilagineum* and *Dictyota dichotoma*.

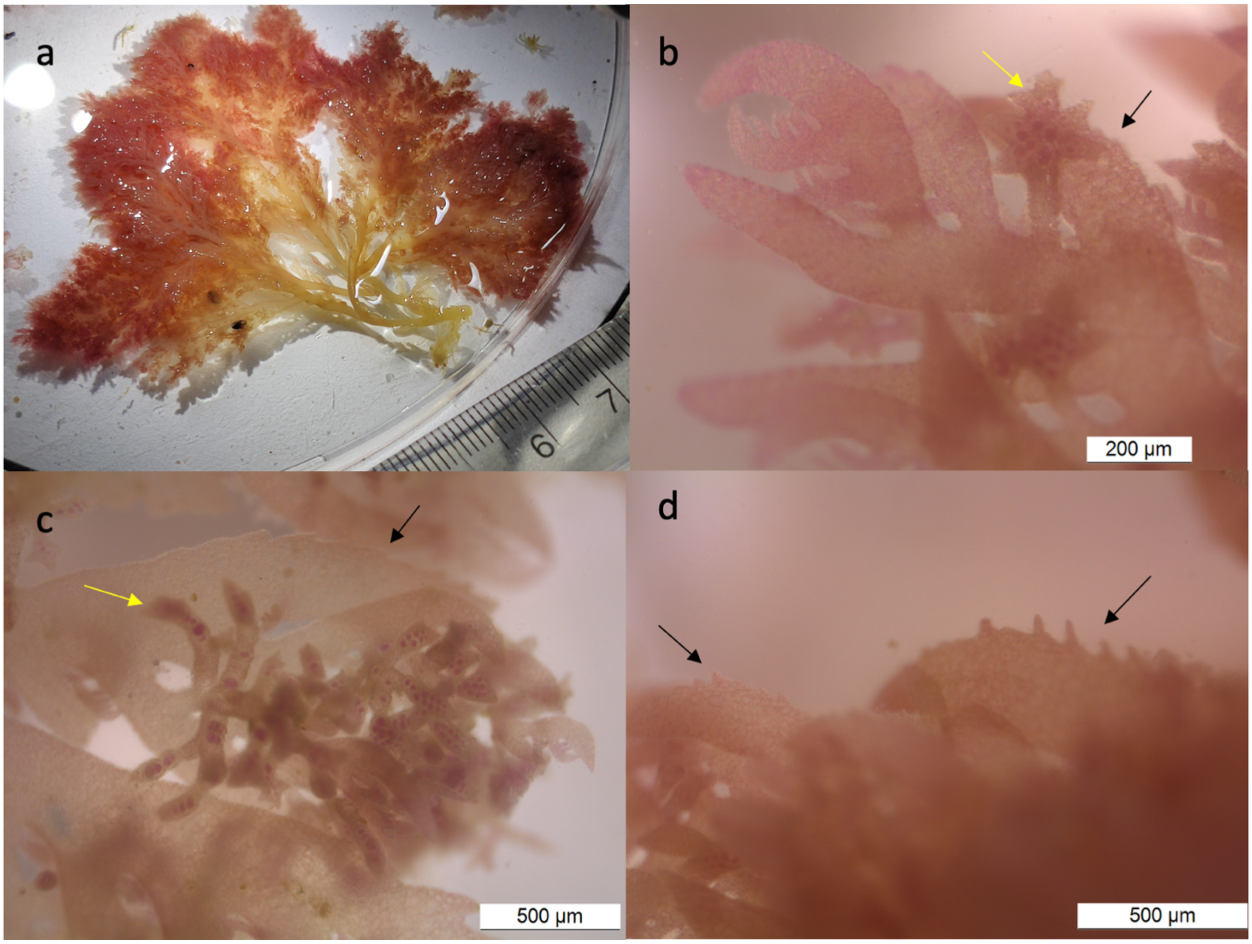

Figure 1. *Plocamium lyngbyanum*, collected in Carrapateira October 2020. **a**: Habit of a fertile tetrasporophyte bearing stichidia (darker reddish parts). **b**: Juvenile stichidia palmately divided (yellow arrow). **c**: Old compound stichidia with third-order ramification (yellow arrow). **d**: Detail of ramuli with serrated margins (black arrow), as also seen in *a*, *b*, and *c*.

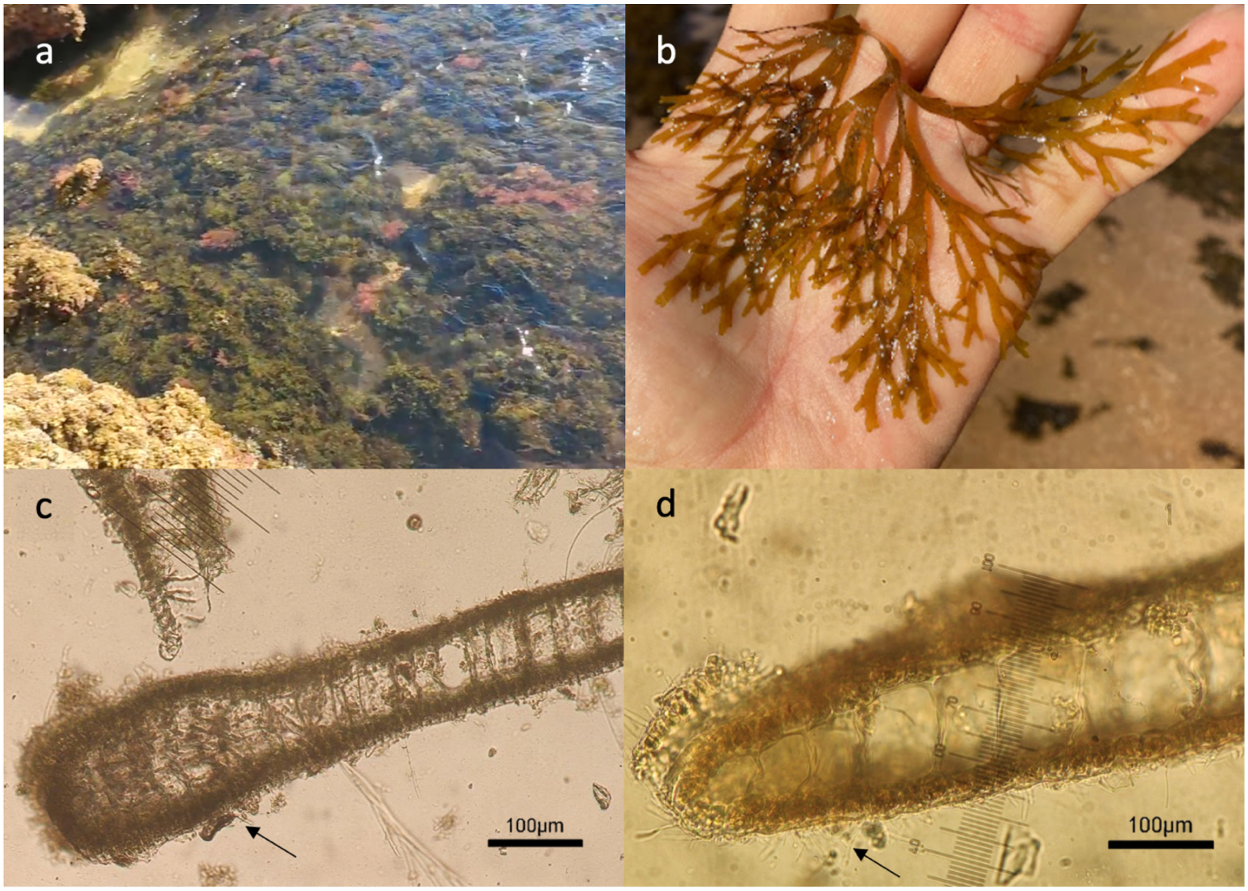

Figure 2. *Rugulopteryx okamurae*, collected in Lagos June 2021. **a**: Upper subtidal covered with *R. okamurae* (brownish) and *Asparagopsis armata* on top (reddish seaweed). **b**: Habit view of *R. okamurae* with its characteristic alternate branching but undulations of the thallus cannot be appreciated. Macroscopic picture taken by Rui Santos. **c**: Transversal section with the multilayered medulla at the margin of the thallus (arrow). **d**: Transversal section of the native species *D. dichotoma* showing a unicellular medulla (arrow).

Regarding the relative abundances, the historical native species are generally less abundant than in the past, if not absent. Also, few species dominate per site, where many species are only present once in one site (see Table 1). The sampling happened at the beginning of Autumn of 2020 and in the late Spring/beginning Summer of 2021. This change in seasonality is noticed in species relative abundances and seasonal species' presence or absence. For example, on one hand, *Cryptopleura ramosa*, *Pterocladiella capillacea,* and *Gymnogongrus griffithsiae* were dominant in the sites of the north in October 2021 but less or absent in May 2020. On the other hand, *Desmarestia ligulata* and *Undaria pinnatifida* were only found in May 2021 (see Table 1). More, *Lyngbya confervoides* and *Rivularia bullata*, cyanobacteria, was found cryptic resembling the seaweed *Ectocarpus spp.* and *Valonia spp.*, respectively.

Table 1. Checklist of the intertidal seaweed, and cyanobacteria, found in the sampling campaigns in 2020 (a) and 2021 (b), and the relative abundance associated (from 1 to 4: 4 = Dominant, 3 = Abundant, 2 = Frequent, 1 = Rare). A, Ancora; M, Montedor; V, Viana do Castelo; C, Carrapateira; S, Sagres; L, Lagos. Order of the checklist followed from Araújo et al. (2009). "": stage of the species above; ?: there is uncertainty of the identification of the species in a particular site.

Phylum	Order	Family	Genus	Species	A	M	V	C	S	L
CYANOBACTERIA	OSCILLATORIALES	OSCILLATORIACEAE	*Lyngbya* C. Agardh	*Lyngbya confervoides* C.Agardh ex Gomont 1892					2b	
	NOSTOCALES	RIVULARIACEAE	*Rivularia* C.Agardh ex Bornet & Flahault	*Rivularia bullata* Berkeley ex Bornet & Flahault 1886					2a	
RHODOPHYTA	BANGIALES	BANGIACEAE	*Porphyra* C. Agardh	*Porphyra linearis* Greville 1830	3b	3b	2b	2b		
				Porphyra umbilicalis Kützing 1843	2b	2a, 1b				
	PALMARIALES	RHODOTHAMNIELLACEAE	*Rhodothamniella* Feldmann	*Rhodothamniella floridula* (Dillwyn) Feldmann 1978		1a				
	AHNFELTIALES	AHNFELTIACEAE	*Ahnfeltia* Fries	*Ahnfeltia plicata* (Hudson) E.M.Fries 1836		2a				
	NEMALIALES	NEMALIACEAE	*Nemalion* Duby	*Nemalion elminthoides* (Velley) Batters 1902	1a, 2b		2b	2a		
		SCINAIACEAE	*Scinaia* Bivona-Bernardi	*Scinaia furcellata* (Turner) J.Agardh 1851	1a, 3b	3b	1a, 3b			
	GELIDIALES	GELIDIACEAE	*Gelidium* J.V. Lamouroux	*Gelidium corneum* (Hudson) J.V.Lamouroux 1813	2a	2b	3a, 3b	1a, 4b		
				Gelidium crinale (Hare ex Turner) Gaillon 1828	3b		1a	1a	2a	1a
				Gelidium pulchellum (Turner) Kützing 1868	4a, 3b	3a, 3b	4a, 3b	3b	1a, 2b	4b
				Gelidium pusillum (Stackhouse) Le Jolis 1863	3a	3a	2a	1a		4a
				Gelidium spinosum (S.G.Gmelin) P.C.Silva 1996				3a, 4b	3a, 3b	2a, 3b
		PTEROCLADIACEAE	*Pterocladiella* Santelices et Hommersand	*Pterocladiella capillacea* (S.G.Gmelin) Santelices & Hommersand 1997	4a, 2b	4a, 3b	4a, 3b	2a, 1b	1a	4a
	GRACILARIALES	GRACILARIACEAE	*Gracilaria* Greville	*Gracilaria gracilis* (Stackhouse) Steentoft, L.M.Irvine & Farnham 1995			2a, 1b			
	BONNEMAISONIALES	BONNEMAISONIACEAE	*Asparagopsis* Montagne	*Asparagopsis armata* Harvey 1855	2a, 3b	1a, 3b	2a, 3b	4a, 4b	2a, 4b	3a, 3b
				''*Falkenbergia rufolanosa*'' (Harvey) F. Schmitz	4a, 3b	2a, 2b	3a	2a	4a	2a
				Asparagopsis taxiformis (Delile) Trevisan 1845						1a, 1b
	CRYPTONEMIALES	DUMONTIACEAE	*Dilsea* Stackhouse	*Dilsea carnosa* (Schmidel) Kuntze 1898	1b		2a, 2b			

Table 2 (continued)

Phylum	Order	Family	Genus	Species	A	M	V	C	S	L
		HALYMENIACEAE	*Cryptonemia* J. Agardh	*Cryptonemia seminervis* (C.Agardh) J.Agardh 1846				1b	2b	
			Grateloupia C. Agardh	*Grateloupia filicina* (J.V.Lamouroux) C.Agardh 1822		1a				
				Grateloupia turuturu Y.Yamada 1941	3a, 4b	2a, 2b	4a, 3b			
		KALLYMENIACEAE	*Metacallophyllis* A. Vergés & L.Le Gall	*Metacallophyllis laciniata* (Hudson) A.Vergés & L.Le Gall 2017	2a	4a, 3b	4a, 3b		1b	
	HILDENBRANDIALES	PEYSSONNELIACEAE	*Peyssonnelia* Decaisne	*Peyssonnelia bornetii* Boudouresque & Denizot 1973						1a
				Peyssonnelia squamaria (S.G.Gmelin) Decaisne ex J.Agardh 1842					2a	2a
				Peyssonnelia coriacea Feldmann 1941						1a
				Peyssonnelia sp. Decaisne 1841					3b	3b
		HILDENBRANDIACEAE	*Hildenbrandia* Nardo	*Hildenbrandia rubra* (Sommerfelt) Meneghini 1841	2b	2b	2a, 3b	2b	1b	2a, 2b
				Hildenbrandia sp. Nardo, 1834				2a, 2b	1a	2a, 2b
	CORALLINALES	CORALLINACEAE	*Corallina* Linnaeus	*Corallina ferreyrae* E.Y.Dawson, Acleto & Foldvik 1964					2a	1a
				Corallina officinalis Linnaeus 1758	2a, 2b	4a, 2b	4a, 2b			
			Ellisolandia K.R.Hind & G.W.Saunders	*Ellisolandia elongata* (J.Ellis & Solander) K.R.Hind & G.W.Saunders 2013	3a, 4b	3a, 4b	4a, 2b	4a, 4b	2a, 4b	4a, 4b
			Jania J.V. Lamouroux	*Jania longifurca* Zanardini 1844	1a	2a, 3b	2a, 2b	3a, 2b	4a, 1b	1a
				Jania rubens (Linnaeus) J.V.Lamouroux 1816	2a, 2b	1a, 2b	2b	2a, 2b	2a	4a, 1b
				Jania sp. J.V.Lamouroux, 1812				2b	1a	2a, 1b
		LITHOPHYLLACEAE	*Amphiroa* J.V.Lamouroux	*Amphiroa beauvoisii* J.V.Lamouroux 1816				1b	2a, 3b	1a, 2b
			Lithophyllum Philippi	*Lithophyllum byssoides* (Lamarck) Foslie 1900	2a, 2b		3a	2a, 2b	2a, 2b	2a, 2b
				Lithophyllum incrustans Philippi 1837	3a, 3b	2a, 2b	2a, 2b	2a, 2b	2a, 2b	1a, 1b
			Titanoderma Nägeli	*Titanoderma pustulatum* (J.V.Lamouroux) Nägeli 1858	3a		4a			
		MESOPHYLLUMACEAE	*Mesophyllum* Lemoine	*Mesophyllum alternans* (Foslie) Cabioch & M.L.Mendoza 1998				2b	3b	

Table 3 (continued)

Phylum	Order	Family	Genus	Species	A	M	V	C	S	L
				Mesophyllum expansum (Philippi) Cabioch & M.L.Mendoza 2003					3b	3b
				Mesophyllum lichenoides (J.Ellis) Me.Lemoine 1928	1a				2a, 2b	2a, 2b
	GIGARTINALES	CAULACANTHACEAE	*Catenella* Greville	*Catenella caespitosa* (Withering) L.M.Irvine 1976			2a, 2b			3b
			Caulacanthus Kützing	*Caulacanthus ustulatus* (Turner) Kützing 1843	2a, 3b	2a, 2b	3a, 4b	4a, 3b	4a, 3b	4a, 2b
		GIGARTINACEAE	*Chondracanthus* Kützing	*Chondracanthus acicularis* (Roth) Fredericq 1993	2a, 4b	2a, 2b	4a, 3b	4a, 4b	4a, 2b	4a, 2b
				Chondracanthus teedei (Mertens ex Roth) Kützing 1843	4a, 3b	4a, 3b	4a, 2b	2a, 3b	1a, 3b	2a, 1b
				Chondracanthus teedei var. lusitanicus (J.E.De Mesquita Rodrigues) Bárbara & Cremades 1996	2a	2a	1a?			
			Chondrus Stackhouse	*Chondrus crispus* Stackhouse 1797	4a, 2b	2a, 2b	4a, 2b			
			Gigartina Stackhouse	*Gigartina pistillata* (S.G.Gmelin) Stackhouse 1809	4a, 4b	3b	4a, 3b			
		CYSTOCLONIACEAE	*Calliblepharis* Kützing	*Calliblepharis ciliata* (Hudson) Kützing 1843	1a		2a, 1b			
				Calliblepharis jubata (Goodenough & Woodward) Kützing 1843	3a,1b	1b	3a, 1b			
			Hypnea J.V. Lamouroux	*Hypnea musciformis* (Wulfen) J.V.Lamouroux 1813			1b?			
		PHYLLOPHORACEAE	*Ahnfeltiopsis* P.C. Silva et DeCew	*Ahnfeltiopsis devoniensis* (Greville) P.C.Silva & DeCew 1992	3a, 2b	1a, 2b	2a, 3b	3a, 4b	3a, 1b	3a
			Gymnogongrus Martius	*Gymnogongrus crenulatus* (Turner) J.Agardh 1851	4a, 2b	1a, 3b	4a	1a	1a, 2b	1a
				Gymnogongrus griffithsiae (Turner) C.Martius 1833		1a	3a			1a
			Mastocarpus Kützing	*Mastocarpus stellatus* (Stackhouse) Guiry 1984	2a, 4b	3a, 3b	2a, 2b			
				‘‘*Petrocelis cruenta*’’ J. Agardh	2b	1b	2a, 3b			
			Phyllophora Greville	*Phyllophora crispa* (Hudson) P.S.Dixon 1964			1a			
	PLOCAMIALES	PLOCAMIACEAE	*Plocamium* J.V. Lamouroux	*Plocamium cartilagineum* (Linnaeus) P.S.Dixon 1967	4a, 2b	4a, 3b	4a, 3b	4a, 3b	4a, 2b	4a, 2b

Table 4 (continued)

Phylum	Order	Family	Genus	Species	A	M	V	C	S	L
				Plocamium lyngbyanum Kützing 1843				1a		
				Plocamium maggsiae G.W.Saunders & Lehmkuhl 2005				2a, 3b	2a	2b
				Plocamium raphelisianum P.J.L.Dangeard 1949				2a, 3b		3a
	RHODYMENIALES	CHAMPIACEAE	*Champia* Desvaux	*Champia parvula* (C.Agardh) Harvey 1853	2a	2a	2a, 1b	4a, 3b	3a	4a
			Gastroclonium Kützing	*Gastroclonium ovatum* (Hudson) Papenfuss 1944	2a, 2b	1a, 2b	4a	2b	1a, 2b	2a, 1b
		LOMENTARIACEAE	*Lomentaria* Lyngbye	*Lomentaria articulata* (Hudson) Lyngbye 1819	1a	1a, 3b	4a, 1b	3a, 3b		2a
				Lomentaria clavellosa (Lightfoot ex Turner) Gaillon 1828				1a		2a
				Lomentaria orcadensis (Harvey) Collins 1937				1a, 3b		
		RHODYMENIACEAE	*Rhodymenia* Greville	*Rhodymenia holmesii* Ardissone 1893			1a	2a, 1b	1a	
				Rhodymenia pseudopalmata (J.V.Lamouroux) P.C.Silva 1952						1a
	CERAMIALES	CALLITHAMNIACEAE	*Aglaothamnion* Feldmann-Mazoyer	*Aglaothamnion feldmanniae* Halos, 1965					1a	
				Aglaothamnion pseudobyssoides (P.Crouan & H.Crouan) Halos 1965					1a	
				Aglaothamnion tripinnatum (C.Agardh) Feldmann-Mazoyer 1941	1a			2a		1a
			Callithamnion Lyngbye	*Callithamnion tetragonum* (Withering) S.F.Gray 1821				2a		
			Gaillona Bonnemaison	*Gaillona hookeri* (Dillwyn) Athanasiadis 2016						2a
			Spyridia Harvey	*Spyridia griffithsiana* (J.E.Smith) G.C.Zuccarello, Prud'homme & H.Stegenga 2004						1a
		CERAMIACEAE	*Centroceras* Kützing	*Centroceras clavulatum* (C.Agardh) Montagne 1846					1a	2a
			Ceramium Roth	*Ceramium ciliatum* (J.Ellis) Ducluzeau 1806	1a		2a, 3b	3a, 4b	4a, 4b	4a, 2b

Table 5 (continued)

Phylum	Order	Family	Genus	Species	A	M	V	C	S	L
				Ceramium echionotum J.Agardh 1844	1a	1a		4a		2a
				Ceramium sp. Roth 1797	4a	4a	4a	4a		2a
			Gayliella Cho, McIvor et Boo	*Gayliella flaccida* (Harvey ex Kützing) T.O.Cho & L.J.McIvor 2008				2a	1a	
			Pterothamnion Nägeli	*Pterothamnion crispum* (Ducluzeau) Nägeli 1862				1a	1a	2a
				Pterothamnion plumula (J.Ellis) Nägeli 1855						2a
		DASYACEAE	*Dasya* C. Agardh	*Dasya hutchinsiae* Harvey 1833				3a	1a	4a
				Dasya ocellata (Grateloup) Harvey 1833				1a		
			Heterosiphonia Montagne	*Heterosiphonia plumosa* (J.Ellis) Batters 1902	2a, 2b	3b	2b			
		DELESSERIACEAE	*Acrosorium* Zanardini ex Kützing	*Acrosorium ciliolatum* (Harvey) Kylin 1924	1b	1b	2a, 3b	1a	2a, 3b	3a, 4b
			Apoglossum J. Agardh	*Apoglossum ruscifolium* (Turner) J.Agardh 1898	1b			2a, 2b	1b	3a
			Cryptopleura Kützing	*Cryptopleura ramosa* (Hudson) L.Newton 1931	4a	1a	4a, 1b	1a		
			Dasysiphonia I.K.Lee & J.A.West	*Dasysiphonia japonica* (Yendo) H.-S.Kim 2012						1a
			Erythroglossum J. Agardh	*Erythroglossum laciniatum* (Lightfoot) Maggs & Hommersand 1993				1a		
			Haraldiophyllum A.D. Zinova	*Haraldiophyllum bonnemaisonii* (Kylin) A.D.Zinova 1981		1a		2a		1a
			Hypoglossum Kützing	*Hypoglossum hypoglossoides* (Stackhouse) Collins & Hervey 1917	1a	1b		2a	2a, 2b	2a
			Myriogramme Kylin	*Myriogramme minuta* Kylin 1924						1a
			Nitophyllum Greville	*Nitophyllum punctatum* (Stackhouse) Greville 1830	2a, 2b	2a, 2b	3b	3a, 4b	4b	1a
		RHODOMELACEAE	*Aphanocladia* Falkenberg	*Aphanocladia stichidiosa* (Funk) Ardré, 1970						1a
			Carradoriella P. C. Silva, 1996	*Carradoriella denudata* (Dillwyn) Savoie & G.W.Saunders 2019				2a		

Table 6 (continued)

Phylum	Order	Family	Genus	Species	A	M	V	C	S	L
			Chondria C. Agardh	*Chondria coerulescens* (J.Agardh) Sauvageau 1897	3a, 4b	2a, 3b	3a, 3b	3b	3a, 3b	1a, 1b
				Chondria dasyphylla (Woodward) C.Agardh 1817	2b	2a, 3b	2a, 1b	2a	1a	
				Chondria scintillans G.Feldmann 1964		2b	2a, 3b			
			Halopithys Kützing, 1843	*Halopithys incurva* (Hudson) Batters 1902						1a
			Herposiphonia Nägeli	*Herposiphonia tenella* (C.Agardh) Ambronn 1880					2a	2a
			Laurencia J.V.Lamouroux	*Laurencia pyramidalis* Bory ex Kützing 1849			1b			
				Laurencia sp. J.V.Lamouroux, 1813			2a	2b	1a	2a, 2b
			Melanothamnus Bornet & Falkenberg	*Melanothamnus harveyi* (Bailey) Díaz-Tapia & Maggs 2017					1a	
			Osmundea Stackhouse	*Osmundea osmunda* (S.G.Gmelin) K.W.Nam & Maggs 1994	2a?		1a?	1a?		1a?
				Osmundea pinnatifida (Hudson) Stackhouse 1809	4a, 3b	3a, 3b	3a, 3b	3a, 4b	2b	
			Polysiphonia Greville	*Polysiphonia caespitosa* (Pocock) Hollenberg 1968						1a
				Polysiphonia elongata (Hudson) Sprengel 1827	3b	3b	1a, 3b	3b	2b	
				Polysiphonia polyspora (C.Agardh) Montagne 1840	1a	1a				
				Polysiphonia sp. Greville, 1823	1a		1a	2a		1a
			Pterosiphonia Falkenberg	*Pterosiphonia complanata* (Clemente) Falkenberg 1897	4a, 2b	1a, 4b	1a, 3b	4a, 3b	3a, 3b	1a
			Symphyocladia Falkenberg	*Symphyocladia marchantioides* (Harvey) Falkenberg 1897				1a		
			Symphyocladiella D.E.Bustamante, B.Y.Won & T.O.Cho	*Symphyocladiella parasitica* (Hudson) D.Bustamante, B.Y.Won, S.C.Lindstrom & T.O.Cho 2019						2a
			Vertebrata S.F. Gray	*Vertebrata fruticulosa* (Wulfen) Kuntze 1891	2a				1a	
				Vertebrata thuyoides (Harvey) Kuntze 1891	1a	1a	2a		1a	
				Vertebrata hypnoides (Welwitsch) Kuntze 1891						4a
				Vertebrata lanosa (Linnaeus) T.A.Christensen 1967			3a, 3b			

Table 7 (continued)

Phylum	Order	Family	Genus	Species	A	M	V	C	S	L
			Xiphosiphonia Savoie & G.W.Saunders	*Xiphosiphonia ardreana* (Maggs & Hommersand) Savoie & G.W.Saunders 2016				2a		
				Xiphosiphonia pennata (C.Agardh) Savoie & G.W.Saunders 2016	2b	2b			2a, 2b	4a
		WRANGELIACEAE	*Anotrichium* Nägeli	*Anotrichium furcellatum* (J.Agardh) Baldock 1976					2a	3a
			Bornetia Thuret	*Bornetia secundiflora* (J.Agardh) Thuret 1855	2a, 1b	1a, 2b	1a	3a, 1b		3a
			Compsothamnion (Nägeli) F. Schmitz	*Compsothamnion thuioides* (Smith) Nägeli 1862		1b				1a
			Halurus Kützing	*Halurus equisetifolius* (Lightfoot) Kützing 1843	2a, 3b	3b		1b		
				Halurus flosculosus (J.Ellis) Maggs & Hommersand 1993				1a		1a
			Griffithsia C. Agardh	*Griffithsia opuntioides* J.Agardh 1842				1a	1a	2a
				Griffithsia sp. C.Agardh, 1817	1a				1a	3a, 2b
			Pleonosporium Nägeli	*Pleonosporium borreri* (Smith) Nägeli 1862						1a
				Pleonosporium flexuosum (C.Agardh) Bornet 1892				1a	1a	2a
			Ptilothamnion Thuret	*Ptilothamnion sphaericum* (P.Crouan & H.Crouan ex J.Agardh) Maggs & Hommersand 1993					4a	1a
OCHROPHYTA	SPHACELARIALES	CLADOSTEPHACEAE	*Cladostephus* C. Agardh	*Cladostephus spongiosus* (Hudson) C.Agardh 1817					1a, 2b	1a, 2b
		SPHACELARIACEAE	*Sphacelaria* Lyngbye	*Sphacelaria tribuloides* Meneghini 1840						1a
		STYPOCAULACEAE	*Halopteris* Kützing	*Halopteris filicina* (Grateloup) Kützing 1843	2a			1a		1a
				Halopteris scoparia (Linnaeus) Sauvageau 1904	1a	2a	2a, 4b	2a	3a	3a
	DICTYOTALES	DICTYOTACEAE	*Dictyopteris* J.V. Lamouroux	*Dictyopteris polypodioides* (A.P.De Candolle) J.V.Lamouroux 1809	3a, 3b	1a, 3b	4a, 2b	3a, 1b	2a	2a
			Dictyota J.V. Lamouroux	*Dictyota cyanoloma* Tronholm, De Clerck, A.Gómez-Garreta & Rull Lluch 2010					2a	
				Dictyota dichotoma (Hudson) J.V.Lamouroux 1809	4a, 4b	3b	4a, 3b	4a, 3b	3a, 3b	3a, 2b
				Dictyota dichotoma var. intricata (C.Agardh) Greville 1830						1a?
				Dictyota fasciola (Roth) J.V.Lamouroux 1809					1a?	
				Dictyota spiralis Montagne 1846?	1b		2a, 2b	1a, 2b		

Table 8 (continued)

Phylum	Order	Family	Genus	Species	A	M	V	C	S	L
			Rugulopteryx De Clerck & Coppejans	*Rugulopteryx okamurae* (E.Y.Dawson) I.K.Hwang, W.J.Lee & H.S.Kim 2009						4b
			Taonia J. Agardh	*Taonia atomaria* (Woodward) J.Agardh 1848	1b					
			Zonaria C.Agardh	*Zonaria sp*. C.Agardh, 1817					1a	
		CHORDARIACEAE	*Asperococcus* J.V. Lamouroux	*Asperococcus fistulosus* (Hudson) W.J.Hooker 1833	1b					
			Leathesia S.F. Gray	*Leathesia marina* (Lyngbye) Decaisne 1842	3b					2b?
		ECTOCARPACEAE	*Ectocarpus* Lyngbye	*Ectocarpus fasciculatus* Harvey 1 841	3a		3a			
				Ectocarpus sp. Lyngbye, 1819	1b		3b			
		SCYTOSIPHONACEAE	*Colpomenia* (Endlicher) Derbès et Solier	*Colpomenia peregrina* Sauvageau 1927		2b	2a, 3b	1a, 2b	3a	
				Colpomenia sinuosa (Mertens ex Roth) Derbès & Solier 1851					1a, 4b	1a, 3b
	DESMARESTIALES	DESMARESTIACEAE	*Desmarestia* J.V. Lamouroux	*Desmarestia ligulata* (Stackhouse) J.V.Lamouroux 1813	3b	3b	3b			
	LAMINARIALES	ALARIACEAE	*Undaria* Suringar	*Undaria pinnatifida* (Harvey) Suringar 1873			1a, 4b			
		LAMINARIACEAE	*Laminaria* J.V. Lamouroux	*Laminaria ochroleuca* Bachelot Pylaie 1824	3a, 2b	3a, 2b	4a, 4b			
		PHYLLARIACEAE	*Phyllariopsis* Henry et South	*Phyllariopsis brevipes* (C.Agardh) E.C.Henry & G.R.South 1987					3b	2b
			Saccorhiza De La Pylaie	*Saccorhiza polyschides* (Lightfoot) Batters 1902	2a, 4b	4b	3a, 3b	3a, 2b		
	FUCALES	CYSTOSEIRACEAE	*Bifurcaria* Stackhous	*Bifurcaria bifurcata* R.Ross 1958	3a, 3b	2a	2a, 3b			
			Cystoseira C. Agardh	*Cystoseira humilis* Schousboe ex Kützing 1860	1a, 2b		1a?		3b	
		FUCACEAE	*Ascophyllum* Stackhouse	*Ascophyllum nodosum* (Linnaeus) Le Jolis 1863			3a, 4b			
			Fucus Linnaeus	*Fucus guiryi* Zardi, Nicastro, E.S.Serrão & G.A.Pearson, 2011		3a, 2b	2a, 1b	2a, 3b		
				Fucus serratus Linnaeus 1753			3a, 2b			
				Fucus spiralis Linnaeus 1753		2b	4a, 2b			
				Fucus vesiculosus Linnaeus 1753			4a, 2b			
			Pelvetia Decaisne et Thuret	*Pelvetia canaliculata* (Linnaeus) Decaisne & Thuret 1845			3a, 3b			
		SARGASSACEAE	*Ericaria* Stackhous e	*Ericaria selaginoides* (Linnaeus) Molinari & Guiry 2020	3a, 3b		3a			
			Gongolaria Boehm er	*Gongolaria baccata* (S.G.Gmelin) Molinari & Guiry 2020		1a	3a, 2b			
				Gongolaria montagnei (J.Agardh) Kuntze 1891					2a	1a

Table 9 (continued)

Phylum	Order	Family	Genus	Species	A	M	V	C	S	L
			Sargassum C. Agardh	*Sargassum flavifolium* Kützing 1849						1a
				Sargassum muticum (Yendo) Fensholt 1955	2a, 2b	1a	4a, 4b		2b	
				Sargassum vulgare C.Agardh, nom. illeg. 1820					2a, 2b	
		BACHELOTIACEAE	*Bachelotia* (Bornet) Kuckuck ex G. Hamel	*Bachelotia antillarum* (Grunow) Gerloff 1959						1a
CHLOROPHYTA	ULVALES	ULVACEAE	*Blidingia* Kylin	*Blidingia minima* (Nägeli ex Kützing) Kylin 1947	2a, 1b	2a		4b	3a, 3b	2a, 3b
			Ulva Linnaeus	*Ulva clathrata* (Roth) C.Agardh 1811	3a	3a, 1b	4a, 4b		4a, 4b	4a, 3b
				Ulva intestinalis Linnaeus 1753	4b	3b	2a, 3b	4b	2b	
				Ulva rigida C.Agardh 1823	4a, 3b	4a, 4b	4a, 2b	4a, 2b	3a, 3b	3a, 2b
				Ulva sp. Linnaeus, 1753	2a	4a	2a	1a	3a, 2b	4a
			Ulvaria Ruprecht	*Ulvaria obscura* (Kützing) Gayral ex Bliding 1969						1a
	CLADOPHORALES	CLADOPHORACEAE	*Chaetomorpha* Kützing	*Chaetomorpha linum* (O.F.Müller) Kützing 1845						1a
				Chaetomorpha tortuosa (Dillwyn) Kleen 1874						1a
			Cladophora Kützing	*Cladophora hutchinsiae* (Dillwyn) Kützing 1845	2a	1a	3a	1a	1a	1a
				Cladophora nigrescens Zanardini ex Frauenfeld 1855					1a	1a
				Cladophora prolifera (Roth) Kützing 1843	4b	3b	3b	2a?, 3b	3b	1a
				Cladophora sp. Kützing, 1843				2a	4a	2a
			Lychaete J.Agardh	*Lychaete pellucida* (Hudson) M.J.Wynne 2017				1a		
		VALONIACEAE	*Valonia* C.Agardh	*Valonia macrophysa* Kützing 1843					2a, 3b	2b
				Valonia utricularis (Roth) C.Agardh 1823					2b	1a
	BRYOPSIDALES	BRYOPSIDACEAE	*Bryopsis* J.V. Lamouroux	*Bryopsis plumosa* (Hudson) C.Agardh 1823				3a	1a	2a
				Bryopsis sp. J.V.Lamouroux, 1809				3b?	1a, 2b?	
		CODIACEAE	*Codium* Stackhouse	*Codium adhaerens* C.Agardh 1822				1a, 3b	3a, 4b	4a, 2b
				Codium tomentosum Stackhouse 1797	1a, 2b	2a, 3b	3a, 3b	2a	1a	
				Codium vermilara (Olivi) Delle Chiaje 1829	2a			2a, 3b	2a, 2b	2a, 2b
		DERBESIACEAE	*Derbesia* Solier	*Derbesia tenuissima* (Moris & De Notaris) P.Crouan & H.Crouan 1867						4a
			Pedobesia MacRaild & Womersley	*Pedobesia simplex* (Meneghini ex Kützing) M.J.Wynne & F.Leliaert 2001					2b	4b

The relative richness of the main groups generally increased in the case of the Cosmopolitan group, especially in Ancora and Montedor. The Lusitanian and the Southern groups approximately maintained their relative richness from the 1960s, although the latter was more present in 2003. Besides the decreasing relative richness, no Northern species were found in the southern sites of Portugal in the sampling done for this study, similarly, the Southern species in the northern sites (Figure 3).

Regarding the absolute number of species, these slightly increased since the 1960s in the case of the Cosmopolitan and the Lusitanian species, compared with 2003 and 2020, but with a decrease in species number in 2021. Even if the observers, expertise, and sampling effort were different, general trends can be seen, such as the species from the Northern and Southern species, which many of them were conspicuous. The Northern species went from 20-21 species in the 1960s-2003 to 7-8 species in 2020-2021, respectively. This decrease represents 62% of the northern species gone in less than 20 years (Figure 4). The 13 missing species are: *Ceramium shuttleworthianum*, *Chorda filum*, *Desmarestia aculeata*, *Dumontia contorta*, *Furcellaria lumbricalis*, *Gaillona gallica*, *Gloiosiphonia capillaris*, *Himanthalia elongata*, *Laminaria hyperborea*, *Palmaria palmata*, *Phyllophora* pseudoceranoïdes, *Plumaria plumosa*, *Rhodomela confervoides*, and *Saccharina latissima*. The Southern species went from 20-36 in the 1960s-2003 to 12-10 in 2020-2021, respectively. Thus, representing a 52% decrease from the 1960s, and a 72% decline from 2003 (Figure 4).

As mentioned above, in late June 2021 in Lagos, *R. okamurae* was found. In 2020, 77 species were found, while in 2021, only 33 species, consequently representing a 57% decrease in species found (Table 2). This can be correlated with the presence of *R. okamuare* as it was extremely dominant, forming a brown soup submerged from the upper subtidal to the upper intertidal in rocky pools. In these pools, large species such as *Sargassum flavifolium* and *Gongolaria montagnei* were found in October 2020 but not in June 2021 (*Table 1*).

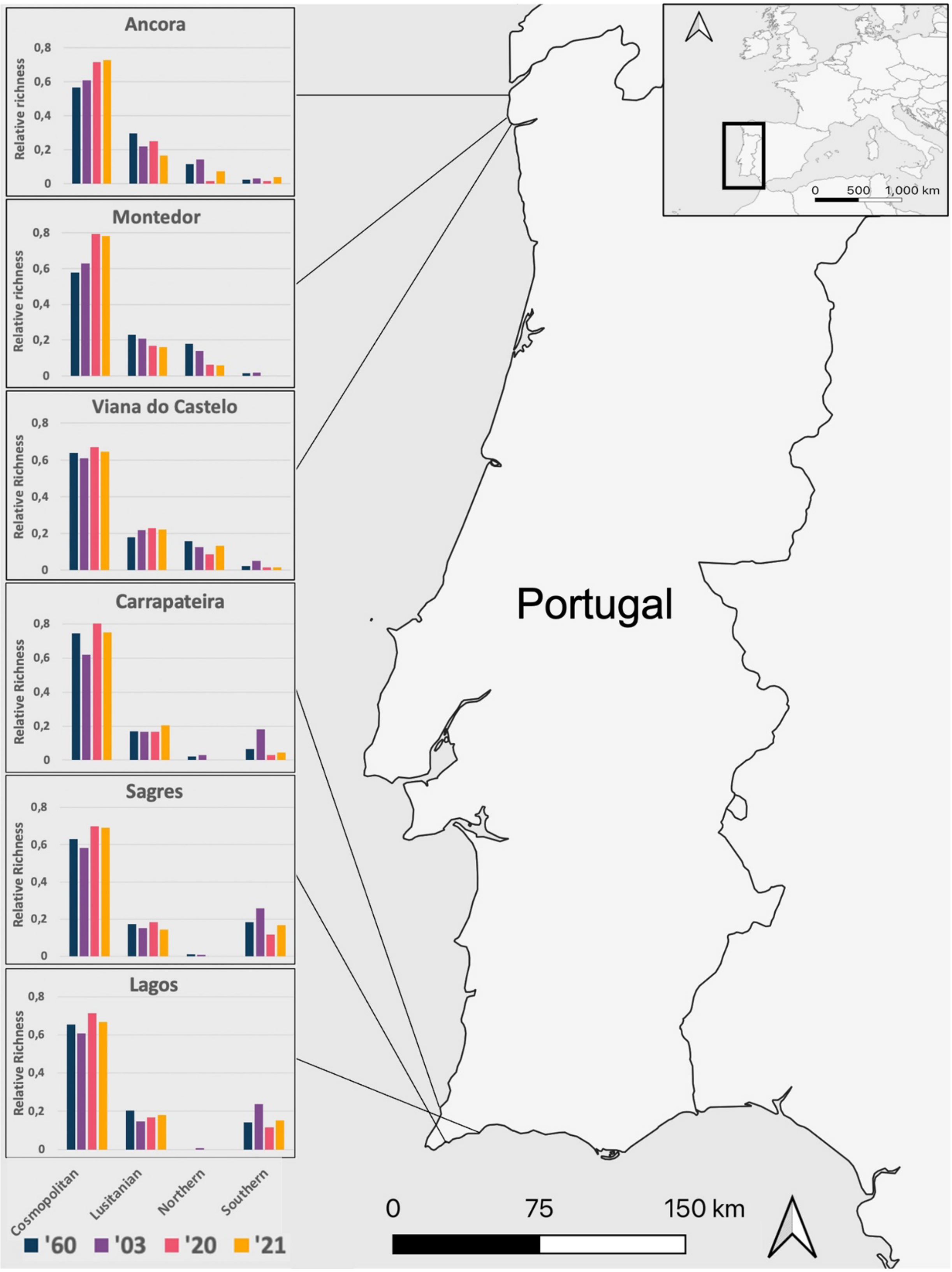

Figure 2. Map of Portugal showing the relative richness of the intertidal macroalgae of the six sampled sites (Ancora, Montedor, Viana do Castelo, Carrapateira, Sagres, and Lagos), the different seaweed groups (Cosmopolitan, Lusitanian, Northern, and Southern) and the different years (the 1960s, 2003, 2020, 2021). The data of 2020 & 2021 comes from this study.

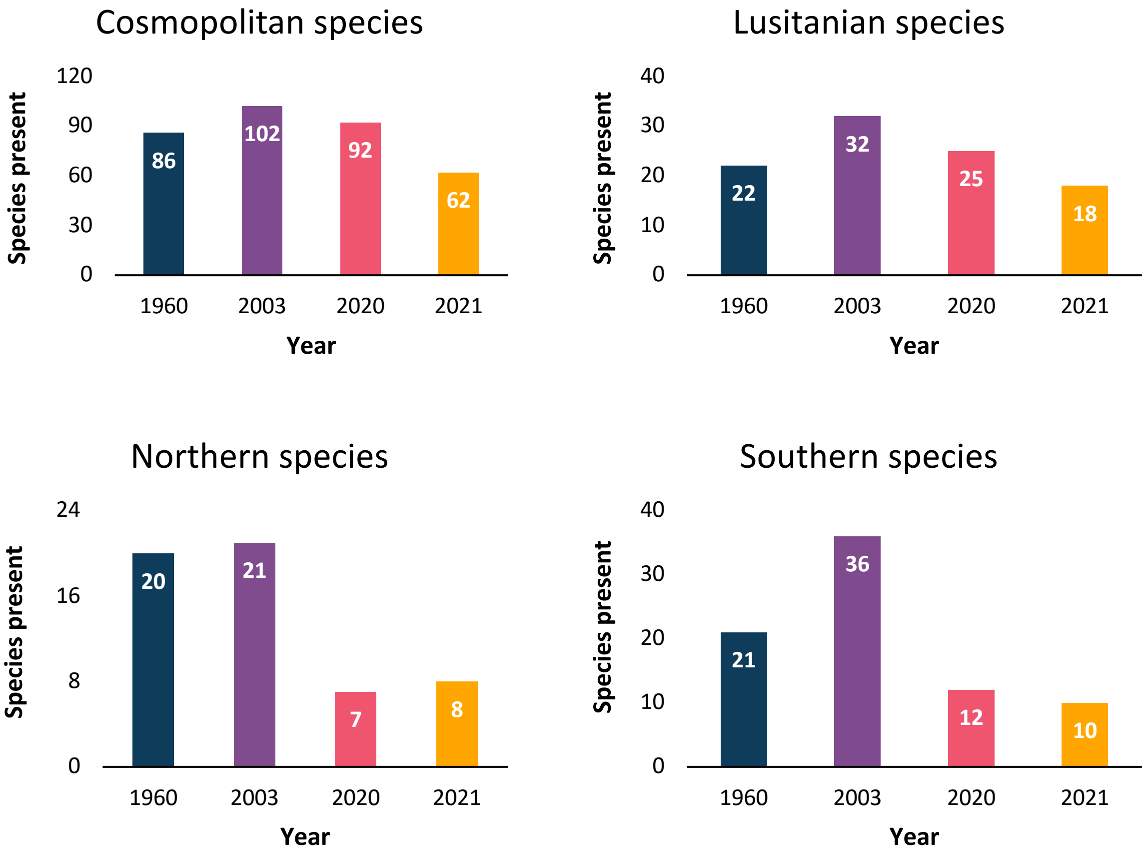

Figure 3. Absolute richness of the intertidal macroalgae of the six sampled sites in Portugal (Ancora, Montedor, Viana do Castelo, Carrapateira, Sagres, and Lagos), the different seaweed groups (Cosmopolitan, Lusitanian, Northern, and Southern) and the different years (the 1960s, 2003, 2020, 2021). The data of 2020 & 2021 comes from this study, and only species used for the relative richness analysis were considered.

Table 10. Number of macroalgal species found in Lagos, Portugal, during the sampling campaigns of 2020 and 2021, separated in the different seaweed groups.

	2020	**2021**
Cosmopolitan	55	22
Lusitanian	13	6
Northern	0	0
Southern	9	5
Total	77	33

Discussion

The present study represents an in-depth study of the intertidal macroalgae found at range edges of cold-water and warm-water species that meet in Portugal, based on 184 taxa from this study and 217 taxa from past studies (Ardré, 1971; Berecibar, 2011), comprising the Phylla Rhodophyta, Ochrophyta, and Chlorophyta. This research is a detailed 60-year long-term study that allows seeing how these communities have been affected by the increasing rate of climate change (IPCC, 2021).

The species list of intertidal seaweeds found in this study is relatively large, agreeing with Portugal hosting a high diversity of macroalgae (e.g., Araújo et al., 2009; Ardré, 1970). Moreover, this allowed a more solid comparison with the previous data collected and compiled in Ardré (1971) and Berecibar (2011). Also, at least 46 species were commonly present in all the sites sampled while there were 44 species specific to one location, not just north or south of Portugal (Table 1). Thus, meaning that all locations are essential for conservation, as three of the 21 sites sampled in the early 1960s disappeared (Peniche, Outão, and Sines) due to coastal development (Lima et al., 2007).

Sampling in different seasons allowed to see seasonality in the macroalgae community, from Autumn in 2020 to the end of Spring and start of Summer in 2021. For instance, the relative abundance changed with the season for the species *Ceramium spp*., *Champia parvula*, *Cladophora hutchinsiae*, *Halopteris spp*., *Vertebrata thuyoides*, among others. Here, the relative abundance of *M. stellatus*, *G. pistillata*, and *G. crenulatus* was higher in Autumn than in Summer, not coinciding with the trends seen in other sites of Portugal (Melo et al., 2021; Pereira & Silva, 2020). This difference could be because this study is semi-quantitative while the others are quantitative, or because seasonal differences increase with ocean warming, especially when combined with the high temperatures of Summer (Wahl et al., 2020). In addition, seasonality could also be seen in the relative richness comparison (see *Figure 1*), as the Northern and Southern species were more represented in 2021. Further, the drop in richness of 2021 could be because half of the Cosmopolitan and Lusitanian species were not detected in Lagos (Table 2), probably due to the presence of *R. okamurae* (Figure 2, a) since it was reported in other sites to dominate the rocky coastline, for instance, a 96% at 15 m of depth (García-Gómez et al., 2021).

More interesting results show up when comparing the richness of the seaweed groups. When looked at the different locations and comparing the relative richness, we can see the globalization of the species, as the proportion of the Cosmopolitan group increases while the others generally decrease (Figure 3). Also, a transition from warmer flora in the south to a colder flora in the north, reveals the relevance of the Portuguese coast in terms of biogeography (e.g., Ardré, 1971; Hoek, 1975). While under increasing rate of climate change rates the non-native species perform better than natives (McKnight et al., 2021), leading to a more Cosmopolitan seaweed composition in the already homogenized seascape (Mineur et al., 2015), an excessive invasive behaviour, such as *R. okamurae*, can outcompete even Cosmopolitan species (Figure 2, a) leading to a les Cosmopolitan composition (Figure 3, Lagos).

The macroalgae database obtained compared relative richness and absolute richness to see how the communities varied in the periods studied and sites sampled. As mentioned in *Materials and methods*, the absolute richness cannot be compared because the sampling and identification efforts were different, because of that, the relative richness was used to account for differences in sampling effort. However, while the Cosmopolitan and Lusitanian species slightly dropped or maintained, it is not the case for Northern and Southern species (Figure 4), since the species list contained conspicuous taxa. Furthermore, from 2003 to present, the decrease in Northern and Southern species is notorious, a reduction of 62% of Northern and 72% of Southern species. This could be due to the warming of the north of Portugal beyond the physiological limits of the species missing, combined with extreme events such as consecutive heatwaves, strong wave action and freshening events (e.g., McKnight et al., 2021; Pereira et al., 2017; Román et al., 2020). From our point of view, the absence of these species is not explained by identification expertise since most of the species are conspicuous and were common in the past (Ardré, 1971), but because conspicuous species were absent in the locations sampled, such as the Northern species listed in *Results* or the Southern species from the genera *Cystoseira*, *Gongolaria*, and *Sargassum*. Some disappearing faster than projected, such as of *L. hyperborea which* is projected to reduce its presence in pessimistic scenarios by 2050-2100 (Jorge Assis et al., 2016), but in this study we already noticed its absence in the north of Portugal.

Even though the kelp *L. hyperborea* might still be present in other subtidal areas under *L.*

ochroleuca (OMARE, 2017)*,* the warm-water *L. ochroleuca* is replacing the cool-water *L. hyperborea*, which has associated up to 12 times more diversity and over 3600 times higher biomass than the warm-water kelp (Teagle & Smale, 2018). Furthermore, last cited *L. hyperborea* in Portugal was in an intertidal pool close to Viana do Castelo in 2010, which had difficulties recovering from a year with bad recruitment (Pereira et al., 2017). Therefore, this species cannot have persisted in the upper subtidal/lower intertidal in Portugal like other organisms from rock pools, as the intertidal wave action is a key factor determining biodiversity and abundance (Carvalho et al., 2021). For example, in December 2019, three extratropical cyclones hit the coast of Portugal (Stojanovic et al., 2021).

In the case of *H. elongata,* until 2006, the range boundary of north of Portugal did not change (Berecibar, 2011). In the present study, this species was not found in Viana do Castelo during this study. Furthermore, this species has drastically decreased in the north of Spain, probably due to increased SST and air temperature (Ramos et al., 2020). Also, as this canopy species, other kelps and fucoids, and the sub-canopy *C. crispus*, almost disappeared and were replaced by warmer-water species, such as *E. selagnoides* and *G. baccata,* in almost 200 km of northern Spain coast (Fernández, 2016). As many cold-water species have a strict survival temperature interval (Casado-Amezúa et al., 2019), consecutive heatwaves are critical for physiological performance (Román et al., 2020). Also, strictly intertidal species are less likely to find deep refugia and more likely to go locally extinct, so it can also be said that they are especially vulnerable as they cannot find deeper local refugia (as in Oliveira et al., 2019). Similarly, the intertidal of Viana do Castelo used to host a wide variety of cold-water species (Ardré, 1971), now the 13 missing Northern species from the sampled northern sites (see Results) most likely disappeared from Portugal's intertidal because of the extreme events that have increased in frequency and intensity (e.g., Stojanovic et al., 2021).

Furthermore, in the sampling performed for this study, turf-like species were found, agreeing with the increasing tendency, while the canopies such as large kelps and fucoids decreased in presence (Meneghesso, 2019). This tendency can also be reinforced by the monopolization of turf communities, limiting the space for other species to recruit and competing for nutrients (overviewed in Filbee-Dexter & Wernberg, 2018), causing kelps such as *S. latissima* to detach faster when growing on turfs and when intense wave action (Feehan et al., 2019). Fact aggravated with the high temperatures which decrease the proteins related to photo-oxidative protection, therefore weakening the individual (Monteiro et al., 2021). These shifts in functional groups make it more challenging for the missing species to return and re-colonize their past ranges. Thus, the cold-water species are important due to their ecological functions and because these populations served as genetic refugia during the last glacial maximum, containing unique haplotypes (Neiva et al., 2014; Provan & Maggs, 2011).

Although the overall tendency of cold-water species to go locally extinct, the presence of *Gelidium corneum* is prevalent and even dominant in Carrapateira in 2021. While this seaweed supports as high temperatures as some of the kelps disappeared (Casado-Amezúa et al., 2019), the area of this species is predicted to be dramatically reduced (de la Hoz et al., 2019). The contradiction with the literature could be due because *G. corneum* grows more exposed to wave action and is rarely emerged, susceptible to the deadly effects of consecutive exposure to air heatwaves (Román et al., 2020); besides the upwelling sustaining the cool temperatures in the south-west coast of Portugal (Leitão et al., 2019).

There are many non-native species found in Portugal, but not all show an invasive behaviour (Berecibar, 2011), such as the novel *P. lyngbyanum* (Figure 1), found in Carrapateira in October 2020. Even though invasive species were found in the north (e.g., *A. armata, G. turuturu, S. muticum, U. pinnatifida*) and in the south (generally *A. armata*), these were not as aggressive as the newly *R. okamurae* found in Lagos in June 2021. This species showed an extreme invasive behaviour that allowed us for a before-after impact comparison. The 57% diversity decrease found after these 8 months may be due to mainly its niche occupation since it was extremely present from the upper subtidal to the rock pools of upper intertidal (Figure 2, a). The undulations of the thallus (Figure 2, b) indicate that the specimen comes from Japan and not from Korea (Hwang et al., 2009). Since this species was found in Gibraltar's Strait, Spain, in 2015, causing devastating consequences to native flora (García-Gómez et al., 2021), it was a matter of time for it to reach Portugal. Finally, climate change affects these populations in the long-term by decreasing biodiversity (this study), shifting the distribution range (Lima et al., 2007), and facilitating biological colonization and invasions (García-Gómez et al., 2021), among others.

Conclusions

In this study, we found 184 taxa in three northern and three southern sites of Portugal, coinciding with the range-edge of cold and warm-water macroalgae species. Portugal contains a large diversity of intertidal seaweeds; seasonal changes can be seen, and up to 44 species are unique to certain locations. As most coastal nations contain priority areas that can substantially achieve biodiversity protection, food provision and carbon storage (Sala et al., 2021), these are worth protecting. When comparing the relative richness found with Ardré (1971), Berecibar (2011), and this study, more Cosmopolitan species were found in 2020 and 2021, while the Lusitanian species maintained the diversity. In contrast, the Southern species decreased 72% in species richness, not only that, but 62% of Northern species were not found in the sampling done in this study. Some of the cold-water missing species were important bioengineers, providing important biomass and diversity, for example: *H. elongata, L. hyperborea*, and *S. latissima*. Novel sightings of *P. lyngbyanum* and *R. okamurae* were seen in the south of Portugal. Furthermore, *R. okamurae* was found extremely invasive, decreasing the diversity found in Lagos by 57% in less than a year. As Northern species are disappearing and the non-native species dominate the seascape, we can suggest that these are probably consequences of climate change on biodiversity.

However, further research is needed to see how the rest of Portugal's flora responded to climate change during this last decade. The resolution of the study might be high, yet collaborations with other experts are needed to confirm more challenging and cryptic species from genera such as *Ceramium, Cladophora, Dictyota, Griffithsia, Polysiphonia.* Furthermore, by the definition of Southern species (see *Materials and methods*), some Lusitanian and Cosmopolitan species could be included in the group. Therefore, this group should be revised as it will always be limited in the Southern species group since newly found species are generally introduced. Last, monitoring the populations of *R. okamurae* should be a priority as the impacts are imperative.

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