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Biogeographic and diversity analysis of intertidal seaweeds and associated peracarids in the Northeast Atlantic

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Análise biogeográfica e de diversidade de algas intertidais e peracarídeos associados no Atlântico Nordeste

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Declaração de autoria de trabalho

Declaro ser a autora deste trabalho, que é original e inédito. Autores e trabalhos consultados estão devidamente citados no texto e constam da listagem de referências incluída.

____ Javier Jiménez Herrero

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Abstract

The distribution and biodiversity patterns of intertidal seaweeds and associated peracarids were studied along the Northeast Atlantic region from 65ºN to 27ºN of latitude. In order to determine what factors drive the geographical distribution of intertidal communities of seaweeds and peracarids, twenty-seven stations and nine abiotic factors were considered (fetch, air temperature, precipitation, insolation, SST, chlorophyll-a, pH, aragonite saturation, OHI). A total of 12779 specimens were sorted and identified to the species or genus level, of which the vast majority belonged to the group of algae. In order to assess biogeographical groups of these species along the Northeast Atlantic, a CLUSTER analysis as well as a NMDS analysis were carried out, resulting in the identification of three ecoregions; 1)Northern Europe, 2)Central Iberian Peninsula and 3)Southern Macaronesia. CCA and NMDS analyses showed high correlations between environmental factors such as precipitation, insolation and SST minimum albeit to a lesser extent, and species distribution. Macaronesian species were correlated with higher temperature and insolation whereas those of the Iberian peninsula were correlated with higher pH and chlorophyll. On the other hand, the abundance that was similar among all species and the results of the SIMPER analysis indicated a certain homogeneity of species without dominance of one over another. Both the species richness (S) and α diversity (indexes of H’, Dsimp and $e^{H'}$) presented a decreasing latitudinal gradient towards higher latitudes. An exception to this pattern was observed for β-diversity, probably due to the homogeneity of abundance of species observed between regions, mainly affected by abiotic factors of the local environment.

Keywords: Distribution, biodiversity, seaweeds, peracarids, abiotic factors

Resumo

Os padrões biogeográficos variam de acordo com as diferentes zonas do oceano; em águas pouco profundas, a distribuição dos organismos fica mais irregular devido a uma variedade de fatores, como características geológicas, efeitos das marés, mas tambem, foi demonstrado que variam de acordo com o tipo de organismo, habitat que ocupam ou condições ambientais a que estão sujeitos. Embora a variabilidade da ocorrência de flora e fauna em diferentes áreas do oceano seja conhecida, os limites biogeográficos de muitas comunidades permanecem obscuros. A classificação global no ambiente marinho permanece limitada na sua resolução espacial. A delimitação dos limites biogeográficos marinhos indica a importância relativa dos fatores que causaram a distribuição atual das espécies marinhas à escala global, como deriva continental, temperatura, aumento do nível do mar e glaciação. O clima, e especificamente a temperatura, é um fator importante na configuração da distribuição geográfica dos organismos e, portanto, o aquecimento global está causando uma redistribuição dos limites geográfico das espécies marinhas. A delimitação de áreas biogeográficas surgiu devido ao aumento das ameaças antrópicas à biodiversidade marinha e à necessidade de proteger a biodiversidade. Além disso, a biogeografia é uma ferramenta comumente usada para a conservação marinha e um critério para a identificação, seleção e designação de Áreas Marinhas Protegidas (AMPs). A região do Atlântico Nordeste tem sido profundamente estudada, no entanto, a maioria dos estudos biogeográficos foram realizados numa faixa latitudinal estreita e fracionada. O objetivo deste estudo é investigar a distribuição geográfica de algas e crustáceos peracarídeos associados a elas ao longo das costas da Europea. Investigamos o papel das variáveis ambientais e da pressão antrópica na determinação da distribuição geográfica, bem como os padrões de biodiversidade de algas intertidais e peracarídeos ao longo do Atlântico Nordeste, cobrindo uma ampla faixa latitudinal, da Islândia (65ºN) para as Ilhas Canárias (27ºN). As questões que queremos responder são: se há diferentes ecorregiões ou áreas com certa homogeneidade interna quanto à composição de algas e espécies de peracarídeos, bem como se os fatores que configuram essa distribuição geográfica são a temperatura superficial do mar (TSM) e o impacto humano. Além a presença de um gradiente latitudinal com diminuição da biodiversidade em direção aos pólos. A fim de investigar essas hipóteses, algas intertidais e amostras de peracarídeos de 27 estações localizadas em uma ampla faixa latitudinal foram colhidas e analisadas. Os organismos foram classificados ao nível da espécie e o conjunto de dados foi analisado. Foi realizada uma análise CLUSTER e um NMDS que revelou a presença de três ecorregiões no Atlântico Nordeste com base na presença de algas e peracarídeos: 1) Norte da Europa, 2) Península Central ou Ibérica, 3) Sul da Macaronésia. Por outro lado, a abundancia destes organismos está distribuída por muitas espécies, pelo que a análise SIMPER revelou uma baixa incidência de cada espécie na distinção entre ecorregiões. Além disso, o baixo endemismo encontrado especialmente na Península Ibérica pode indicar esta área como uma zona de transição entre a ecorregião Norte e Sul ou Macaronésia. Quando exploramos a relação da distribuição geográfica das espécies com as variáveis ambientais, as análises de CCA e NMDS mostraram, ao contrário do que se esperava, uma maior influência das variáveis como fetch, insolação, precipitação e clorofila do que da temperatura (exceto para o mínimo SST) e impacto humano. Isso pode ser devido ao fato de que os organismos que ocupam a zona entremarés estão expostos a condições ambientais extremas, na interface do ambiente marinho e terrestre e, portanto, são os mais afetados por esses tipos de fatores ambientais. Cada ecorregião foi caracterizada por uma série de condições ambientais: as espécies da ecorregião da Macaronésia correlacionaram-se com altas temperaturas, típicas desta área, bem como com elevada insolação, enquanto as espécies presentes na Península Ibérica se caracterizaram por elevadas concentrações de pH e clorofila, possivelmente devido a upwelling presente na costa de Portugal. Por fim, foi estudada a relação da biodiversidade desses organismos com a latitude. Para a biodiversidade local, foram obtidos tanto a riqueza de espécies quanto a diversidade alfa (índices H ', Dsimp e eH'), que descrevem um gradiente latitudinal com decréscimo para latitudes mais elevadas e com uma diferença marcante entre as ecorregiões norte e os sítios do sul (ecorregião Ibéria e Macaronésia). Porém, para a diversidade beta, a análise de correlação (r pearson) não mostrou relação com a latitude, o que indica que não há substituição ou troca de espécies entre estações ou ecorregiões, e a presença de habitats semelhantes dentro de cada ecorregião e entre elas. Além disso, os resultados de evenness (J ') que mostram valores elevados para as três ecorregiões indicam que dentro de cada ecorregião a abundância é distribuída entre as diferentes espécies sem predominância de uma sobre as outras, essas condições são mantidas para as três ecorregiões. Uma das causas para que a diversidade beta não siga esse padrão pode ser a pouca influência que a temperatura exerce na distribuição dessas espécies de algas e peracarídeos na região do Atlântico Nordeste. Este estudo pode melhorar o conhecimento da biogeografía da região do Atlântico Nordeste, fornecendo uma visão em maior escala dos padrões de distribuição de algas e peracarídeos que habitam a zona entremarés. Além disso, a partição espacial do Nordeste do Oceano Atlântico é valiosa para as políticas de gestão de ecossistemas marinhos, o tamanho relativamente grande das unidades aqui definidas é justificado pela grande conectividade entre os ecossistemas marinhos e ajudará a compreender as escalas espaciais em que devem aplicar ações de gestão das AMPs. Também pode ajudar a aumentar o conhecimento sobre os fatores que determinam a distribuição e diversidade desses organismos, o que pode ser útil para pesquisas futuras sobre as previsões de possíveis mudanças causadas pelas mudanças climáticas. No entanto, mais estudos biogeográficos são necessários nesta região para confirmar esta divisão espacial.

Palavras-chave: Distribuição, biodiversidade, algas marinhas, peracarídeos, fatores abióticos.

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Abbreviations

ADONIS	Permutational Multivariate Analysis of Variance
CCA	Canonical Correspondence Analysis
ENACW	East North Atlantic Central Water
ENSO	El-Niño Southern Oscillation
IPCC	Intergovernmental Panel on Climate Change
MPAs	Marine Protected Areas
NAD	North Atlantic Drift
NMDS	Non-metric multidimensional scaling
NOAA	National Oceanic and Atmospheric Administration
N-S	North-South
OHI	Ocean Health Index
OSPAR	Oil Spill Prevention Administration And Response
SIMPER	Similarity Percentage
SPMW	Subpolar Mode Water
SST	Sea Surface Temperature
UPGMA	Unweighted pair group method using arithmetic averages
VIF	Variable Inflation Factors

1. Introduction

1.1 Marine biogeography

Marine biogeographic regions, which have been recognized for over 150 years, are based on distinct floras and faunas (Forbes, 1859). MacArthur in 1972 defined biogeography as the study of biological patterns that can be mapped, but it also included the study of the distribution of organisms in the past and present, and of related patterns of variations over the earth (Brown and Lomolino, 1998). This term is more useful when it refers to areas of evolutionary transformation or refuge of older persistent biota, parts of the ocean that host unique biotas (Briggs and Bowen, 2011). Although the oceans have been and are connected, few are the species that have distributed around the globe (Gaither et al., 2015), most of the marine species are endemics, presenting a range often defined by the edges of biogeographic regions (Briggs J. C., 2016).

Biogeographic patterns vary from the different zones of the ocean. In the pelagic environment and deep-sea where the environmental conditions are uniform present very broad distribution, whereas they are more linear and belt-like along continental slopes and shelves due to the geophysical structure (Dinter, 2001). Besides, in shallow waters the distribution of the organisms gets patchier due to more various influences by a variety of factors such as geological features, tidal interactions, and riverine outflows (Angel, 1993). Defining marine biogeographical regions on a global or large regional scale has been proposed by a number of authors. A first approach was the delimitation of the continental shelf in three regions: warm, temperate and polar waters; based on zoogeographic barriers and endemism (Ekman, 1953). Later, very large regions of coastal, benthic, or pelagic ocean that hold similar biotas at higher taxonomic levels were defined as realms (Udyardy, 1975). Nested within the realms are the provinces, large areas defined by the presence of distinct biotas that have at least some cohesion over evolutionary time frames. Provinces will hold some level of endemism, principally at the level of species (Spalding et al. 2007). Briggs (1974) defined biogeographic provinces as shallow (<200m) marine regions presenting at least a 10% of endemism. The definition of provinces by 10% endemism has been generally accepted for the past 35 years (Briggs and Bowen, 2011). Finally, ecoregions are the smallest-scale units defined by Spalding (2007) as: Areas of relatively homogeneous species composition, clearly distinct from adjacent systems. Unlike provinces, endemism is not a key determinant factor in the delimitation of the ecoregions, they usually have important levels of endemism though (Spalding et al. 2007).

While the variety in the occurrence of flora and fauna in different areas of the ocean is known, the biogeographic boundaries of many communities remain unclear (Costello et al., 2017). The global classification in the marine environment remains limited in their spatial resolution (Spalding et al., 2007). Delimitation of marine biogeographic limits would indicate the relative importance of factors that have caused the present distribution of marine species at a global scale, such as continental drift, temperature, sea-level rise, and glaciation (Costello et al., 2017). A debate that persists over the years is the placement of temperate and tropical waters in different regions, considering there is a close relationship between warm-temperate province and tropical (Vermeij, 2005). Many organisms cover the tropical and warm-temperate regions, whereas only a few extend into the cold-temperate regions (Grant et al., 2010). The boundaries between these biogeographic provinces are frequently associated with continents, sharp ecological gradients, or vast expanses of open ocean (Briggs J. C., 2016). However, the role of fronts in marine biogeography is not yet fully understood (Acha et al., 2015). Unlike terrestrial biogeography, the marine environment presents a greater variety of variables that make its study more difficult. A specific set of environmental variables can demarcate the distribution of a biological community, providing an ecological niche for its members (Dinter, 2001). In a continuous transglobal medium, the major barriers that constitutes these boundaries are geographic. Historically, several geographic barriers have been recognized to be important drivers of organisms distribution. Open oceans and rivers flows are also known to be barriers in the marine realm (Briggs J. C., 2016).

The quantitative study of patterns of distribution and abundance of species provide a better understanding of the assemblages of organisms (Andrew and Mapstone 1987; Underwood et al. 2000). The distribution of species and delimitation of these ecological borders are usually tied to climatic conditions (Repasky, 1991), specifically, distribution of planktonic communities have been shown to have a close relationship to environmental characteristics (Acha et al., 2020). In addition, the relationship between competition and predation (Hersteinsson and McDonald 1992), as well as, food selection and habitat complexity also play an important role in distribution and abundance of marine organisms (Duffy and Hay 1991; Edgar and Robertson 1992).

The delimitation of biogeographical areas has emerged due to the increase of the anthropogenic threats to marine biodiversity and the need for the protection of biodiversity (Hayden et al. 1984). To get representativeness of biodiversity on a higher scale of a zonation and regionalization above the level of habitats, biocoenoses, and species, it is necessary to distinguish different biogeographical areas. Besides, biogeography is a commonly used tool for marine conservation and a criterion for the identification, selection, and designation of Marine Protected Areas (MPAs)(Dinter, 2001). It is also of practical interest to many governmental and intergovernmental organizations who wish to identify naturally similar areas for reporting on the state of the environment, for prioritizing conservation action, or providing funding for conservation or ecodevelopment (Costello et al., 2017). The few publications that have aimed to use biogeographic regionalization in global marine conservation planning (e.g., Kelleher et al. 1995, Olson and Dinerstein 2002) have been qualitative, and have expressed concern about the lack of an adequate global classification. Only about a 0.5% of the surface area of the oceans is currently protected (Chape et al. 2005), and therefore there is a need for tools to improve an effective and representative marine conservation.

1.2 North-east Atlantic Ocean

1.2.1 Water masses and ocean dynamics

The Atlantic Ocean did not exist until approximately 165 million years ago when seafloor spreading started to divide southern Gondwana during the Jurassic with a main formation of the Atlantic in the Cretaceous (Sclater and Tapscott, 1979). This relatively young age (in geological terms) did not provide much time for evolutionary differentiation and speciation and thus makes biogeographic approaches using endemism rates more difficult for the Atlantic compared to other oceans (Dinter, 2001).

A better understanding of the Atlantic fauna has been possible due to phylogeographic analyses (Floeter et al., 2008). Several studies have identified the origins of Atlantic genera from different sources; Thesys origins (Dercourt et al., 1986), New World (West Atlantic-East Pacific) (Coates & Obando, 1996), radiations within the Atlantic, and invasions from the Indo-Pacific via southern Africa (Briggs and Bowen, 2013).

The ocean is formed by several large water masses, with no clear boundaries. There is a gradual and mixed process between them (Castro et al., 1998). The main characteristic in the division of the water masses is the density, in the Atlantic Ocean they are distributed in four vertical layers separated by equal density in the surface. The main water mass in the upper layer of our study sites is the East North Atlantic Central Water (ENACW). This water mass is formed during winter and gets subducted in the west of the Iberian Peninsula (Liu and Tanhua, 2019). In addition, one component of the Subpolar Mode Water (SPMW) is carried by the south branch of North Atlantic Current and mixed, contributing to the properties of this water mass (McCartney and Talley, 1982) so that ENACW shows a typical linear temperature-salinity (T-S) relationship (Pollard et al., 1996). ENACW advects in the general southern direction along the south branch of the North Atlantic Current, passes northwest Africa, and then turns southwest into Canary basin passes northwest Africa, and then turns southwest into Canary basin (Arhan et al., 1990).

The principal current that covers the Eastern Atlantic Ocean is the North Atlantic Drift (NAD). This current flows from the Gulf Stream beyond the Grand Bank of Newfoundland. The Coriolis effect forces the NAD to cross the Atlantic Ocean in easterly direction (Haedrich and Judkins 1979, Bearman et al., 1989). In the middle of the North Atlantic, a division of this current take place resulting in the Azores Current that flows south-eastward (Gould et al., 1985). Later divisions are the south-eastward bound (Portugal), Canary Current and the Irminger Current flowing towards the north-west. The former two currents are part of the North Atlantic Subtropical Gyre while the stronger western branch of latter forms the characteristic Polar Front together with the cold and less saline waters of the south-westward going East Greenland Current off south-east Greenland (Malmberg et al., 1985). A weak and variable eastern branch of the Irminger Current flows coast-near around North-West Iceland influencing the North Icelandic coastal waters in an interference with cold and less saline East Iceland Current waters (Stefánsson 1962 and Gudmundsson 1969) (Figure 1.1).

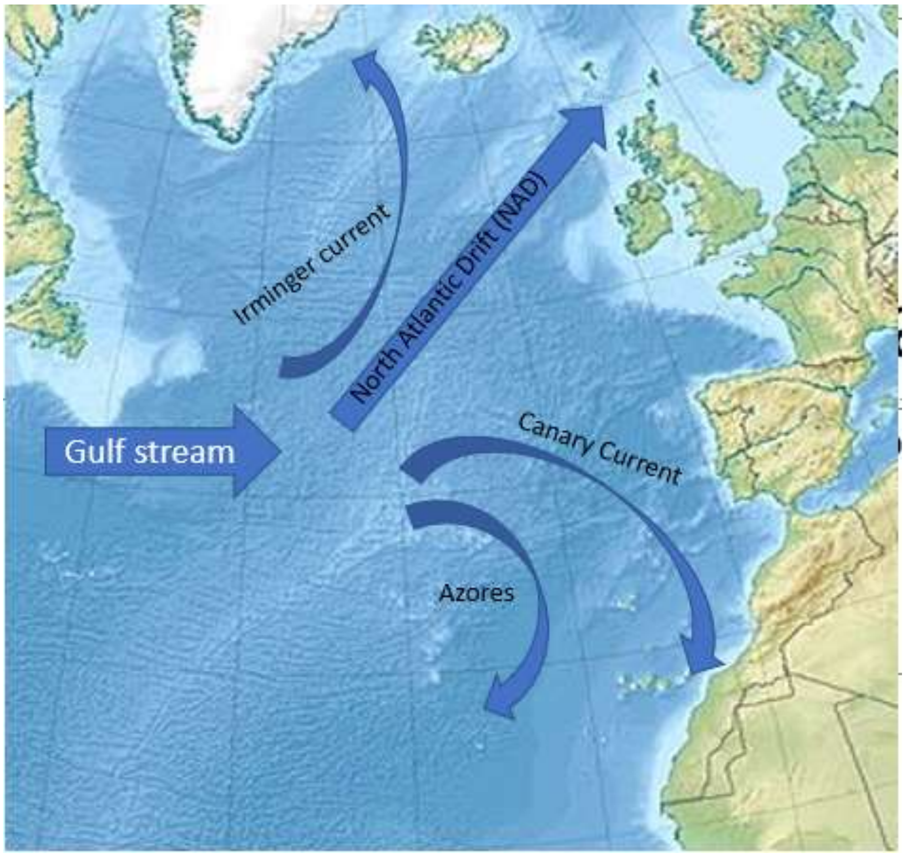


Figure 1.1. Main currents of the North Atlantic Gyre, flowing in a clockwise direction, and part of the North Atlantic Subpolar Gyre further north. Image adapted from Gonzalez-Pola (2018).

The ocean dynamic is a factor that plays an important role in the distribution patterns of marine organisms and the borders of the different ecological regions correspond with the distribution limits of the species (Gaines et al., 2009). Therefore, large areas defined by the presence of distinct biotas that have at least some cohesion over evolutionary time frames and hold some level of endemism (Briggs J. C., 2016), usually named as provinces, take place where the limits of the different water masses are set (Gaines et al., 2009).

1.2.2 Marine ecoregions

The boundaries of biogeographic regions usually vary considerably, not only due to the methods used by biogeographers but also between flora and fauna, benthic or pelagic organisms or different taxonomic groups (Dinter, 2001). In addition to taxonomic discrimination, there are other attributes to consider such as abundance, biomass and biotic interactions which may be useful to describe the structure and function of communities (Rice et al., 1994). Looking at the very different approaches and uncertainties, we can venture to state that biogeography still needs further exploration and study. However, during the last decade there has been a notable improvement in the biogeography, and more specifically in the Atlantic region (Dinter, 2001).

The Temperate Eastern Atlantic Region can be divided in Lusitania and Northern European seas provinces (Spalding et al., 2007) (Figure 1.2). The warm-temperate waters from the southern end of the English Channel down to southern Morocco and eastward to include the Mediterranean as well as the Azores, Madeira, and the Canary Islands circumscribe the province of Lusitania. However, Almada et al. (2013) have subsequently argued that the Macaronesian archipelagos are highly distinct from the mainland coasts of the Lusitanian Province, and these should not be grouped together. On the other hand, the Northern European seas province encompasses the waters from the Norwegian archipelago and Barents Sea to the southern entrance of the English Channel, including as well Iceland and the Faroe Islands. Iceland's unusual biota has made it the center of debate; this region has a low endemism and has been located within the Eastern Atlantic Boreal region (Briggs J. C., 2016). Nevertheless, the eastern side of the North Atlantic holds the richest biota of this ocean (Vermeij, 2005).

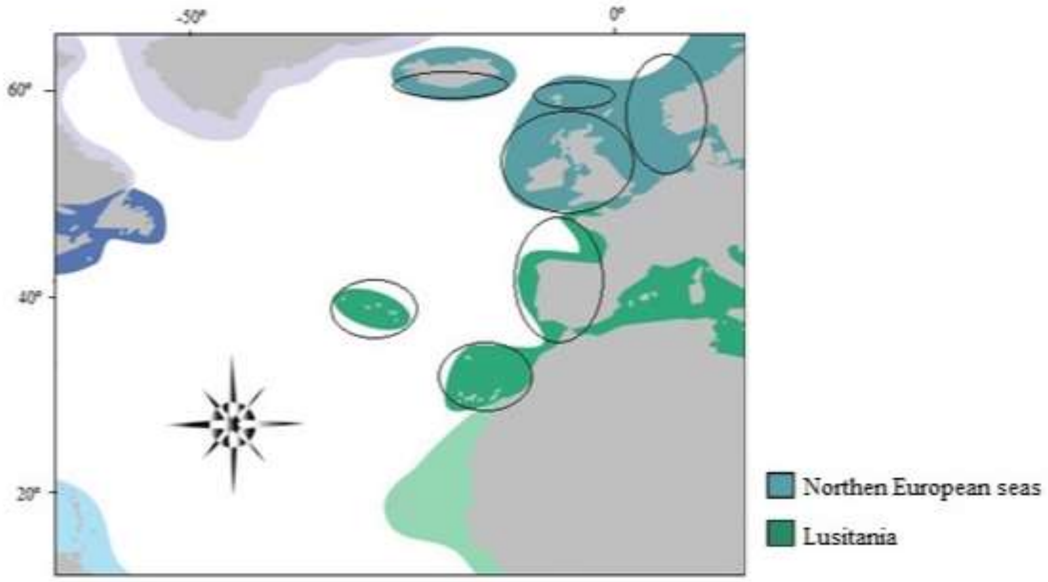


Figure 1.2. Map of the North-east Atlantic Ocean provinces. Each province is represented by a distinct color with ecoregions outlined. Image adapted from Briggs J. C., 2016 and Spalding et al., 2007.

1.3 Intertidal seaweeds and associated peracarids

Distribution models have been widely applied to land based organisms (Hortal et al., 2004), but they have rarely been used for intertidal species (Lima et al., 2007). These species occupy the interface of land and sea, enduring atmospheric and oceanic stress conditions frequently close to their physiological tolerance thresholds (Helmuth et al., 2002). An important feature of these organisms is that they can be used as bioindicators of climate-driven changes (Southward et al., 1995). Specifically, intertidal algae provide shelter and food resources for different organisms, as well as being structural engineers in rocky shores (Chapman et al., 1995). Thus, distribution models of these organisms may be used as powerful tools for tracking and forecasting changes in coastal systems (Martínez, Viejo, Carreño and Aranda, 2012). Algal phytogeography has been a subject of great controversy (Garbury and South 1989) and it has been constrained by a near total reliance on presence/absence data, species lists and floras (Adey and Hayek, 2011). Biogeographic regions were redefined by Van den Hoek (1975), but they were based on the appearance and disappearance of species, rather than by the zoologists' percentage of endemics, while Lüning (1990) preferred summer/winter isotherms. Another used method, which establishes gradients instead of distinguishing between regions, is to calculate a numerical index that is a ratio of red plus green algae to brown algae (Mathieson et al. 1991). Besides, biogeographic regions are often characterized with endemic and rare species on the "tail of the curve", where they are least abundant, and most variable, rather than with abundance data based in means and statistical analysis (Adey and Hayek, 2011).

Rocky substrates are very abundant in many coastal areas along the Northeast Atlantic biogeographic region, holding a wide variety of benthic communities that are dominated, in most cases, by different species of macroalgae (Van den Hoek, 1975; Borja et al., 2004). The benthic marine alga flora of the North Atlantic has been subjected to extensive analysis and therefore the genera distribution patterns of the species are reasonably well-known (Robin South et al., 1987). The general pattern of algal distribution in the North Atlantic region follow temperature trends, which can be seen more significantly in the N-S orientated coastlines (Joosten &Hoek, 1986). In addition, algal distributions show marked differences in latitudinal range as a result of the Gulf stream deflection (Robin South et al., 1987).

In the last 25 years, the Northeast Atlantic has experimented an increase in the sea surface temperature of 0.5ºC per decade (Gonzalez-Taboada, 2012; Lima and Whetey, 2012) which has caused shifts in the species distribution (Fernández, 2016). Large brown seaweeds such as kelps and fucoids which are cold key structural organisms of the Atlantic coast of Europe, have experienced a significant declined (Dinter, 2001; Lima et al., 2007; OSPAR, 2010). The North-east Atlantic is dominated by cold temperate species such as *Laminaria hyperborea, Himanthalia elongata, Chondrus crispus, Fucus serratus* and warm-temperate species such *as Cystoseira baccata, Cystoseira tamariscifolia, Gelidium corneum, Bifurcaria bifurcata and Ellisolandia elongata* (Fernández, 2016). Further studies of the Atlantic flora are needed in order to establish the boundaries of the North-east Atlantic biogeographic regions which may have changed during the last years (Fernández, 2016).

Numerous species of intertidal macroalgae are an important habitat-forming substrate, harboring many epiphytes as well as sessile and mobile associated fauna which are mainly peracarid crustaceans (Kersen et al., 2011; Guerra-García et al., 2011). Crustaceans present one of the most morphological diverse organisms, however, it is believed that almost the 40% belongs to the Peracarida group (Kaestner 1980). This group is constituted of small benthic crustaceans found from the littoral to hadal regions of the oceans and some species which occupies terrestrial and freshwater habitats (Holdich and Bird 1986, Jaume and Boxshall 2008). Furthermore, peracarids play an important role in the structuring of benthic assemblages. They are a source of food for other benthic animals and fishes of commercial importance and important contributors to benthic production (Moreira et al., 2008).

The vast majority of peracarids are bottom-dwelling organisms, either infaunal or epifaunal, and they have a wide variety of feeding habits (Gudmundsson et al., 2000; Guerra-García and Tierno de Figueroa, 2009). Changes in food supply is believed to be an important factor in the distribution of these species and the diversity patterns in the benthic environment (Izquierdo and Guerra-García, 2010). Recently, this group has been the focus of numerous biogeography studies (Chavanich and Wilson 2000; Thiel 2002; Castellanos et al. 2003; De Broyer et al. 2003; Chiesa et al. 2005; Winfield et al. 2006; Myers and Lowry 2009), mainly because this group lacks pelagic larvae and their capacities for long-distance movement are limited in adults (Izquierdo and Guerra-García, 2010). Furthermore, they have been shown to be important contributors to benthic production (Mancinelli and Rossi, 2002) and good indicators of environmental changes (Conradi and Lopéz González, 2001; Guerra García et al., 2009). In spite of their interest, only a few researchers have studied the zonation patterns of rocky intertidal peracarids (Tararam et al., 1986; Buschmann, 1990; Krapp-Schickel, 1993; Baldinger and Gable, 1995).

Knowledge on the distribution of peracarids in the North Atlantic is still fragmentary. During the last decades, most of the studies have been focused on the Iberian Peninsula and specifically on the Strait of Gibraltar (Guerra-García, 2009; Izquierdo and Guerra-García, 2010), very scarce research has been undertaken on other Atlantic coasts (Guerra-García, 2009). Jimeno and Turón (1995) studied the ecological distribution of Gammaridea and Caprellidea from the northeast coast of Spain, and Pereira et al. (2006) studied the biogeographical patterns of intertidal peracarids, including isopods, tanaids and cumaceans, and their associations with macroalgal distribution along the Portuguese coast. Other studies of the distribution of these organisms have focused their interest in the deep Atlantic communities (Gage et al., 2004), however there is a lack of knowledge of the distribution patterns in the intertidal along European shores.

1.4 Drivers of distribution patterns

1.4.1 Environmental factors

Several mesoscale studies have attempted to relate the geographic distribution of different communities with biotic and abiotic processes (Blanchette et al., 2008). Studies in different parts of the world such as South Africa (Bustamante & Branch, 1996; Sink et al., 2005), Chile (Broitman et al., 2001), New Zealand (Menge et al., 1999, 2003), the US west coast (Connolly & Roughgarden, 1998; Schoch et al., 2006; Blanchette & Gaines, 2007), Japan (Nakaoka et al., 2006), British Columbia, Canada (Zacharias & Roff, 2001) and Santa Cruz Island, California, USA (Blanchette et al., 2006) has shown a strong link between oceanographic conditions and geographical variation in species assemblages, and specifically climate has been considered as a major determinant of species distribution (Grinnell et al,. 1917). Nevertheless, this interaction between environmental conditions and species distribution remain unexplored, limiting the prediction of the effects of climate change in the marine environment (reviewed in Darling and Côté 2008). Moreover, most of the predictions are based merely on the latitudinal variation of climate, without taking into account the differences in physical factors between the global, local and regional scale (Christensen et al. 2006; Helmuth et al. 2006; Jump et al. 2006; Austin and van Niel 2011).

One of the main environmental factors that play a key role in the distribution patterns of marine communities is temperature. This factor has been well-studied in biogeography and provide a useful quantifiable metric of ocean conditions (Blanchette et al., 2008). There are numerous fossil evidences that demonstrate the influence of temperature on the distribution of the organisms, such as the shift of marine faunas polewards as sea surface temperatures (SST) rose during the Pleistocene-Holocene transition (Hubbs, 1960; Addicott, 1969; Moore et al., 1980). But also short-term events such as El-Niño Southern Oscillation (ENSO), which causes sea surface temperature variations, can impact on species distribution limits (Pearcy & Schoener, 1987; Tanasichuk & Cooper, 2002; Zacherl et al., 2003; Keister et al., 2005). Commonly, the geographical limits of macroalgae have been linked to ocean isotherms, showing either lethal or sublethal conditions that limit growth and/or reproduction (Luning, 1990). In addition, several studies attribute recent shifts in distributions of macroalgae to the rising ocean temperatures (Mieszkowska et al., 2006; Lima et al., 2007a). Furthermore, future patterns of thermal stress should be considered in the context of biogeographical distributions (Blanchette et al., 2008). Present temperatures and predicted near future increases in thermal stress might not vary consistently with latitude in coastal marine systems (Helmuth et al., 2002, 2006a), and organisms could be most at risk in hotspots well removed from their current biogeographical range edge (Blanchette et al., 2008).

The organisms that occupy the intertidal are exposed to environmental conditions at the extreme edge of both the marine and terrestrial environment and therefore they are the most affected by the potential effects of climate change (Harley et al., 2006; Helmuth et al., 2006b). But also, other non-climatic physical factors are critical in shaping the vertical and latitudinal distributions of marine intertidal organisms (e.g. Harley 2003). In intertidal macroalgae distribution, various non-climatic factors may be determinant variables. For instance, the colonization of seaweeds depends on wave action and the availability of hard substrata for attachment (Luning, 1990; Vadas et al., 1992). The differences in the timing of the low tide may create “hot spots” of thermal stress (Helmuth et al. 2006). When emerged, the intertidal communities suffer water loss and significant overheating which may lead to physiological damage (Chapman 1995; Davison and Pearson 1996; Livingstone 2001).

High irradiance is another factor that affects these organisms (Häder and Figueroa 1997; Figueroa and Viñegla 2001). Ultraviolet is common in intertidal macroalgae and its negative effects on these organisms have been shown to increase with high temperature (Altamirano et al. 2003). However, this may vary with cloudiness and wind regimes, which modify air temperature, humidity and irradiance (Dromgoole 1980; Helmuth 2006), conditions hard to predict. Therefore, most distribution models for intertidal species do not include these physical factors and only account for large-scale changes in ocean temperature (Lüning et al,. 1990). Wave exposure has been acknowledged as a key process molding the composition of coastal communities (Ballantine 1961, Kingsbury 1962, Lewis 1964). The most noticeable effect is the exclusion of those organisms with inadequate attachment mechanisms (Zacharias and Roff, 2001). This physical factor not only affect the organisms but also their interactions acting directly as a mechanical stressor (McQuaid and Branch 1985, Menge and Sutherland 1987, Denny 1988) and indirectly by altering temperature (West and Salm 2003), sedimentation (Airoldi 2003, Schiel 2006), nutrient intake (Hearn et al. 2001) and productivity (Hurd et al,. 2000). Long periods affected by waves can also increase light attenuation through sediment resuspension, limiting photosynthesis as well as burying communities in sediments (Zacharias and Roff, 2001). Several studies have studied the relationship between the structure of intertidal communities and this physical factor (Lewis 1964, Seapy & Littler 1978). There are several tools in the assessment of this factor such as topographical indices based on the openness of the coastline and combined with local wind data, commonly showed as fetch models (Burrows et al. 2008).

Although it is believed, that salinity has a little effect on the marine communities' distribution (Mann & Lazier, 1996) in small scales this factor gains importance, specifically in intertidal communities that can be affected by salinity ranges from near 0 to >30ppt over shorth distances (Zacharias and Roff, 2001). In estuaries, salinity is one of the major environmental variables (Attrill 2002; Day et al. 2013) and it is modulated by several factors, such as tidal currents, evaporation, rainfall and riverine discharge (Day et al. 2013). Witman and Grange (1998) showed that high precipitation rates may affect local salinity and subsequently subtidal community structure by altering the spatial distributions of key predators.

Another factor that is taken into account in the distribution of species is productivity, dependent or independent of temperature and in many occasions related to upwelling processes (Field et al. 1998). The intensity and frequency of this oceanographic phenomenon have been pointed to act as a leading process structuring marine benthic communities in many temperate regions (Menge, 2000; Fenberg et al., 2014). The primary productivity is regulated by the availability of nutrients; the high turnover rates of phytoplankton makes primary producers to respond rapidly to nutrient levels which have led to the study of the relationship between primary productivity and assemblages of species (Huston and Wolverton ,2009). Chlorophyll levels in the sea can give us an idea of the primary productivity, which is commonly greater in coastal areas (Field et al. 1998), and can affect the fauna by increasing carrying capacities, population densities and diversity (Huston and Wolverton ,2009). In the case of algae, high productivity not only has a direct influence on the organisms themselves, but can also affect the associated organisms either directly or indirectly (Cole and McQuaid, 2010). Huston (1979) suggested that where there is greater diversity and greater densities of foundation species, there is more vacant space and consequently more dependent species. Previous studies have approached the effects of high productivity on the biogeography of intertidal organisms, however whether these responses can be generalized to include the fauna inhabiting biogenic habitats remain unknown (Cole and McQuaid, 2010).

1.4.2 Human impact

Furthermore, anthropogenically-forced environmental stresses are increasing in parallel with global warming, which can also cause a change in the distribution of organisms (Beaugrand et al., 2003; Richardson & Schoeman, 2004; Roessig et al., 2004; Harley et al., 2006; Portner & Knust, 2007). There are numerous models indicating that the greenhouse gas emissions could cause an increase on the acidification and warming of the ocean surface (Conners, Hollowed & Brown, 2002). Other human impacts such as overfishing may have indirect effects not only on the exploited populations, but also on ecosystem structure and function (Myers & Worm, 2003; Frank et al., 2005). In addition, one of the major threats affecting coastal marine ecosystems is anthropogenic eutrophication (Cloern, 2001).

Due to the increase in recent years of these anthropogenic stressors, the importance of biodiversity conservation and the state of habitats have been highlighted (Hunter and others, 1988; May, 1994). However, many of these studies focus on the terrestrial realm. But the marine realm will also undergo changes on species distribution (Richmond, 1993; Norse, 1993). Increasing world population in coastal areas is putting marine ecosystems at risk zone (IGBP, 1990; Leatherman, 1991; Norse, 1993) and it is timely, to evaluate the probable and known effects of anthropogenic global change and habitat disturbance on nearshore ecological communities (Ray, 1991).

Human disturbance and destruction of coastal habitats is likely to have a greater effect on the marine ecosystems than global warming (Bugnot et al., 2020). Tropical regions characterized by high diversity, high numbers of endemic species, and by high numbers of rare species will be subject to the greatest risks from human impact (Conners, Hollowed & Brown, 2002). Predictions indicate that precipitation and temperatures will become more variable and extreme weather events will be more frequent and extreme (e.g., heat waves, droughts, and floods) (Easterling et al. 2000; IPCC 2007). These factors may also affect pH fluctuations which could become more pronounced, nonetheless little research has focused on the impact of pH fluctuations on marine species distribution (Conners, Hollowed & Brown, 2002). Several factors contribute to these fluctuations including temperature (influencing the solubility of CO2), salinity (influencing alkalinity), photosynthesis rates (affecting uptake of CO2), respiration (affecting release of CO2), and upwelling of CO2-rich deep water (Bates et al. 1996; Raven et al. 2005; Lee et al. 2006; Wootton et al. 2008)

Species living in coastal and intertidal zones will therefore be particularly exposed if fluctuations in seawater pH increase (Marchini et al., 2019). Especially, organisms such as peracarids are more at risk of being negatively affected by ocean acidification. Their cuticle contains magnesium calcite (Hild et al. 2008), which is highly soluble and the surface seawater is predicted to become undersaturated with respect to this mineral in the near future (Feely et al. 2004; Andersson et al. 2008; Neues and Epple 2008). The decreased of pH in the ocean has been mainly caused due to the ocean's capacity to act as a sink of anthropogenic carbon. Changes in pH lead to major changes in the seawater chemistry, namely an increase of bicarbonate and a decrease of carbonate ions as well as of the saturation state of calcium carbonate and aragonite. Among marine ecosystems, calcareous organisms such as peracarids or some algae will be the most affected by a decrease in pH (Martin and Gattuso, 2009; Bijma et al., 2013; Kamenos et al., 2013)
However, for the moment many studies fail to establish limits on the natural variability of benthic communities, and therefore we still are unable to discriminate many of the ecological

responses registered because of natural or anthropogenic disturbances (e.g. Echavarri et al.,2007). Establishing the relationship between stressors and causes at the species or community level is a difficult task that requires the use of multiple lines of evidence (Adams, 2005). Thus, there is an urgent need for tools that contribute to the effects of human activities in the marine environment, by providing indicators that measure the extent of impact of an activity on part of the ecosystem (Rogers and Greenaway, 2005).

Harlpem (2012) developed an index to quantify the human impact on the ocean. The index allows to simultaneously evaluate disparate metrics, allowing for an integrated assessment of changes in, for example, fish stocks, extinction risks, coastal jobs, water quality and habitat restoration. The Ocean health index (OHI) comprises ten goals which can be considered separately or aggregated into an overall score for a region, country or entire ocean (Figure 1.3). The index is calculated as a linear weighted sum of the scores for each of the ten public goal indices and the appropriate weights for each goal. Each goal score is a function of its present status and an indication of its likely near-term future status. The global index score was 60 out of 100, nevertheless it varied greatly by country. For instance, Northern Europe showed a high score while African countries scored poorly. Developed countries tended to score higher than developing countries showing that index scores are significantly correlated with the human development. This is because developed countries tend to have stronger economies, better regulations and infrastructure to manage pressures and greater capacity to pursue sustainable resource use (Harlpem., 2012).

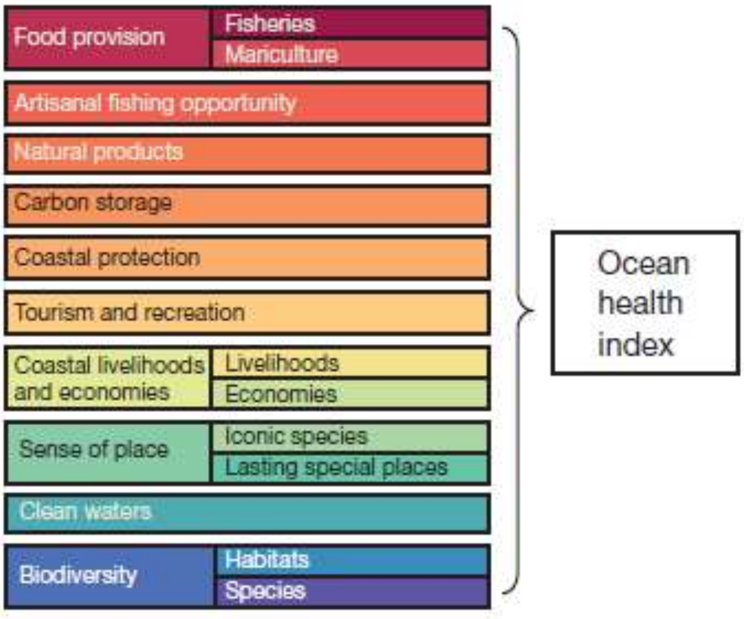


Figure 1.3. Public goals and sub-goals of Ocean health index (OHI). Source: Harlpem, 2012.

1.5 Biodiversity

Biological diversity is “the variety of life” and encompasses variations at all levels of biological organization (Gaston and Spicer, 2004). This range of different levels of organization goes from the genetic variation between individuals and populations, to species diversity, assemblages, habitats, landscapes and biogeographical provinces. The term most used in many studies to describe biodiversity is *species richness* which refers to the number of species in a given area (Gray, 2000) and it is worth stressing that the richness in a region should be determined by a balance between the rates of extinction, migration and origination of species (Wiens & Donoghue, 2004; Mittelbach *et al*., 2007). However, the number of species alone does not describe the structure of the assemblage of species in a given area because the number of individuals per species varies (Gray, 2000). The richness of any region is a consequence of the richness of each of the smaller areas that compose it, and the turnover in species composition among them (Whittaker 1960). In order to take into account the proportional abundance of species, a variety of indices are used (Magurran et al., 1984). These indices consider both species richness and how evenly the individuals are distributed among species (evenness or equitability) (Gray, 2000).

Several scales of species richness have been proposed; the number of species found in a sample or the richness of taxa at a particular community was named *apha* (or within habitat) *diversity* and it was described as the basic unit of diversity. Alpha diversity measures capacity within a community and thus reflects how finely species are dividing ecological resources (Sepkoski, 1988). Several indices of species diversity are used to measure alpha diversity. A commonly used index is that referred to as ‘Shannon’s Index’ or ‘H’. Another widely used indices for community analysis are Simpson’s and Gini-Simpson’s. But these indices are not themselves diversities, therefore, in order to measure the true diversity, “the effective number of species” was proposed (Jost, 2006). This can be defined as the number of equally-common species required to give a particular value of an index. Converting indices to true diversities (effective numbers of species) gives them a set of common behaviors and properties (Cao and Hawkins, 2019). After conversion, diversity is always measured in units of number of species, no matter what index we use. This lets us compare and interpret them easily, and it lets us develop formulas and techniques that don't depend on a specific index. It also lets us avoid the serious misinterpretations spawned by the nonlinearity of most diversity indices (Jost, 2006). In addition, species diversity can be shown as *beta* (or between habitat) *diversity*, and it can also be measured at a larger scale, *gamma diversity* (Whittaker et al., 1960).

The spatial structure of communities is linked with ecological processes by beta diversity, and therefore it can also be defined as the taxonomic differentiation of fauna or flora between sites or communities (Sepkoski, 1988). These ecological processes include neutral processes such as dispersion limitation and niche-based processes (e.g. limiting similarity and environmental filtering) (Dobrovolski, Melo, Cassemiro and Diniz-Filho, 2011). Beta diversity can be used to measure the amount of turnover in species composition along environmental gradients and therefore, it can reflect the extent of habitat selection or specialization (Sepkoski, 1988). Besides, this measurement of diversity provides a better understanding on how ecological processes operate along environmental gradients (Qian and Ricklefs, 2007). Only a few studies focused on beta diversity for marine biota, especially at a large scale (Smit, Bolton and Anderson, 2017). Beta diversity can be divided into two components: spatial turnover and nestedness (Baselga, Jiménez-Valverde and Niccolini, 2007). The latter measures the ordered deconstruction of assemblages due to non-random processes of species loss, leading to the formation of local sets poorer in the number of species. On the other hand, spatial turnover describes the replacement of species as a result of ecological processes (Wright and Reeves, 1992). Turnover and nestedness are complementary and main drivers of dissimilarity patterns between communities (Baselga, Jiménez-Valverde and Niccolini, 2007), and it has become possible within the last decade (Baselga et al., 2010).

The latitudinal gradient of diversity, specifically species richness is still one of the most important patterns in macroecology and biogeography (Pianka, 1966;Willig et al., 2003;Wiens & Graham, 2005; Mittelbach et al., 2007). Latitude is a surrogate for a number of primary environmental gradients (e.g., temperature, insolation) that interact and are correlated to each other, making the study of this gradient difficult and controversial (Willig, Kaufman & Stevens, 2003). Global-scale patterns of biodiversity is one of the most studied in ecology and biogeography, consistent trends are repeatedly documented in both terrestrial and marine environments (Gaston et al., 2000). One of the main factors that influence this latitudinal gradient of biodiversity is the spatial scale but it is also dependent on the historical, geographic, biotic, abiotic and stochastic forces (Schemske 2002). Several studies confirm an increase in species diversity from the poles toward the tropics (Willing 2003; Hillebrand 2004). This phenomenon was described by Rapoport in 1982 and it refers to the tendency for species geographical ranges to become smaller towards the tropics. Although many explanations have been proposed for this pattern (Pianka 1966; Stevens 1989; Rohde 1992; Koleff & Gaston 2001), its underlying causes remain unresolved (Currie et al. 2004; Martin & McKay 2004; Mittelbach et al. 2007).

There are numerous theories that aim to explain this latitudinal gradient of species diversity. For example, the *species–area hypothesis* support that larger areas can harbor more individuals and populations thus reducing extinction risk, while also containing more barriers that promote allopatric speciation (Rosenzweig 1995, Chown and Gaston 2000). Kaspari (2004) proposed the *species–energy hypothesis* that attempt to explain the pattern by the faster metabolic and speciation rates associated with warmer temperatures, and the climatic stability that characterizes the tropics. The *species–productivity hypothesis* suggests that greater energy inputs will support more individuals and promote specialization, however the relationship between species numbers and productivity appears to be highly scale dependent (Rosenzweig 1995, Chase and Leibold 2002). This latitudinal gradient has also been observed in beta diversity (referring to the turnover of species). The increase of beta diversity of species between habitats towards the equator might contribute to high diversity at both local and regional scales, and it could be explained by less-seasonal environments in the tropics which allow a greater habitat specialization (Stevens et al., 1989). Few studies have examined the relationship between latitude and beta diversity at any scale, and results are inconsistent.

Despite its generality, exceptions to the latitudinal gradient of species diversity are common in both terrestrial and marine realm (Stevens, 1989; Stephens & Wiens, 2003; Willig et al., 2003; Smith et al., 2005; Kindlmann et al., 2007; Fernández et al., 2009; Pyron & Bur brink, 2009). For instance, the temperate Pacific coast of South America harbors many different marine taxa and it presents an inverse latitudinal gradient in seaweeds (Meneses & Santelices, 2000; Santelices et al., 2009) and peracarids crustaceans (Lancellotti &Vásquez, 2000; González et al., 2008). Others regions have also shown an inverse latitudinal gradient of diversity of benthic organisms (Willig et al., 2003). Biodiversity patterns may be the result of different physical properties of the water such as light penetration and absorbency of radiation, salinity, temperature or oxygen concentration. They can shape the latitudinal gradient which may affect in the delimitation of the marine biogeographic boundaries (Hayden et al., 1984). Although, a decrease of diversity from the equator to the poles can be found in pelagic, benthic and even deep-sea species, there are exceptions such as peracarids in North Atlantic waters that do not follow this pattern (Brandt et al., 1996).

Reductions in biological diversity have been observed during the last decades, mainly due to factors such as habitat destruction, pollution and climate change (Dornelas et al., 2014). Beta diversity has gained great importance in marine ecology and biogeography (Thrush et al., 2010) because it can describe changes in community composition and structure along spatial and environmental gradients (Anderson et al., 2011). Diverse environmental factors such as organic matter input (Hecker 1990), currents (Blake & Grassle 1994), macrohabitat heterogeneity (Gooday et al. 2010), temperature (Howell et al. 2002), oxygen concentration (Levin et al,. 2000) among others, may be responsible for determining beta diversity patterns. While there is a growing body of literature on the subject, large gaps remain in the understanding of biodiversity patterns. Thus, one of the most important objectives in ecology and biogeography remains the ‘‘development of a markedly improved understanding of the global distribution of biodiversity’’ (Gaston et al., 2000).

2. Objectives

Coastal marine systems are among one of the most important in terms of economic and social contribution to the world population. Marine habitats are estimated to provide over US$14 trillion worth of ecosystem goods and services per year, or c. 43% of the global total (Costanza et al. 1997). Nevertheless, many scientists around the world agree that coastal marine systems, along with the goods and services they provide, are threatened by anthropogenic global climate change (IPCC 2001). During the last decade there has been a growing concern about species distribution changes in marine systems. Climate is considered one of the major drivers of species distribution (Grinnel, 1917). There are numerous studies that have suggested climate driven species distribution shifts (Lima et al. 2007; Hawkins et al. 2009). However, the interaction between the factors that drive the distribution of organisms remain unexplored, thus limiting the capacity to predict changes on species distribution by climate change (Dornelas et al., 2014). In addition, biodiversity has been reduced in recent years, mainly due to habitat destruction, pollution and overharvesting, and ecosystem function is changing as a result (Butchart et al., 2005). The implementation of conservation and management decisions is typically at the scale of local to regional ecosystems, knowledge of biodiversity change within assemblages is essential to inform policy ("AIBSnews", 2004).

There are several biogeographic studies focused on the distribution of seaweeds (Robin South, 1987; Fernández, C., 2016.), peracarids (Beaugrand, 2002; Guerra-García, Sánchez and Ros, 2009) and their relationship (Izquierdo and Guerra-García, 2010; Guerra-Garcia and Sanchez, 2009), however most have been carried out on a regional scale, especially in the Iberian peninsula. In this study, we aim to gain a broader idea of the distribution of seaweeds and associated peracarids. We focus on the role of environmental variables and anthropogenic pressure in the determination of the geographical distribution as well as biodiversity patterns of intertidal seaweeds and peracarids along the Northeast Atlantic, covering a wide latitudinal range, from Iceland to Canary Islands. This study will provide a larger-scale view (North-east Atlantic region) of the distribution patterns of the algae and peracarids that inhabit the intertidal zone. It can also help to expand the knowledge on what are the factors that determine the distribution and diversity of these organisms, which can be useful for future research on the predictions of possible changes caused by climate change.

Considering ecoregion as an area of relatively homogeneous species composition, clearly distinct from adjacent systems, we hypothesize the presence of ecoregions in the Northeast Atlantic, based on the occurrence of both algae and associated peracarid species and that the main factors that drive the separation of ecoregions are the sea surface temperature (SST) and anthropogenic pressure. In addition to the presence of a biodiversity latitudinal gradient, decreasing towards the poles.

In order to verify these hypotheses, samples of a wide latitudinal range were analyzed and a biogeographic analysis was carried out including different environmental factors as well as anthropogenic pressures to reveal which of them have a greater effect on the distribution. In addition, the biodiversity of the different seaweeds and peracarids communities was studied and, they were compared with different latitudes.

The intent of this study was 1) to determine ecoregions for the North-east Atlantic (25ºN-65ºN) based on intertidal seaweeds and associated peracarids species distributions; 2) to explore the relationship between ecoregions and environmental variables, including anthropogenic pressure, and 3) to compare and contrast diversity of seaweeds and peracarids from intertidal sites at geographically widely dispersed areas to ascertain if there are trends with latitude.

3. Material and methods

3.1 Study area

This study encompasses the North-east Atlantic region. Samples were taken at nine sites and twenty-seven stations along a wide latitudinal gradient from Reykjavik in Iceland (65° 59' 59.9856" N, 21° 19' 10.776" W) to Canary Island (Spain) in the south of the North-east Atlantic region (27° 59' 8.7144" N, 15° 22' 30.756" W)(Figure 3.1). The sites were selected in order to cover the greatest range of latitudinal environmental conditions and they are strongly influenced by the Gulf Stream which is divided in several currents producing great differences in the oceanographic conditions of the sites.

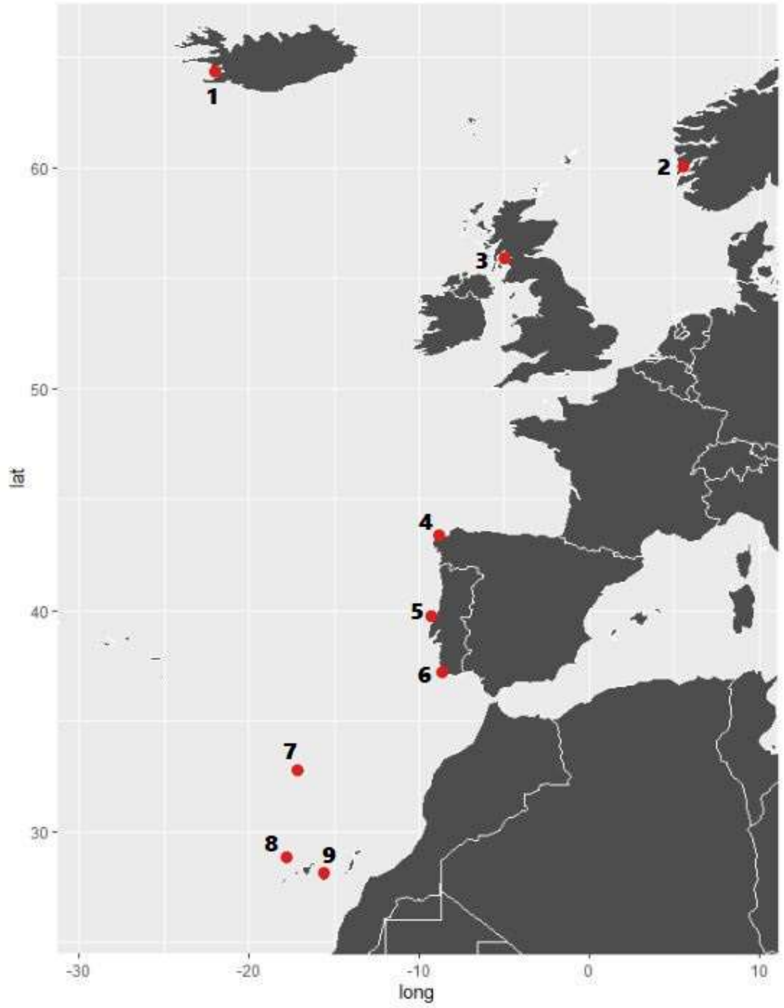


Figure 3.1. Study area showing the sampling sites, with three stations for each site. 1)Iceland, 2)Norway, 3)Scotland, 4)Galicia, 5)West Portugal, 6)South Portugal and the islands of 7)Madeira, 8)La Palma and 9)Gran Canaria.

The primary goal of the sampling design was to cover all relevant habitats in the intertidal zone to maximize diversity sampling. The design used was based on the tidal zonation levels. The rocky intertidal shore was divided into three levels, upper, middle and lower, according to the zonation scheme of Lewis (1964) and within each level, four habitats were considered, according to two abiotic variables that determine the distribution of algae in the intertidal zone, exposure to light (sun/shadow) and exposure to the sea (submerged/emerged).

The limits were set by the margins of distribution of indicator species and the reason for this is that the degree of exposure decouples the vertical distribution of species from the levels of high or low tide, except in sheltered shores. Although the Lewis system only considers two divisions: the littoral fringe and the eulittoral, the latter can be subdivided depending on the relative abundance of the dominant species. Therefore, the criteria used here were: 1) Upper, above the barnacle limit. It is here that occurs *Melarhaphe neritoides* and other littorinids in other regions (and also the lichens), 2) Middle, between the upper limit of the barnacle belt and the upper limit of the mussel belt which is usually coincident with the upper limit of heavy algal cover. This is where the heavy dominance of barnacles occurs (although decreasing up-shore) and also the limpets, 3) Lower, bellow the upper limit of the mussel belt.

3.2 Environmental variation along the European latitudinal range

The environmental variables used in the present study were selected due to the important role that they play on the distribution of marine organisms. Temperature, salinity and chlorophyll as a proxy of productivity can change the distribution and the occurrence of marine organisms (Rohde, 1992; Ingole & Parulekar, 1998; Gaston, 2000; Yasuhara et al., 2012). At the coast, other abiotic factors, such as wave fetch, tidal amplitude, insolation, are critical at local level to structure marine communities (Gaston, 2000; Gartner et al., 2013; Kroeker et al., 2016). Also human disturbances and the effect caused by climate change, can act both on small and large scales, affecting the distribution of organisms (Airoldi & Beck, 2007; Brierley & Kingsford, 2009; Crain et al., 2009; Coll et al., 2010). Thus, to better understand the pattern of diversity and distributions of marine organisms, we need to consider this set of abiotic factors.

The latitudinal gradient along the sampling stations was characterized by the following environmental variables fetch, air temperature, chlorophyll-a minimums SST, insolation, precipitation. Ocean acidification was studied by the addition of pH and aragonite saturation values, which were obtained from NOAA Dataset. Besides, Ocean Health Index (OHI) was included, developed by Halpern in 2012, which encompasses different human actions that can change the state of the ocean. The index (OHI) score is the weighted sum of ten goal-specific index scores (1):

$$I = \sum_{i=1}^{N} \alpha i I i \qquad (1)$$

where α is the goal-specific weight ($\sum\alpha_i=1$; $\alpha_i= 1/N$) and I_i is the average value of present and likely future status, for each goal i. In this study, index values for 2015 were included, they were the most recent data found from Halpern.

3.3 Sampling and species classification

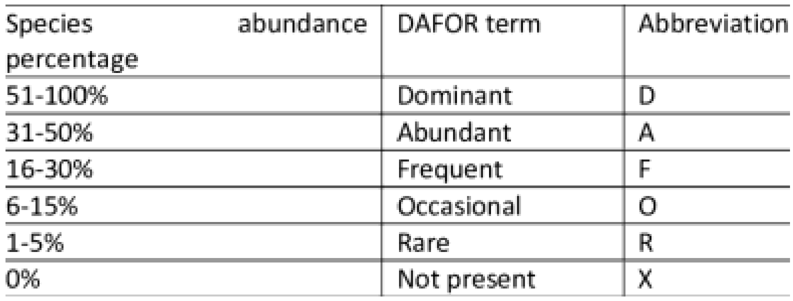
Sampling was conducted from spring to fall 2011 (from April to October) and consisted of 20 cm x 20 cm quadrats within each intertidal zone, one per habitat. Each quadrat area was scratched and organisms were completely removed. Three replicates were taken from each habitat. All habitats within each level were explored and every species observed were collected. A minimum of 15 individuals of the most common species and the complete collection of the rest of organisms was established, however, this procedure slightly varied depending on the habitat; In the Upper level collect at least for 15 person*min. In the Middle and Lower levels collect for at least for 30 person*min. Then, the samples collected in the different habitats were placed in previously labeled bags and subsequently preserved in a preservative solution (40% salt water, 40% ethanol (70%), 10% glycerin, 10% formalin (4% formalin).

3.4 Sample processing

The samples were then processed. Firstly, in order to separate the peracarids from the algae, they were immersed in fresh water for 5 min, agitating to release the organisms. Then, the algae were removed and water was sieved through a 500 micra mesh. Finally, the organisms were preserved in alcohol. In the laboratory, samples were identified, whenever possible, to the species, with a Carl Zeiss Magnifier, STEMI 2000C and a Carl Zeiss Microscope, Axioskop 2 PLUS, and the representative specimens of the different species and locations were stored in liquid medium (KEW), since this process facilitates future uses of biological material. The identification of the species was carried out through a diverse bibliography (e.g. Dixon & Irvine 1977, Irvine 1983, Burrows 1991, Maggs & Hommersand 1993 and Afonso Carrillo & Sansón 1999).

In the last phase, data was introduced in a table, with each species classified according to two scales of semi-quantitative abundances. The first uses values between 0 - 4, with 0 - absent, 1 - present or rare, 2 - little abundant, 3 - common and 4 - very abundant. The second, the

DAFOR scale, quantifies organisms as D - dominant, A - abundant, F - frequent, O - occasional and R - rare. In the case of the peracarids, absolute abundance were scaled and adapted to the DAFOR scale (Table 3.1).



Species abundance percentage	DAFOR term	Abbreviation
51-100%	Dominant	D
31-50%	Abundant	A
16-30%	Frequent	F
6-15%	Occasional	O
1-5%	Rare	R
0%	Not present	X

Table 3.1. DAFOR scale used to determine species abundance. Source: Kenneth F. D. Hughey (2012).

3.4 Data analyses

First, the data set containing all the species that were sampled was cleaned, removing those that only appeared in one site. Then, a presence and absence matrix with sites in the rows and species in the columns was created in order to analyze the distribution pattern. Using the *Vegan* package of the statistical software RStudio, the affinities among sites based on presence-absence matrix with a total of 412 species were measured through a CLUSTER analysis using UPGMA (unweighted pair group method using arithmetic averages), based on the Bray-Curtis similarity index. The results were shown in a dendrogram and a K-means cluster plot was used for a better visualization of the groups. The number of groups or clusters (k) was chosen, based on the elbow method. In addition, the similarity of the sites based on the occurrence of species was shown performing a non-metric multidimensional scaling (NMDS), distinguishing by colors the different biogeographic regions obtained in the cluster analysis. Finally, the percentage of endemism corresponding with each biogeographic division was calculated.

Before proceeding with the analysis of the environmental data, normality was verified using Shapiro-Wilk test and the environmental variables were plotted against latitude. The relationships between environmental measures and species assemblages were studied by a Canonical Correspondence Analysis (CCA) (Izquierdo and Guerra-García, 2010) and by fitting the environmental variables with the NMDS plot using the *envfit* function

(Dixon, 2003). Both analysis were carried out using the package *Vegan* from the RStudio software. In order to study the significance of the environmental variables represented in the CCA, a permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001), using the 'adonis' function of the 'vegan' package (Oksanen et al., 2017), with 999 permutations was carried out. Furthermore, multicollinearity between the different environmental variables was detected using the VIF (Variable Inflation Factors) method.

After this point, an abundance matrix with sites in the rows and species in the columns was used, and abundance was scaled to the DAFOR scale. The similarity percentages breakdown (SIMPER) procedure (Clarke, 1993) was used to assess the average percent contribution of each specie to the dissimilarity between the three ecoregions obtained in the previous analysis. Biodiversity was also analyzed by measuring *alpha* and *beta* diversities. Species richness (S), Shannon-Wiener Index (H') (2), Simpsons Index (DSimp) (3), Evenness (J') (4) and effective number of species (5) were calculated for each station. The indices were calculated as the following:

$$H' = -\sum_{i=1}^{s}(p_i)(logp_i) \qquad (2)$$

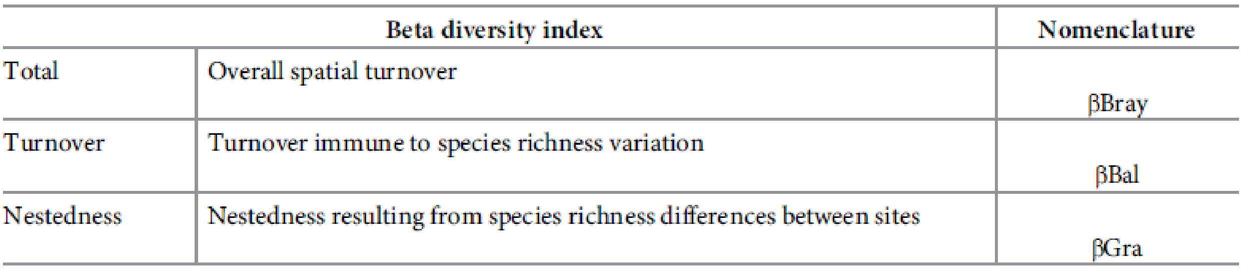
Being p the proportion (n/N) of individuals of one particular species found (n) divided by the total number of individuals found (N). Natural logarithm was used in order to calculate the effective number of species.

$$D = \sum_{i=1}^{s}\frac{n_i\,(n_i-1)}{N(N-1)} \qquad Dsimp = 1 - D \qquad (3)$$

$$J' = \frac{H\prime}{\ln S} \qquad (4)$$

$$Effective\ number\ of\ species = e^{H\prime} \qquad (5)$$

On the other hand, beta diversity was partitioned into overall beta diversity, turnover and nestedness components following the methods proposed by Baselga in 2009 (Table 3.2). This procedure was performed using the function "beta.sample.abund" in the R package betapart.



Beta diversity index		Nomenclature
Total	Overall spatial turnover	βBray
Turnover	Turnover immune to species richness variation	βBal
Nestedness	Nestedness resulting from species richness differences between sites	βGra

Table 3.2. Beta diversity index and their nomenclatures used in the present study. Source: Dalmolin, Tozetti & Ramos Pereira, (2019).

In order to study if there is a relationship between the latitude and biodiversity, the Pearson correlation coefficient was calculated for all the biodiversity indices. Furthermore, the indices that showed a high correlation were plotted against latitude, differentiating the three main biogeographic regions by color.

4. Results

4.1 Cluster analysis of intertidal seaweeds and peracarids

A total of 12779 specimens were sorted and examined, out of which more than 74% were algae. In this study, 332 species of algae were identified of which almost 16% belonged to the Rhodomelaceae family, followed by Cladophoraceae and Ceramiaceae and 80 different species of peracarids were found. Amphipoda was the dominant group represented by the family Hyalidae with a 14% of the total of the peracarids specimens analyzed. When examining the cluster dendrogram based on Bray-Curtis similarity, two main groups can be differentiated (Figure 4.1) at 0.8 dissimilarity. One that includes the stations 10-27 (Madeira, Canary Islands and Iberian Peninsula) and another that includes the stations 1-9 (Iceland, Norway and Scotland). At 0.6 dissimilarity another division occurs, separating the stations 19-27 (Madeira and Canary Islands) and the stations 10-18 (Iberian Peninsula). It is worth highlighting the distinction of a station in each of these last two groups, corresponding to station 14 (Moel) in the Iberian Peninsula and station 6 (Viksoy) for the northern region.

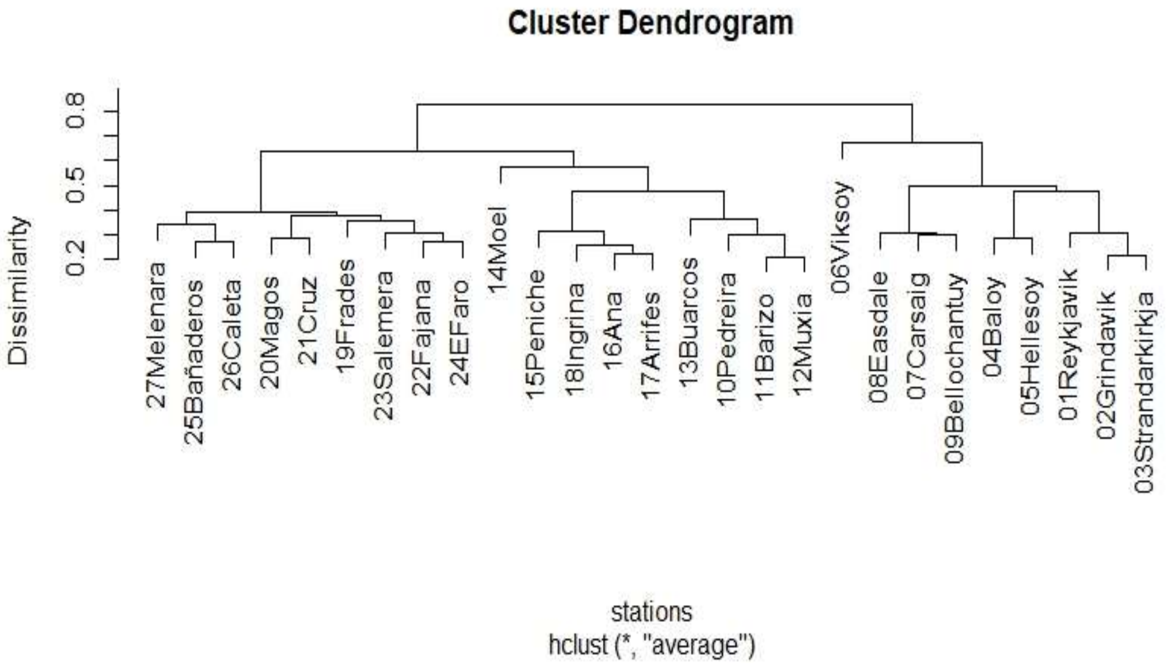


Figure 4.1. Cluster dendrogram based on the seaweed and peracarid composition of each station.

The k-means cluster analysis gives us a better visualization of the groups (Figure 4.2). The number of clusters was predefined using the elbow method which the optimal number of clusters correspond to the bend in the knee (or elbow) (Figure 4.3). The results of the graph agree with those shown in the dendrogram, separating the sites into three large groups. The northern region which encompasses from Iceland, Norway and Scotland, shown in red, the green cluster includes the Iberian Peninsula or central region and the southern region is represented by the blue cluster. In addition, a greater amplitude in terms of dissimilarity can be observed for the Iberian Peninsula and North regions, where, as in the dendrogram, the little similarity of the station 14 (Moel) and 6 (Viksoy) with the rest present in the area stands out. On the other hand, the stations that belong to the southern region (Madeira and Canary Islands) showed a greater grouping, indicating less dissimilarity between them.

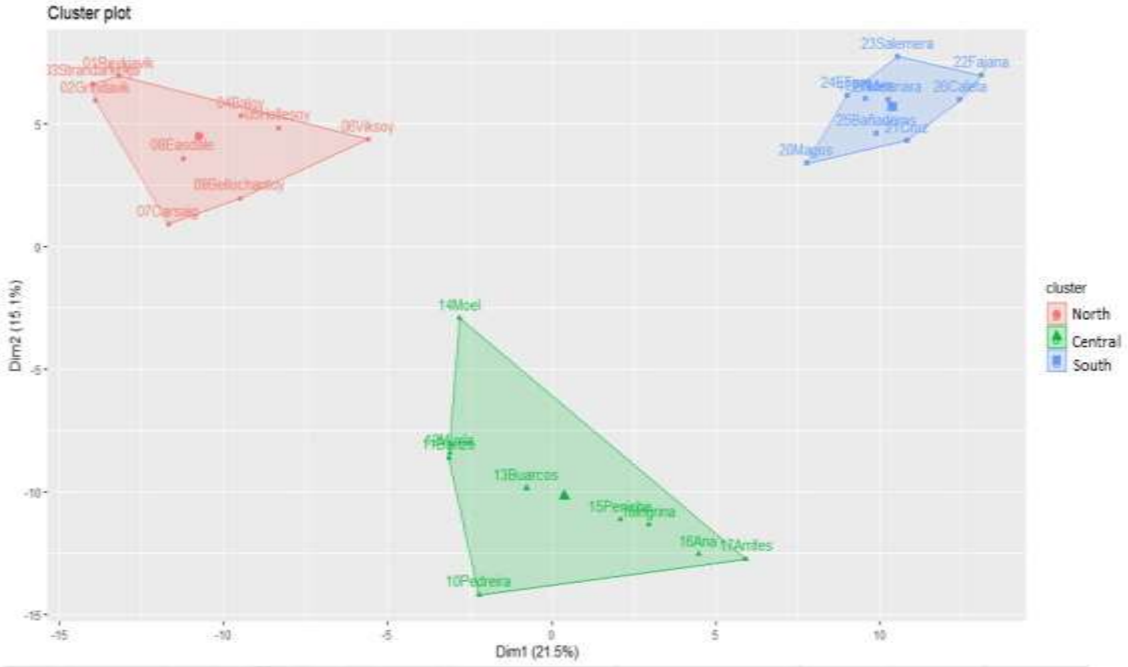


Figure 4.2. Graph showing the results of the k-means cluster analysis based on the occurrence of seaweeds and peracarids along the different stations.

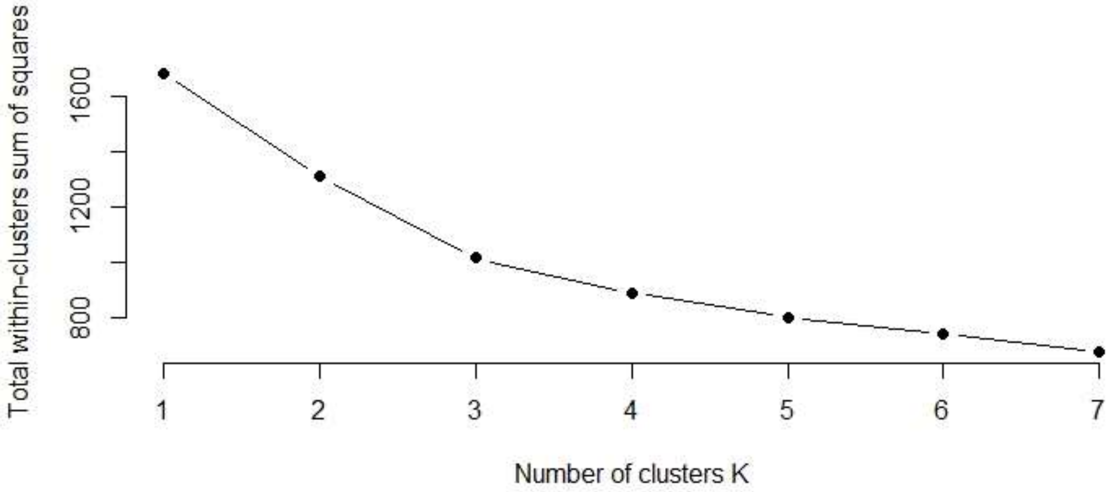


Figure 4.3. Elbow method which display the best k mean fitting or optimal number of clusters predefined for the k-means cluster analysis.

Finally, distinct groups of stations emerge from the 2-dimensional picture produced by the non-metric multidimensional scaling (NMDS) (Figure 4.4) and match well those produced by the CLUSTER and k-means analysis. The three distinct groups were considered as different biogeographic regions, corresponding with the stations in the north (blue), central region or Iberian Peninsula (orange) and those in the south (green), the latter which includes Madeira and Canary Island is also known as Macaronesia (Almada et al. 2013). Furthermore, the low stress level (0.054) indicates a good fit and therefore we can assume that the ordination is not arbitrary.

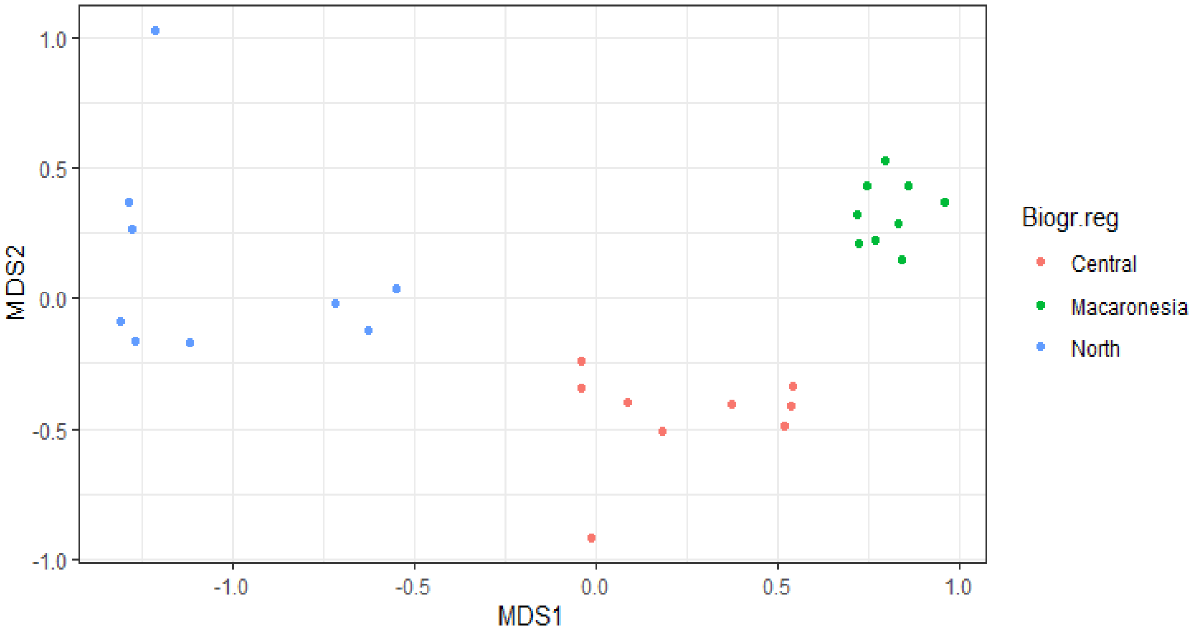
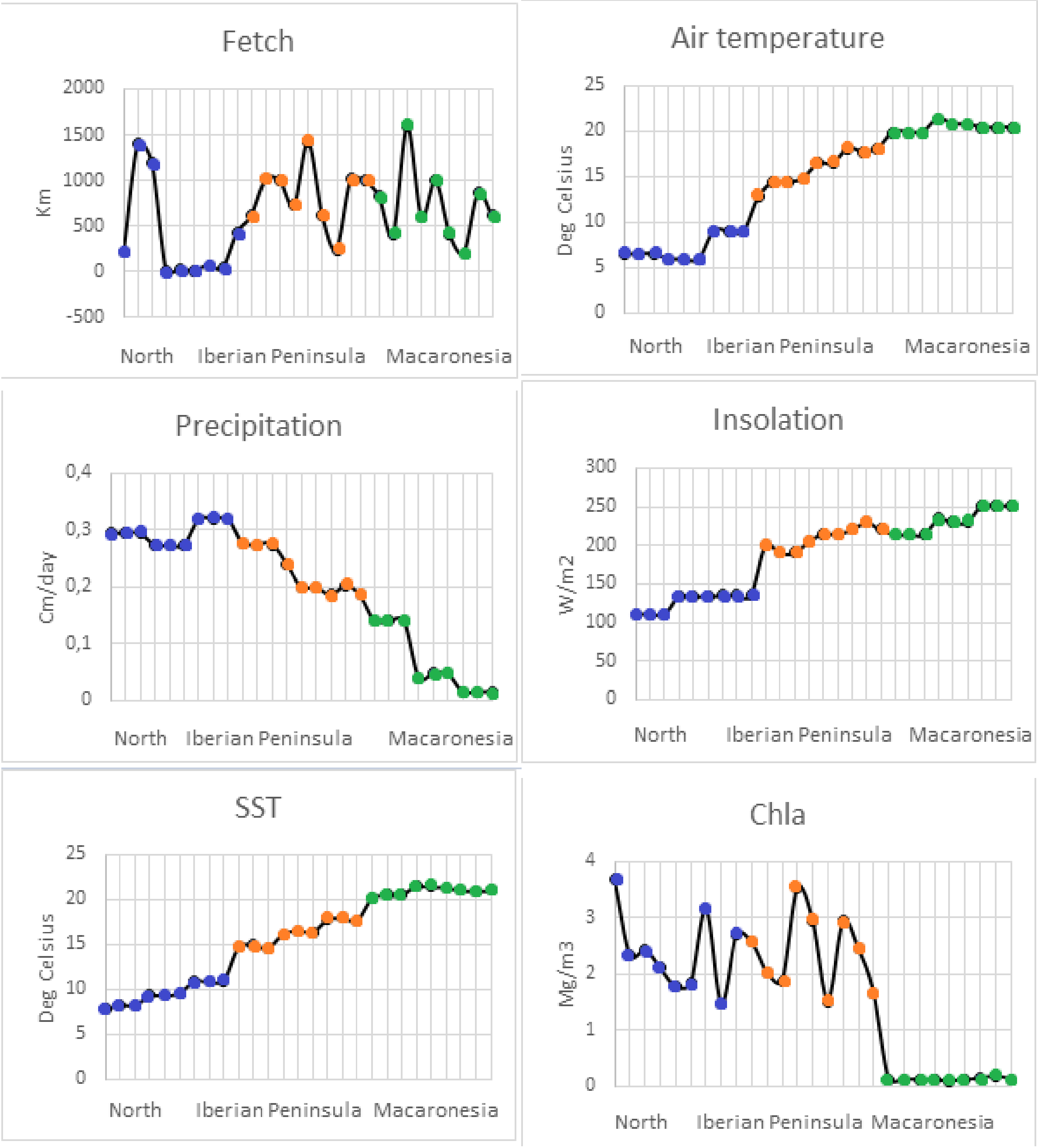


Figure 4.4. Graph representation of the non-metric multidimensional scaling analysis (NMDS), where colors represent the different biogeographic regions and points represent each station.

4.2 Relationship between abiotic data and the distribution of seaweeds and associated peracarids

Regarding the latitudinal variation of the environmental parameters along sampling stations, low latitudes were represented by higher air temperatures, SST, insolation, pH and aragonite saturation while northern sites were dominated by higher precipitation and chlorophyll-a. It was observed that contrary to all the other variables, fetch did not show a clear latitudinal variation. Higher values of fetch were observed at the stations 2 (Grindavik) in the North, 14 (Moel) in the Iberian Peninsula and 21 (Cruz) in Madeira. As well OHI did not show a definite trend and remains relatively stable along the latitudinal gradient, ranging from 60 (stations 1, 2 and 3) to 80 (stations 19, 20 and 21). Stations located in the Macaronesia (19-

27) showed higher temperature values both in the air and on the seawater surface as well as a greater energy received by insolation than the station along the northern Atlantic coasts (Figure 4.5). Oppositely, precipitation and chlorophyll-a concentration were really low for the southern sites, on the other hand the fetch or area (km) affected by the wind varied across all the stations, showing no definite trend. When focusing on the saturation of aragonite and pH (in the latter, with the exception of stations 1, 2 and 3) increased as we approach regions located farther south with a significant difference from the stations 1-9 (North) that showed lower values.



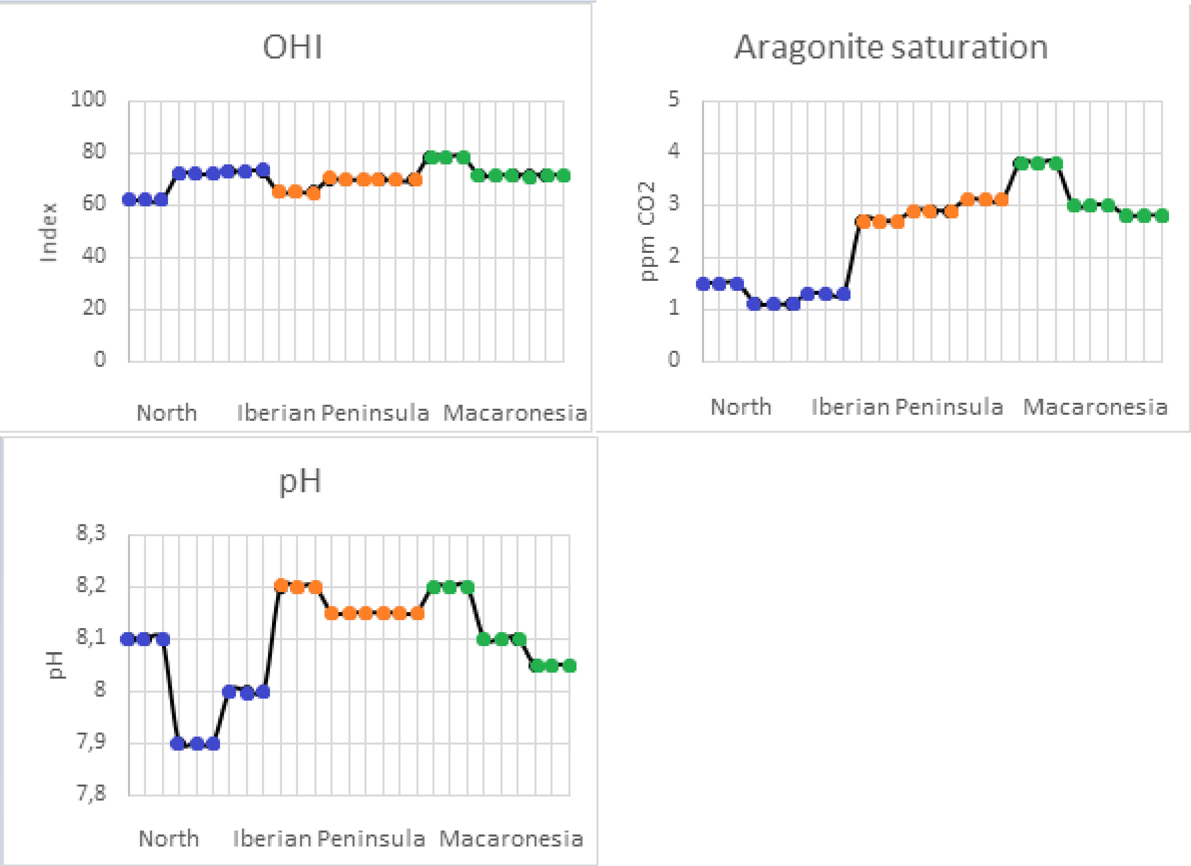


Figure 4.5. Variation of abiotic variables along sampling stations (points). The stations corresponding to the northern region were represented in blue, orange for the Iberian Peninsula and green for the stations of the Macaronesia.

The non-metric multidimensional scaling analysis (NMDS) (Figure 4.6) based on the occurrence of seaweeds and peracarids revealed a grouping of the stations in three main regions, corresponding with Macaronesia, Iberian Peninsula and North, the latter showed marked differences between Norway, Iceland and Scotland. In addition, the analysis showed the relationship of these groups with the environmental variables; the communities from the stations 1-9 (North) tended to be associated with colder temperatures, more chlorophyll-a concentration minimums, lower insolation and aragonite saturation than those in the stations 19-27 (Macaronesia). While the communities from Central or Iberian Peninsula (stations 10-18) were associated with higher precipitation and chlorophyll-a concentration as well as higher fetch and pH, the latter with a longer arrow indicate a “stronger” predictor than the fetch. On the other hand, the OHI was associated with the southern stations and showed a low correlation with other environmental variables such as aragonite saturation, insolation and air temperature. Besides, the stress level (0,058) obtained showed a good ordination of the stations.

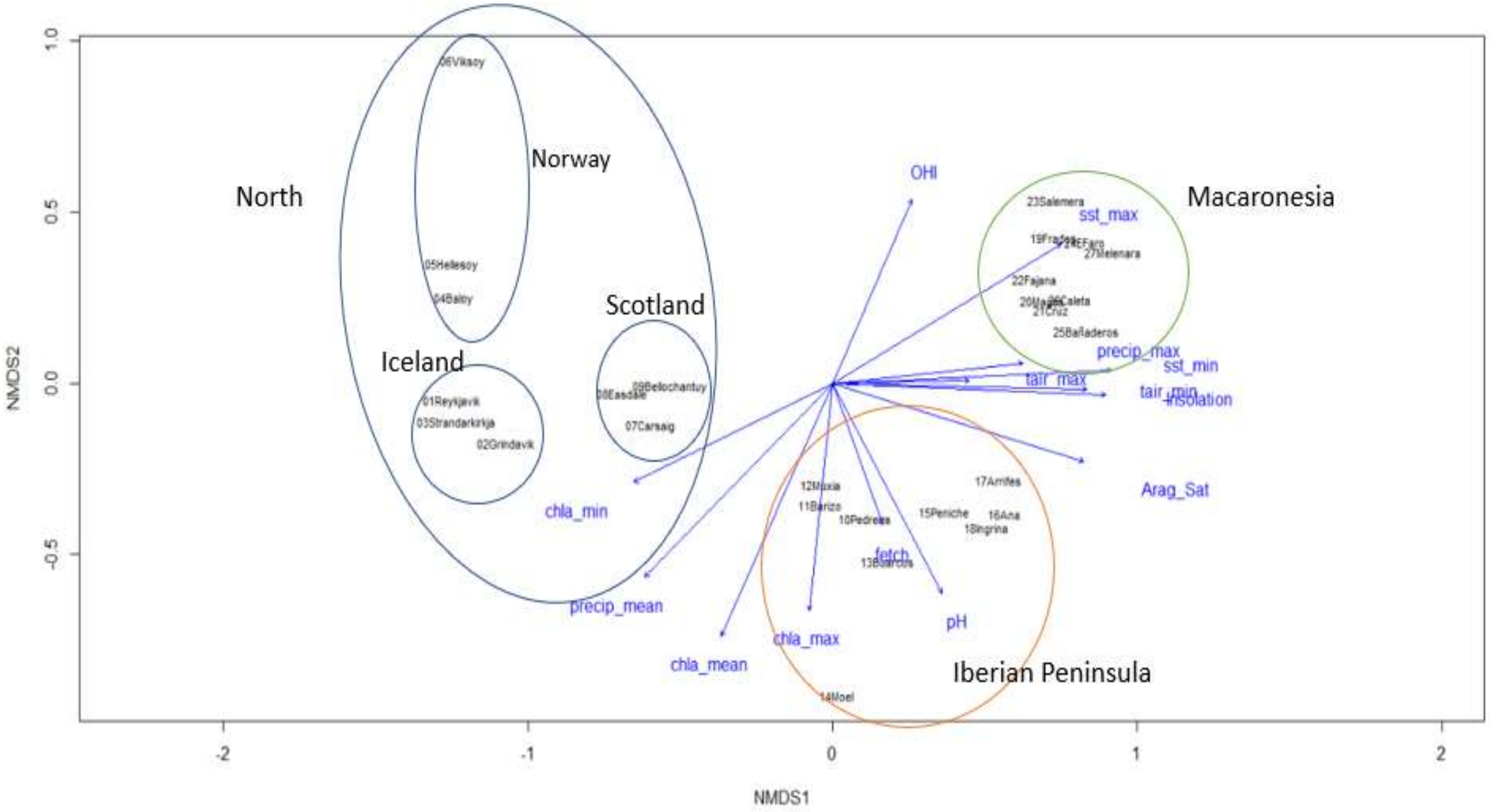


Figure 4.6. Non-metric multidimensional scaling (NMDS) based on Bray-Curtis distances. Arrows show vector fitting of the environmental variables and biogeographic regions are delimited by the colored circle.

The Figure 4.7 and Table 4.1 show the results of the Canonical Correspondence Analysis (CCA). Based on the significance of the model ($p\text{-value} < 0.05$) it can be concluded that the ordination was not arbitrary and therefore that the environmental variables are significantly correlated with the sampling stations. The total inertia or the total variance in stations and species distribution was 3.588 while the environmental variables represented by the constrained inertia, significantly explained almost the 70% (0.6978) of the total. The results of the CCA represented in the graph (Figure 4.7), agree with those shown in the NMDS. There are three groups of stations (points), north to south from left to right, the Iberian Peninsula being a transition zone. The distribution of species can be observed in red, the grouping of the stations in Macaronesia indicated a more homogeneous species distribution within this region than the rest. The first axis, which explained 21% of total variance, was highly correlated with insolation, precipitation, chlorophyll-a, SST maximum, air temperature, OHI and aragonite saturation, whereas the second axis explained 12% of total variance and was mainly correlated with SST minimum, chlorophyll-a maximum and pH, on the other hand fetch was the only variable more correlated with the third axis (Table 4.1).

Table 4.1. Summary of the results of the CCA analysis.

Importance of components:

	CCA1	CCA2	CCA3
Eigenvalue	0.6072	0.3557	0.1617
Proportion Explained	0.2174	0.1274	0.0579
Cumulative Proportion	0.2174	0.3448	0.4027

Partitioning of scaled Chi-square:

	Inertia	Proportion
Total	3.588	1.0000
Constrained	2.503	0.6978
Unconstrained	1.084	0.3022

Correlation with environmental variables:

	CCA1	CCA2	CCA3
fetch	0.2137	-0.13707	0.40703
precip_max	0.6180	-0.01981	0.09533
Insolation	0.9583	-0.07309	0.08517
chla_mean	-0.6535	-0.62719	0.11000

sst_min	0.9833	0.10669	0.08660
sst_max	0.9329	0.09683	-0.02541
tair_max	0.4604	-0.32791	-0.13606
tair_min	0.8628	0.20305	0.23699
precip_mean	-0.8096	-0.47653	-0.11541
chla_min	-0.7652	-0.15752	-0.25256
chla_max	-0.2651	-0.77949	0.14100
OHI	0.4990	0.37009	-0.43878
Arag_Sat	0.8837	-0.14694	0.23364
pH	0.4383	-0.49016	0.40146

When observing the environmental variables, the length of the ordination vectors (arrows) represents the importance of the abiotic variables in the distribution of the sites (Figure 4.7). Some do not show any relationship between them, such as pH and precipitation or maximum chlorophyll-a and aragonite saturation. Variables such as SST, air temperature, precipitation, aragonite saturation distinguished Macaronesia and Iberian Peninsula from the North. Macaronesia was marked by higher OHI. Fetch, chlorophyll-a and pH maximums characterized the Iberian peninsula while the North region was dominated by lower temperatures, precipitation maximums, insolation and aragonite saturation. In addition, the results of the Permutational Multivariate Analysis of Variance (ADONIS) (Table 4.2) indicated that the environmental variables that have a greater influence on the distribution of organisms were fetch, precipitation maximum, insolation, chlorophyll-a, SST minimum and precipitation (p-value < 0.05).

	Df	***SumofSqs***	***MeanSqs***	***R^2***	***Pr(>F)***
fetch	1	0.4870	0.48697	0.06554	0.003 **
precip_max	1	1.1668	1.16678	0.15705	0.001 ***
Insolation	1	1.4023	1.40227	0.18874	0.001 ***
chla_mean	1	0.8589	0.85887	0.11560	0.001 ***
SST_min	1	0.4718	0.47180	0.06350	0.001 ***
SST_max	1	0.2063	0.20626	0.02776	0.100 .
tair_max	1	0.1716	0.17164	0.02310	0.137
tair_min	1	0.1718	0.17181	0.02313	0.146
precip_mean	1	0.3877	0.38767	0.05218	0.012 *
chla_min	1	0.1235	0.12354	0.01663	0.344
chla_max	1	0.1325	0.13248	0.01783	0.294
OHI	1	0.1977	0.19772	0.02661	0.106
Arag_Sat	1	0.1271	0.12705	0.01710	0.294
pH	1	0.1595	0.15949	0.02147	0.163

Residuals	12	1.3652	0.11377		
Total	26	7.4296	1.00000		
Signif. codes:	**0 ‘***’**	**0.001 ‘**’**	**0.01 ‘*’**	**0.05 ‘. ’**	**0.1 ‘ ’**

Table 4.2. Results of the Permutational Multivariate Analysis of Variance using distance matrices (ADONIS). Df: Degrees of freedom, Sqs: Squares and Pr(>F): p-value.

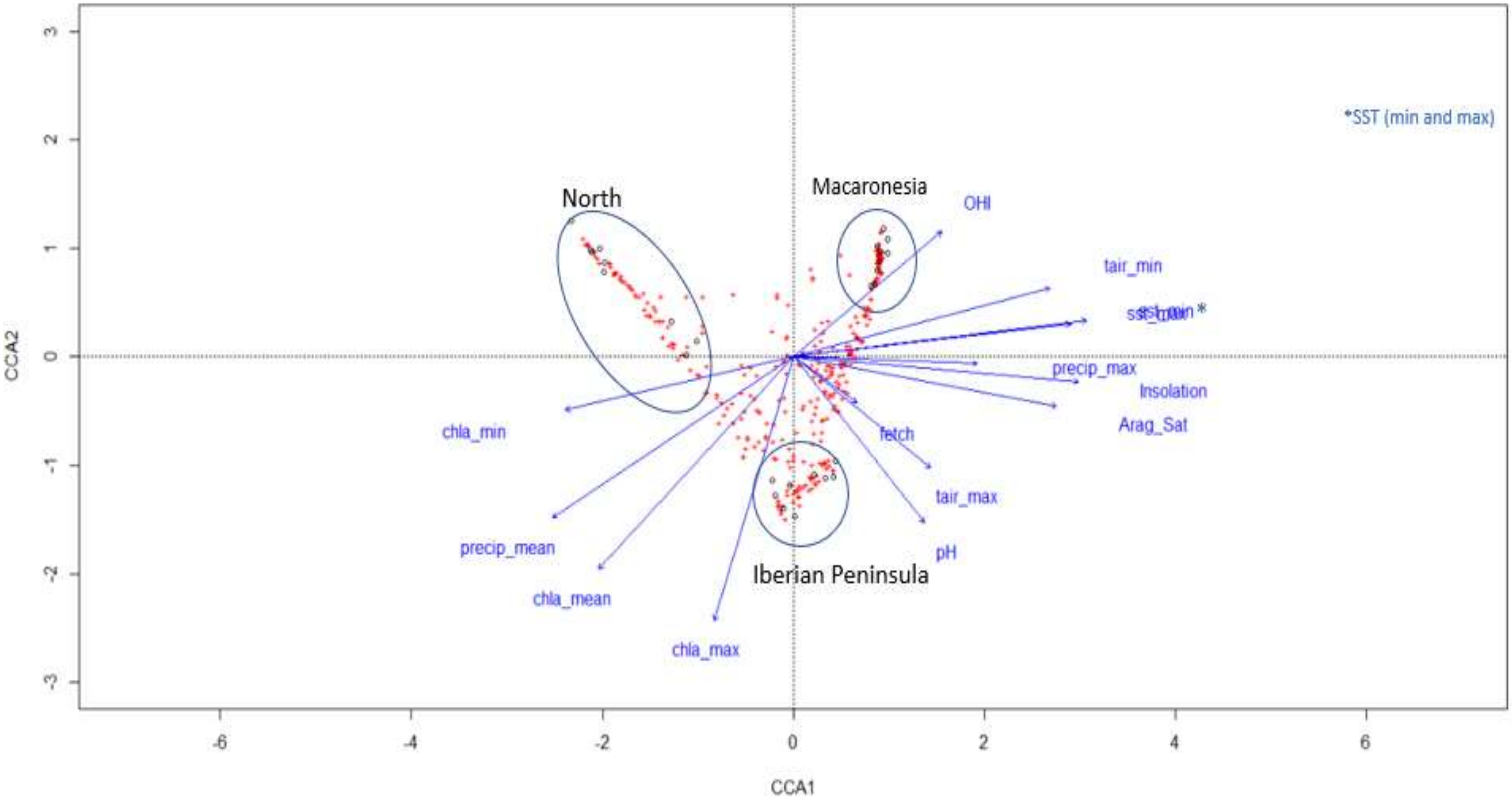


Figure 4.7. Graph representation of the stations (points) and seaweeds and peracarids species (red) with respect to the first two axes of the Canonical Correspondence Analysis (CCA).

4.3 Abundance data and species assemblage

The region of the Iberian Peninsula concentrated the greatest abundance of organisms, both algae and peracarids. The sites where highest abundance of organisms was obtained, were 4.Baloy, 5.Hellesoy, 8.Easdale which belong to the northern region. The three biogeographic regions were characterized by species common to each area, with a greater abundance of algae. Some species were only found at one ecoregion, and compared with their typical distribution from the literature (Algaebase) (Table 4.3). Species such as *Vertebrata lanosa* and *Ascophyllum nodosum* were only found in the North. On the other hand, a greater number of species only observed in Macaronesia was found while the organisms in the Iberian Peninsula shared the distribution with other ecoregion. However, the North, Iberian Peninsula and Macaronesia showed low endemism (<10%), being 2, 0 and 4%, respectively.

Organism/Species	Ecoregion	Distribution
Algae/*Vertebrata lanosa*	North	North and Iberian Peninsula
Algae/*Pelvetia canaliculata*	North	North and Iberian Peninsula
Algae/*Elachista fucicola*	North	North and Iberian Peninsula
Algae/*Ascophyllum nodosum*	North	North, Iberian Peninsula
Algae/*Padina pavonica*	Macaronesia	North, Iberian Peninsula and Macaronesia
Algae/ *Jania capillacea*	Macaronesia	Macaronesia
Algae/ *Cladophora coelothrix*	Macaronesia	North, Iberian Peninsula and Macaronesia
Algae/*Gracilaria dura*	Macaronesia	Iberian Peninsula and Macaronesia
Algae/*Spyridia filamentosa*	Macaronesia	North, Iberian Peninsula and Macaronesia
Algae/*Palisada perforata*	Macaronesia	Iberian Peninsula and Macaronesia
Algae/*Lophosiphonia reptabunda*	Macaronesia	North, Iberian Peninsula and Macaronesia
Algae/ *Heterosiphonia crispella* var.laxa	Macaronesia	Iberian Peninsula and Macaronesia

Table 4.3. Species that have only been found in one of the ecoregions. Ecoregion indicates in which of them it is present and distribution refers to the areas that these species are known to occupy using AlgaeBase as a source.

The SIMPER analysis (Table 4.4) revealed which species were responsible for the separation between the three biogeographic regions. Only the species with contributions greater than 0.75%

are presented. The dissimilarity among regions, using the SIMPER routine, revealed a poor distinction due to the low contribution of each species. The highest contribution was 1.27% for *Vertebrata lanosa* and it occurs between the north and Iberian peninsula, followed by algae such as *Pelvetia canaliculate*, *Elachista fucicola* and *Fucus spiralis* that also help to the distinction of these regions (Table 4.4A). Between the north and south or Macaronesia region, the species that most contribute to the separation of the biogeographical regions coincide with the previous ones, with the exception of some species such as *Padina pavonica, Herposiphonia secunda* and *Jania capilacea* with contributions of 0.93%, 0.87% and 0.86%, respectively (Table 4.4B). On the other hand, the separation of the Iberian peninsula and the south was represented by a greater number of species, however they presented lower contribution values, being the highest 1.12% for *Padina pavonica* (Table 4.4C). For all the species shown in table 4.4, the type of organism was defined as well as the region in which it appears with the highest occurrence. In general, the species that were obtained from the north and south regions are the ones that provide the greatest distinction between the biogeographic regions.

North-Iberian P	**average**	**sd**	**% Contrib**
Vertebrata lanosa(A)-North	0,01037950	0,0049935	1,27369894
Pelvetia canaliculata(A)-North	0,00858750	0,0052161	1,05379735
Elachista fucicola(A)-North	0,00791350	0,002045	0,97108883
Fucus spiralis (A)-North	0,00684290	0,004902	0,83971236
Cladophora rupestris(A)-North	0,00671970	0,0026146	0,82459413
Hyale.stebbingi(P)-Iberian	0,00666490	0,0034059	0,81786946
Caulacanthus ustulatus(A)-Iberian	0,00650440	0,0024565	0,79817403
Gelidium pusillum (A)-Iberian	0,00627030	0,0030574	0,76944693
Ascophyllum nodosum (A)-North	0,00626540	0,0042174	0,76884564
Ectocarpales(A)-Iberian	0,00613750	0,0048359	0,75315065

(A)

North-South	**average**	**sd**	**%Contrib**
Vertebrata.lanosa (A)-North	0,011092	0,0052005	1,21444768
Fucus spiralis (A)-North	0,0092011	0,0041767	1,00741566
Pelvetia canaliculata(A)-North	0,0091593	0,0054561	1,00283904
Padina pavonica (A)-South	0,0085467	0,0018414	0,93576632
Elachista fucicola (A)-North	0,0084372	0,0019808	0,92377731
Herposiphonia secunda (A)-South	0,0080069	0,0016244	0,87666436
Jania capilacea (A)-South	0,0079376	0,0016711	0,8690768

Apohyale prevostii (P)-North	0,0078408	0,0028949	0,85847831
Hyale stebbingi (P)-Iberian	0,0073995	0,0018074	0,81016098
Mastocarpus stellatus (A)-North	0,0073387	0,002883	0,80350407
Hypnea musciformis (A)-South	0,0072879	0,001882	0,79794205
Cladophora rupestris (A)-North	0,0072308	0,0027631	0,79169025
Cladophora coelothrix (A)-South	0,0072269	0,001653	0,79126325
Valonia utricularis (A)-South	0,0072176	0,0019086	0,790245
Gracilaria dura (A)-South	0,0072081	0,0017092	0,78920486
Corallina officinalis (A)-North	0,0071694	0,0029265	0,78496765
Spyridia filamentosa (A)-South	0,0070631	0,0021078	0,77332901
Centroceras clavulatum (A)-South	0,0068709	0,0015265	0,7522853

(B)

Iberian P-South	**average**	**sd**	**%Contrib**
Padina pavonica (A)-South	0,0065546	0,001108	1,12403405
Ectocarpales (A)-Iberian P	0,0062869	0,0036438	1,07812676
Jania capilacea (A)-South	0,0060905	0,0010179	1,04444656
Cladophora coelothrix (A)-South	0,0055477	0,0010588	0,95136297
Gracilaria dura (A)-South	0,0055259	0,0010627	0,94762453
Spyridia filamentosa (A)-South	0,0054101	0,0013999	0,92776624
Palisada perforata (A)-South	0,005245	0,0029585	0,89945361
Centroceras clavulatum (A)-South	0,0050197	0,0013978	0,8608174
Cystoseira humilis (A)-South	0,0049398	0,0038514	0,84711552
Hypnea musciformis (A)-South	0,0049006	0,002081	0,8403932
Valonia utricularis (A)-South	0,0048907	0,0020501	0,83869547
Lophosiphonia reptabunda (A)-South	0,0048312	0,001971	0,82849195
Ulvaria obscura (A)-Iberian P	0,0046594	0,0019572	0,79903034
Caulacanthus ustulatus (A)-Iberian P	0,0046586	0,0023476	0,79889315
Heterosiphonia crispella var.laxa (A)-South	0,0046515	0,0024678	0,79767559
Osmundea pinnatifida (A)-Iberian P	0,004567	0,0020181	0,78318486
Plocamium cartilagineum (A)-Iberian P	0,0044818	0,0018171	0,7685741
Sphacelaria cirrosa (A)-South	0,0044688	0,0025996	0,76634476
Pterothamnion crispum (A)-Iberian P	0,004432	0,0015405	0,76003401
Lichina pygmaea (A)-Iberian P	0,0043861	0,0042577	0,75216272

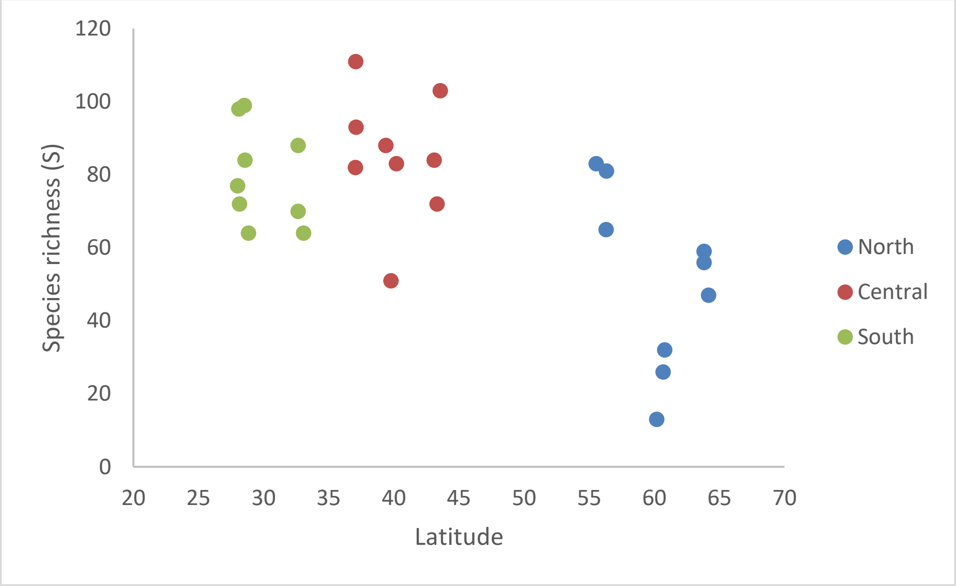
(C)

Table 4.4. Results of the SIMPER analysis, showing the main species that help to the separation into three biogeographic regions (North, Iberian peninsula and south or Macaronesia). The type of organism was defined as A for algae and P for peracarids and the region with greater presence of each species was described. The average contribution and standard deviation (sd) were also

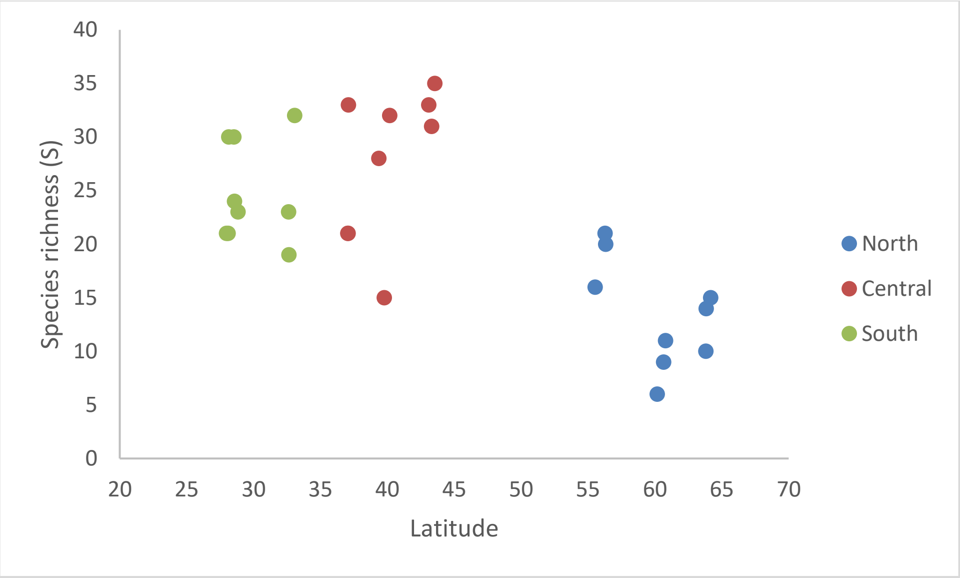
shown as well as the percentage that each species represented of the total contribution (% contrib).

4.4 Latitudinal variation of biodiversity

For both algae and peracarids, an inverse latitudinal gradient with species richness (S) decreasing towards the poles was shown (Figure 4.8). Pearson's correlation coefficient (r) was -0.63 for peracarids and -0.61 for algae, which indicated that species richness (S) was highly correlated with latitude. The algae showed higher values of species richness in Macaronesia and Iberian Peninsula than in the North region, being the station 17Arrifes (Iberian Peninsula) the one that reached the highest value with 111 species. Peracarids showed the same trend with an important decrease of species richness in the stations located in the North region. Alpha (α) diversity was measured with three diversity metrics such as Shannon-Wiener Index (H'), Simpson Index of diversity (Dsimp), effective number of species ($e^{H'}$) and evenness (J'). The Shannon index for algae and peracarids showed its maximum in stations located in the Iberian Peninsula (stations 10Pedreira and 16Ana), with values of 4.65 for algae and 3.5 for peracarids (Table 4.5). The lowest values were grouped in the northern stations.



(A)



(B)

Figure 4.8. Latitudinal change in species richness (S). Latitudinal change in richness of algae (A) and peracarids (B), with the three biogeographic regions differentiated by colors: North (Blue), Iberian Peninsula (Red) and South or Macaronesia (Green).

Stations	Latitude	S	H'	Dsimp	$E^{H'}$	S	H'	Dsimp	$E^{H'}$
1	64,16	15	2,678093	0,9290513	14,557306	47	3,758679	0,9746574	42,8917286
2	63,83	14	2,604202	0,9236625	13,5204317	59	3,993653	0,9801298	54,252713
3	63,82	10	2,273495	0,8940067	9,71328951	56	3,952876	0,979472	52,0849479
4	60,80	11	2,332773	0,8968755	10,3064818	32	3,363204	0,9624317	28,8815794
5	60,66	9	2,133725	0,8745364	8,44627064	26	3,174113	0,9548639	23,9056062
6	60,17	6	1,712941	0,8062349	5,54524609	13	2,436646	0,9532922	11,4346246
7	56,32	20	2,954177	0,9459578	19,1859262	81	4,302379	0,9851305	73,8753342
8	56,29	21	2,990635	0,9468379	19,8983139	65	4,068265	0,9812406	58,4554543
9	55,53	16	2,713318	0,9294988	15,0792255	83	4,312338	0,9851166	74,6147344
10	43,56	35	3,500591	0,9681626	33,135029	103	4,562756	0,9888685	95,8472712
11	43,32	31	3,380578	0,9642246	29,3877523	72	4,194622	0,9835443	66,3286546
12	43,09	33	3,416406	0,9645507	30,4597457	84	4,354999	0,9860966	77,8667475
13	40,18	32	3,433713	0,9666856	30,9915008	83	4,373003	0,9883011	79,2813565
14	39,77	15	2,656373	0,9262663	14,2445304	51	3,876355	0,9900218	48,2480301
15	39,37	28	3,282464	0,960921	26,6413361	88	4,42785	0,9867566	83,7511582
16	37,09	33	3,475997	0,9683556	32,3300455	93	4,486608	0,982252	88,8196581
17	37,08	21	2,996171	0,947729	20,0087765	111	4,653614	0,9840189	104,96364
18	37,05	21	3,012292	0,9490792	20,333952	82	4,361779	0,9871338	78,3964778
19	33,07	32	3,449834	0,9676695	31,4951637	64	4,09422	0,9886256	59,9925267

20	32,65	19	2,911298	0,9435047	18,3806412	70	4,191595	0,9863231	66,1281813
21	32,63	23	3,094818	0,9529484	22,083219	88	4,412642	0,9819258	82,4871068
22	28,52	30	3,350707	0,9631173	28,5228922	99	4,532897	0,9838371	93,0276723
23	28,57	24	3,121463	0,9530715	22,6795355	84	4,359089	0,9885608	78,1858746
24	28,84	23	3,075699	0,9507423	21,6650205	64	4,084225	0,9819258	59,3958881
25	28,15	30	3,337414	0,9617981	28,1462463	72	4,196937	0,9838371	66,4823833
26	28,10	21	3,005131	0,9483796	20,1888607	98	4,525989	0,9885608	92,3872517
27	27,99	21	3,009386	0,949019	20,2749473	77	4,269348	0,9850424	71,4750187

Table 4.5. Diversity parameters of seaweeds (green) and peracarids (orange). S: Species richness; H’: Shannon-Wiener Index; Dsimp: Simpson Index of diversity; $e^{H'}$: Effective number of species.

For both algae and peracarids, the Simpson Index of diversity (Dsimp) and the effective number of species ($E^{H'}$) showed a similar trend with the stations 10Pedreira and 14Moel in the Iberian Peninsula representing the greater values and the northern region characterized by lower values. When investigating the relationship of these diversity metrics with latitude, Pearson's correlation coefficient (r) showed a significant correlation with values that ranged between -0.5 and -0.6, with the exception of the evenness (J’) that did not show any correlation with latitude. Algae and peracarids showed a latitudinal gradient between the northern and southern stations, however the Macaronesia and Iberian Peninsula did not described any variation with latitude (Figure 4.9).

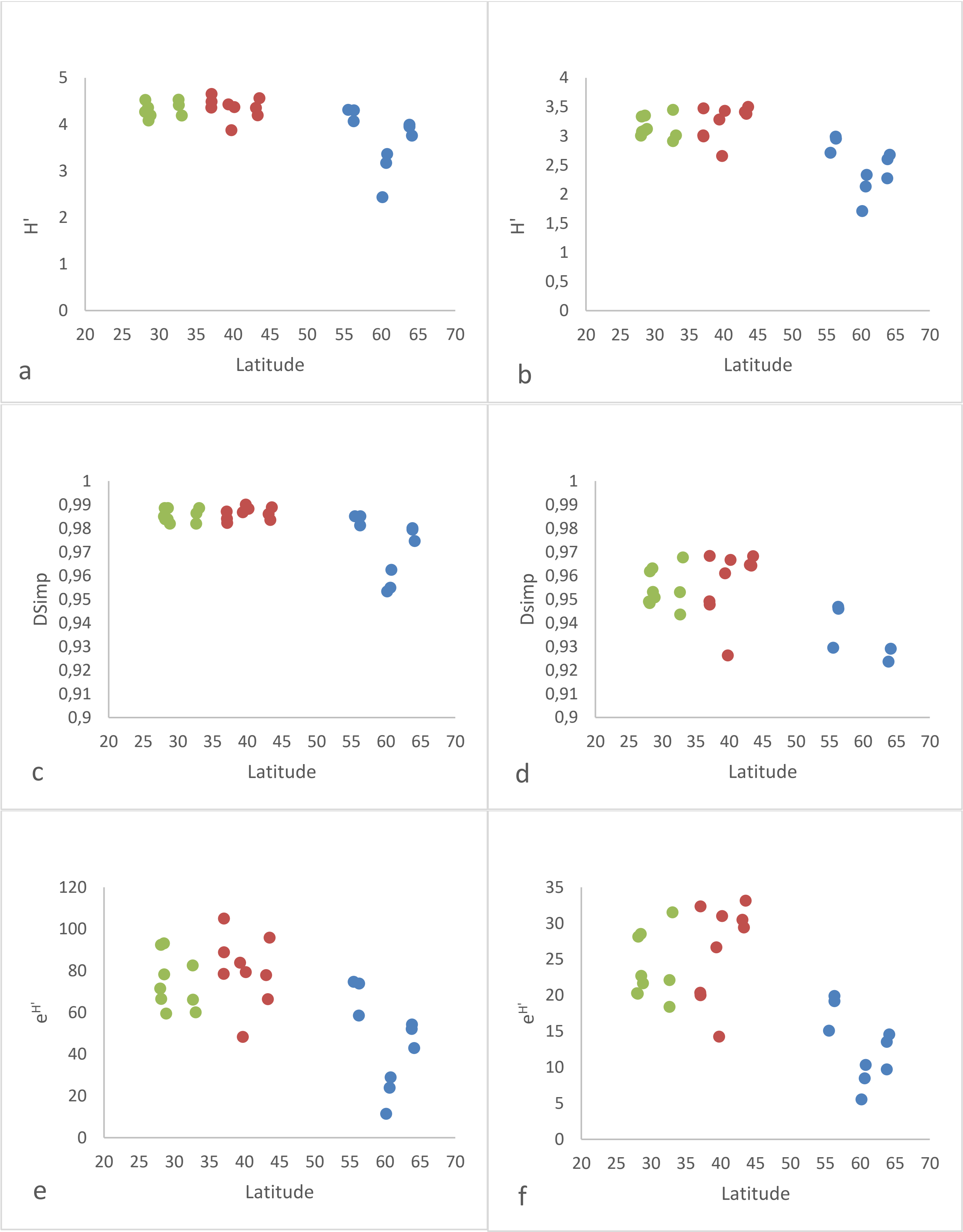


Figure 4.9. Graphic representation of the relationship between Shannon-Wiener Index (H’) (a, b), Simpson Index of diversity (Dsimp) (c, d) and Effective number of species ($e^{H’}$) (e, f) with

latitude. Algae is represented by the left graphs and peracarids by the right, with colors distinguishing the three biogeographic regions; North (blue), Iberian Peninsula (red) and Macaronesia or South (green).

Beta (β) diversity was partitioned into turnover and nestedness components. For seaweeds, the turnover or the balanced variation in abundance, the nestedness or abundance gradient and the overall dissimilarity showed the highest values in stations located in the North (Table 4.6). However there was no significant difference between the stations (p-value > 0.05) while peracarids; both the highest and lowest values are distributed among the three biogeographic regions. On the other hand, when we analyze the relationship of beta diversity with latitude, Pearson's correlation coefficient (-0.02 for algae and -0.04 for peracarids) determined that there was no linear relationship between beta diversity and latitude (n=27). The three components of beta diversity were also studied for the three biogeographic regions (North, Iberian Peninsula and Macaronesia) (Table 4.7) showing no significance differences between them (p-value > 0.05). In addition, the mean of all stations was obtained for the overall dissimilarity of beta diversity, showing a greater value for algae (0.84 ±0.01) than peracarids (0.80 ±0.02).

Stations	turnover	nestedness	overall dissimilarity	turnover	nestedness	overall dissimilarity
1	0.7165044	0.09839222	0.8148966	0.7893555	0.06185371	0.8512092
2	0.7104616	0.08958367	0.8000452	0.7790438	0.06218763	0.8412314
3	0.7498781	0.06497283	0.8148509	0.8080106	0.03043159	0.8384421
4	0.7485193	0.05934235	0.8078616	0.8108392	0.03684939	0.8476886
5	0.7104512	0.10497087	0.8154221	0.7785954	0.05556959	0.8341650
6	0.7188976	0.09960771	0.8185053	0.7941466	0.04657258	0.8407192
7	0.7064529	0.06931246	0.7757653	0.7865950	0.04771584	0.8343108
8	0.6929796	0.08321767	0.7761973	0.8220335	0.03299132	0.8550248
9	0.7172927	0.05623321	0.7735259	0.7840443	0.02749186	0.8115362
10	0.7292764	0.0582418	0.7875183	0.7851827	0.0487733	0.8339561
11	0.6665652	0.1317361	0.7983013	0.7869359	0.0604405	0.8473764
12	0.7401997	0.0334217	0.7736214	0.7916111	0.0657850	0.8573962
13	0.7041403	0.0948789	0.7990192	0.8164312	0.0284874	0.8449186

14	0.7550386	0.0609533	0.8159920	0.8064383	0.0477129	0.8541512
15	0.6894550	0.0876460	0.7771011	0.8232930	0.0214974	0.8447904
16	0.7397229	0.0877861	0.8275090	0.8076383	0.0385917	0.8462301
17	0.7005158	0.1095034	0.8100193	0.7960416	0.0556798	0.8517214
18	0.7508184	0.0707446	0.8215630	0.8048440	0.0287068	0.8335508
19	0.7509160	0.0744349	0.8253510	0.7947870	0.0476955	0.8424826
20	0.7208550	0.0625119	0.7833670	0.7851327	0.0252972	0.8104299
21	0.7132637	0.0677377	0.7810015	0.7729947	0.0354360	0.8084307
22	0.7223213	0.0935433	0.8158647	0.8086084	0.0515529	0.8601614
23	0.7129333	0.0909554	0.8038887	0.7834717	0.0504333	0.8339050
24	0.7640831	0.0597673	0.8238505	0.7994650	0.0414997	0.8409647
25	0.6717200	0.0897003	0.7614203	0.7783451	0.0743625	0.8527076
26	0.7334331	0.0788906	0.8123238	0.7994615	0.0399334	0.8393949
27	0.7085472	0.0976929	0.8062401	0.8133694	0.0486688	0.8620382

Table 4.6. Beta diversity partitions; turnover, nestedness and overall dissimilarity for peracarids in orange and for seaweeds in green, at each sampling station.

Ecoregions	**turnover**	**nestedness**	**Overall dissimilarity**
North	0.8125102	0.02579470	0.8383049
Central	0.7782997	0.07042215	0.8487218
South	0.8139615	0.03901771	0.8529792

(A)

Ecoregions	**turnover**	**nestedness**	**Overall dissimilarity**
North	0.7206107	0.07512859	0.7957393
Central	0.7151279	0.07236415	0.7874920
South	0.7541785	0.07641384	0.8305924

(B)

Table 4.7. Beta diversity partitions; turnover, nestedness and overall dissimilarity. Seaweeds (A) and peracarids (B) for the three different ecoregions.

5. Discussion

The results of the present study revealed three ecoregions in the northeast Atlantic, however, with certain homogeneity in terms of the abundance of species. Only a few species were characteristic of a single ecoregion, and none in the Iberian Peninsula. Regarding environmental variables, those of the local environment such as precipitation, insolation and fetch, as well as minimum SST and chlorophyll drove the distribution of algae and associated peracarids in the northeast Atlantic. Additionally, our analysis support the existence of an inverse latitudinal gradient of seaweeds and peracarids local diversity. Consistent with previous reports, alpha or local diversity showed a decrease from southern regions (Macaronesia and Iberian Peninsula ecoregions) to the poles (North ecoregion) while beta diversity did not show any latitudinal pattern.

5.1 Ecoregions

Our analysis revealed 3 different ecoregions, North ecoregion, Iberian Peninsula or Central ecoregion and Macaronesia or South ecoregion, which are areas of relatively homogeneous species composition, clearly distinct from adjacent systems (Spalding et al., 2007). These results agree with Breeman & van den Hoek (1990) who studied the distribution patterns of 42 species of the genus Chlorophyceae. A similar pattern has also been reported for other organisms in the Northeast Atlantic, however, Norway, Scotland and Iceland were considered as different ecoregions (Spalding et al., 2007). On the other hand, our results which show very low endemism, differ from those proposed by Briggs (2016), which divides this area into different biogeographic provinces. The distinction between Iberian Peninsula ecoregion and Macaronesia ecoregion have already been proposed by Almada (2013) who argued that Macaronesian archipelagos are highly distinct from the mainland coast of Iberian Peninsula, and these should not be grouped together.

The grouping of the stations by the presence of algae and peracarid species matches with their corresponding coasts, however there are exceptions such as the station of Moel (14) and Viksoy (6), which present some dissimilarity with the rest of the stations on their ecoregion. This indicates different species composition from the rest of stations within the ecoregion. Both, the cluster analysis (Figure 4.2) and the NMDS (Figure 4.4 and 4.6) showed a greater grouping for the stations located in Macaronesia, in addition to the fact that the other ecoregions presented stations with greater dissimilarity, this homogeneity of species in Macaronesia may be due to the fact that these islands closest to the tropics presents more stable climatic conditions as well as lower seasonal variation than the European coast (Keith, Kerswell & Connolly, 2013).

Some species were found only in one of the ecoregions described above (Table 4.3) which may help to characterize the distinctness of the flora of each ecoregion as well as changes in the distribution of the species. All of the species found in one ecoregion were algae, probably due to the greater number of these organisms that were obtained in the sampling. The Macaronesia was the ecoregion that held more species present only in this region, followed by the North ecoregion, this confirms the homogeneity in the presence of species from Macaronesia. *Vertebrata lanosa* and *Ascophyllum nodosum* were species found only at the North ecoregion, *V. lanosa* is usually attach to *A. nodosum* and therefore they usually share similar geographic distribution. Besides, these species had already been described as characteristic of the North Atlantic (Bjordal, Jensen & Sjøtun, 2019). Macaronesian species such as *Padina pavonica* had also been reported to this region before (Haroun & Cruz-Reyes, 2000). In addition, the distribution limits between the Iberian peninsula and the north are less marked, it may be caused by the division of the Gulf Stream into the North Atlantic Drift (NAD) and the Canary Current towards the south, promoting more similar oceanographic conditions between the Iberian peninsula and the North ecoregion. Nevertheless, the Iberian peninsula did not show any species only found in this area, which may implies that this ecoregion represents a transition zone between the southern or Macaronesia ecoregion and the north.

When comparing the ecoregions in which the species have been found with the usual distribution, we can observe how some species are reducing their distribution area (Table 4.3). Shifts in distribution of marine populations are the most commonly reported changes in relation to shifting oceanographic conditions (Perry et al. 2005; Dulvy et al. 2008). Given the importance of the impacts of global warming on the biota (Harley et al., 2006) we can presume that these shifts in distribution are a result of the effects of the rising temperatures. Some species previously found in the three ecoregions have moved north, while others have become established in the southern region. These results are consistent with other studies such as Bianchi & Morri (2003) who observed a greater occurrence of subtropical species in temperate waters, however other species showed more affinity for warmer water moving to these areas. Despite these results, further analysis is necessary to address this hypothesis.

5.2 Relationship between abiotic variables and species distribution

There are several studies (Blanchette et al., 2008; Guerra-García, Baeza-Rojano, Cabezas & García-Gómez, 2011) that show the influence of temperature on the distribution of benthic organisms. Furthermore, the increasing anthropogenic pressure and all the changes in oceanographic conditions that it entails have been shown to produce variations in the distribution of marine organisms (GREGORY, CHRISTOPHE & MARTIN, 2009). The results of the non-metric multidimensional scaling (Figure 4.6) agree with the literature, showing a greater importance (longer arrows) to environmental variables such as chlorophyll-a, SSTmax, precipitation and others driven by anthropogenic pressure such as OHI, aragonite saturation and pH. The main characteristic that diverges Macaronesia from the rest of the ecoregions is the maximum temperatures, which as it was expected is higher at the southern sites. However, it has been shown how hot events driven by climate change are occurring more often and can lead to changes in the distribution patterns of different organisms (Lima & Wethey, 2012). On the other hand, the Iberian peninsula is marked by higher values of pH, chlorophyll-a and fetch, the latter being less important in the differentiation of this area. In particular, the station of Moel(14), which presents a different occurrence of species than the rest of this ecoregion, is highly related to maximum values of chlorophyll-a concentration, which may be due to the upwelling present along the Portuguese coast (Oliveira, Nolasco, Dubert, Moita & Peliz, 2009). The environmental variables associated with the North ecoregion and that make the distribution differ from the rest are minimum temperatures both on the surface of the water and in the air, as well as lower values of insolation. It is known that many species have an optimal temperature range which can limit their geographic distribution (Stuart-Smith, Edgar & Bates, 2017). In addition, since they are organisms that inhabit the intertidal zone, insolation and air temperature are of greater importance and may also affect their distribution. Some studies (Guerra-García, Baeza-Rojano, Cabezas & García-Gómez, 2011) have shown the importance of these factors in the distribution of intertidal marine organisms.

Regarding the correlation between the abiotic variables, the variance inflation factor (VIF) showed high values for pH and aragonite saturation, which indicates correlation with the other variables. However, the NMDS (Figure 4.6) showed no correlation between pH and SST maximums, and between aragonite saturation and chlorophyll-a. The fetch has a local effect (in km) and is not directly affected by environmental conditions presented in this study, thus, it was not correlated with all the other variables. Therefore, despite the fact that most of the abiotic variables presented certain correlation between them, they were included in the analyzes since they explained a great proportion of the grouping of the stations according to the occurrence of species.

The Canonical Correspondence Analysis (CCA) presented a "V" shape in terms of the arrangement of the species (Figure 4.7), this could be due to environmental variables such as fetch, pH, maximum chlorophyll-a or maximum air temperature. However, the analysis was repeated without these variables, and the CCA showed a similar shape but with a lower proportion explained by environmental variables. This fact may imply that the arrangement of species is triggered by the whole set of abiotic variables. However, it is clear how the pH and chlorophyll peaks make the stations located in the Iberian Peninsula differ in species composition from the rest. These stations coincide with an upwelling zone as well as areas of great river discharge, which would explain these maximums of chlorophyll concentration. In addition, this primary production proxy could affect high concentrations of phytoplankton, consuming a large amount of CO2 and thus increasing the pH. Several studies (Estrada, 1980; Silva, Palma & Moita, 2008) indicate that upwelling conditions that lead to increased concentrations of chlorophyll-a can change the distribution of organisms such as phytoplankton but also other organisms such as copepods (Peterson & Hutchings, 1995). In addition, these results are consistent with those proposed by Agostini (2018) who indicated pH and therefore acidification as one of the main factors causing changes in the geographical distribution of many species, mainly peracarids and algae with calcareous structures (Bijma et al., 2013; Kamenos et al., 2013).

On the other hand, the division between the North and South ecoregion or Macaronesia is marked by the minimum and maximum temperatures in the water (SST max and min). Macaronesia, in particular, is highly associated with the human impacts compilated in the OHI. Despite these results, the ADONIS analysis revealed low significance of the minimums and maximums of SST (Table 4.2) while the anthropogenic pressure had no significant influence (p-value > 0.05) on the distribution of algae and peracarids. Oppositely, the abiotic factors of the local regime such as fetch, precipitation, insolation and chlorophyll-a showed a greater effect on the distribution of these organisms. As other studies suggested (Jacinto & Cruz, 2016), this may be due to the importance of these environmental variables in benthic communities that inhabit the intertidal zone, which are more exposed to environmental conditions, which may limit their distribution. In addition, Guerra-García (2011) demonstrated the seasonal variation of algae and associated peracarids of the intertidal, mainly caused by factors such as the wave exposure or the length of the day. Another possible explanation for the reduced significance of ocean temperature is that biological interactions play a more important role in the distribution of species as it was proposed by Keith, Kerswell and Connolly (2013). They showed how the biotic interactions such as predation or competition had greater importance at low latitudes while environmental variables are more influential at high-latitude boundaries.

5.3 Species abundance and biodiversity patterns

Although the highest abundance of organisms, both for algae and peracarids, was found in the Iberian Peninsula, the SIMPER analysis (Table 4.4) showed few species located in this region that have a greater influence on the distribution of the stations. The north and south or Macaronesia ecoregions presented a majority of species with the greatest contribution to the distribution patterns, which support that the Iberian Peninsula acts as a transition zone. Other researchers (Pereira et al., 2006; Izquierdo and Guerra-García, 2010) have developed this idea before, they proposed that the Iberian Peninsula represented a transition between warm-water (from north Africa and Mediterranean Sea) and cold-water taxa (from the North Sea and the Arctic). The species *Vertebrata lanosa* showed the highest percentage of contribution in the delimitation of the northern ecoregion with the rest. This algae, being an obligate epiphyte of *Ascophyllum nodosum* (Bjordal, Jensen & Sjøtun, 2019), makes it have very specific characteristics. By depending on another species, its presence in a certain region makes it differ from the rest. Other algae such as *Padina pavonica* characterize Macaronesia, the distribution of this species, however, has been attributed to colder areas such as the Iberian peninsula, which may indicate a change in its distribution patterns (Barceló, M.C., Gómez Garreta, A., Ribera, M.A. & Rull Lluch, J, 1998). Only a few species of peracarids were attributed importance by the SIMPER analysis, this may be due to the fact that a greater number of algae was obtained in the sampling. In addition, the very low contribution values of the species in the delimitation of the distribution could indicate that there were many species with similar abundances, and none of them dominates in particular, which implies a certain homogeneity in terms of the biomass of these organisms for the three ecoregions.

Biodiversity analysis showed different results for alpha (α) and beta (β) diversity. Species richness, which takes into account the number of species in each season, presented a negative trend towards higher latitudes. The decrease in biological diversity from equatorial to polar regions is one of the oldest and most fundamental patterns in macroecology and biogeography (Brown & Lomolino 1998, Gaston 1996a, Rosenzweig 1995, Willig 2001). Specifically, the latitudinal gradient of species richness has been the focus of research for years. Our results (Figure 4.8) are consistent with several studies that demonstrate this inverse gradient of species richness in both marine (Willig et al., 2003; Hillebrand, 2004) and terrestrial organisms (Qian & Ricklefs, 2007). In turn, other measures of alpha diversity such as Shannon-Wiener, Simpson' Index and Effective number of species also showed the same trend (Figure 4.9). As well as for the species richness, a great difference was found between the north and the southern regions (Iberian peninsula and Macaronesia), which presented a more similar local diversity indicating greater homogeneity and matching with other studies (Vermeij, 2005) that showed a close relationship between warm-temperate province and tropical. This may be due to the fact that most of the environmental variables presented more similar values in these two regions (Figure 4.5), which may lead to more marked differences in diversity with the north. Despite extensive research focused on this topic, few studies include these measures of diversity, and some of them presented exceptions such as Okuda, T., Noda, and Yamamoto (2004) who showed how Simpson Index did not describe a latitudinal gradient while species richness did follow this pattern. There are several hypotheses proposed for this latitudinal trend of diversity, interaction between species (migration and extinction) (Wiens & Donoghue, 2004), origin of species

(Mittelbach et al., 2007) or space (as the tropics occupy more surface area, they can host a greater number of species) (Dornelas et al., 2014). Others (Currie, 1991; Rosenzweig, 1995; Evans *et al*., 2005) proposed that this pattern is a consequence of environmental factors such as temperature (which can enhance predation and herbivory) or productivity. In the present study, since an important influence of local abiotic factors in the distribution of species has been observed, it might also be what triggers this variation in local diversity with latitude. In addition, the difference observed in the alpha diversity values (Table 4.5) between peracarids and algae, the latter with a greater diversity can be attributed to the greater amount of algae found in the sampling, which would allow sustaining a greater biodiversity.

Regarding beta and its components (turnover, nestedness and total diversity), several studies have observed a latitudinal gradient in both terrestrial (Qian & Ricklefs, 2007) and marine organisms (Smit AJ, Bolton JJ and Anderson RJ, 2017). However, the present study did not show any latitudinal pattern of beta diversity which indicates that there is no replacement or exchange of species between stations or ecoregions. Furthermore, the similar evenness (J') results showing high values for the three ecoregions give us a clue of which may be the cause that beta diversity does not follow any trend with latitude. This indicates that within each ecoregion the abundance is distributed among the different species without dominance of one over the others, these conditions are maintained for the three ecoregions. Exceptions to this diversity latitudinal gradient have been described for marine flora. Bolton (1994) investigated the distribution and abundance of seaweeds from 29 floras throughout the world and no consistent latitudinal trend in diversity was detected. Crow (1993) corroborated this finding for aquatic angiosperms from throughout North and Central America. More specifically, higher levels of angiosperm richness existed at warm temperate sites than at tropical sites. The reasons remain unknown. Some studies (Tittensor et al., 2010; Straub et al., 2016; Stuart-Smith et al., 2017) have attributed the existence of this latitudinal gradient to temperature. In the present study, the SST did not present a highly significant effect on the distribution of the species, but local abiotic factors such as insolation, precipitation or fetch were more important. This may explain why alpha diversity does follow this pattern, unlike beta diversity, which indicates the presence of similar habitats within each ecoregion and between them.

6. Conclusions

Seaweeds and associated peracarids in the northeastern Atlantic can be grouped into three ecoregions, 1) North, that includes the coasts of Iceland, Norway and Scotland, 2) Central or Iberia that includes the stations located in Spain and Portugal, and 3) South or Macaronesia that corresponds to the Canary Islands and Madeira. Several abiotic factors appear to separate the ecoregions but in contrast to what was expected, abiotic factors of the local regime such as fetch, precipitation and insolation showed a greater influence on the distribution of these intertidal marine organisms than temperature. In addition, the anthropogenic pressure as well as the environmental variables affected by this impact did not show a great effect on the distribution of the species. On the other hand, the different measures of alpha diversity as well as the number of species or richness showed a latitudinal gradient, decreasing towards the poles. This biodiversity pattern, that has been deeply studied in ecology and biogeography, is confirmed in the present study, however, beta diversity did not show relationship with latitude. We suggest that this disjunction result from the implication of local environmental variables in the shaping of the distribution of species.

Climate change may lead to a modification of many boundaries in the ocean due to expected changes in temperature, circulation, stratification, etc. studying the spatial patterns of ecoregions is particularly valuable for analyzing long-term trends (Spalding et al., 2012; Spalding et al., 2007). Our results may improve the knowledge in biogeography and they can be used as a baseline for future studies on the effects of climate change on the distribution of species in a regional scale. Moreover, the spatial partitioning of the northeastern Atlantic Ocean is valuable for marine ecosystem management policies, and the relatively large size of the units defined here is driven by the great connectivity between marine ecosystems and will aid in understanding the spatial scales at which management actions must be applied. However, further biogeographic studies on this region are necessary to confirm this spatial division. Also, in order to know the effects of climate change and human impacts on the distribution of species, historical data on environmental variables are necessary. Despite this, the present study gives a broad vision of which factors are the most influential in shaping the distribution of algae and associated peracarids, as well as the effect on biodiversity patterns encompassing a wide range of latitude.

7. References

Acha, E., Viñas, M., Derisio, C., Alemany, D. and Piola, A., 2020. Large-scale geographic patterns of pelagic copepods in the southwestern South Atlantic. *Journal of Marine Systems*, 204, p.103281.

Adey, W. and Hayek, L., 2011. Elucidating Marine Biogeography with Macrophytes: Quantitative Analysis of the North Atlantic Supports the Thermogeographic Model and Demonstrates a Distinct Subarctic Region in the Northwestern Atlantic. *Northeastern Naturalist*, 18(mo8), pp.1-128.

Beaugrand, G. (2002). Reorganization of North Atlantic Marine Copepod Biodiversity and Climate. *Science*, *296*(5573), 1692-1694.

Blanchette, C., Melissa Miner, C., Raimondi, P., Lohse, D., Heady, K. and Broitman, B., 2008. Biogeographical patterns of rocky intertidal communities along the Pacific coast of North America. *Journal of Biogeography*, 35(9), pp.1593-1607.

Briggs, J. and Bowen, B., 2011. A realignment of marine biogeographic provinces with particular reference to fish distributions. *Journal of Biogeography*, 39(1), pp.12-30.

Briggs, J. and Bowen, B., 2013. Marine shelf habitat: biogeography and evolution. *Journal of Biogeography*, 40(6), pp.1023-1035.

Cole, V. and McQuaid, C., 2010. Bioengineers and their associated fauna respond differently to the effects of biogeography and upwelling. *Ecology*, 91(12), pp.3549-3562.

Conners, M., Hollowed, A., & Brown, E. (2002). Retrospective analysis of Bering Sea bottom trawl surveys: regime shift and ecosystem reorganization. *Progress In Oceanography*, *55*(1-2), 209-222.

Costello, M., Tsai, P., Wong, P., Cheung, A., Basher, Z. and Chaudhary, C., 2017. Marine biogeographic realms and species endemicity. *Nature Communications*, 8(1).

Dobrovolski, R., Melo, A., Cassemiro, F. and Diniz-Filho, J., 2011. Climatic history and dispersal ability explain the relative importance of turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 21(2), pp.191-197.

Dornelas, M., Gotelli, N., McGill, B., Shimadzu, H., Moyes, F., Sievers, C. and Magurran, A., 2014. Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss. *Science*, 344(6181), pp.296-299.

Fernández, C., 2016. Current status and multidecadal biogeographical changes in rocky intertidal algal assemblages: The northern Spanish coast. *Estuarine, Coastal and Shelf Science*, 171, pp.35-40.

Guerra-García, J., Cabezas, P., Baeza-Rojano, E., Espinosa, F., & García-Gómez, J. (2009). Is the north side of the Strait of Gibraltar more diverse than the south side? A case study using the intertidal peracarids (Crustacea: Malacostraca) associated to the seaweed Corallina elongata. *Journal Of The Marine Biological Association Of The United Kingdom*, *89*(2), 387-397.

Guerra-García, J., Sánchez, J., & Ros, M. (2009). Distributional and ecological patterns of caprellids (Crustacea: Amphipoda) associated with the seaweed Stypocaulon scoparium in the Iberian Peninsula. *Marine Biodiversity Records, 2*.

Gage, J., Lambshead, P., Bishop, J., Stuart, C. and Jones, N., 2004. Large-scale biodiversity pattern of Cumacea (Peracarida: Crustacea) in the deep Atlantic. *Marine Ecology Progress Series*, 277, pp.181-196.

Gray, J., 2000. The measurement of marine species diversity, with an application to the benthic fauna of the Norwegian continental shelf. *Journal of Experimental Marine Biology and Ecology*, 250(1-2), pp.23-49.

Harley, C., Randall Hughes, A., Hultgren, K., Miner, B., Sorte, C., & Thornber, C. et al. (2006). The impacts of climate change in coastal marine systems. *Ecology Letters*, *9*(2), 228-241.

Izquierdo, D. and Guerra-García, J., 2010. Distribution patterns of the peracarid crustaceans associated with the alga Corallina elongata along the intertidal rocky shores of the Iberian Peninsula. *Helgoland Marine Research*, 65(2), pp.233-243.

Jost, L. (2006). Entropy and diversity. *Oikos*, *113*(2), 363-375.

Jueterbock, A., Tyberghein, L., Verbruggen, H., Coyer, J., Olsen, J. and Hoarau, G., 2013. Climate change impact on seaweed meadow distribution in the North Atlantic rocky intertidal. *Ecology and Evolution*, 3(5), pp.1356-1373.

Keith, S., Kerswell, A., & Connolly, S. (2013). Global diversity of marine macroalgae: environmental conditions explain less variation in the tropics. *Global Ecology And Biogeography*, *23*(5), 517-529.

Kerswell, A. (2006). GLOBAL BIODIVERSITY PATTERNS OF BENTHIC MARINE ALGAE. *Ecology*, *87*(10), 2479-2488.

Lima, F., & Wethey, D. (2012). Three decades of high-resolution coastal sea surface temperatures reveal more than warming. *Nature Communications*, *3*(1).

Liu, M. and Tanhua, T., 2019. Distribution of Water Masses in the Atlantic Ocean based onGLODAPv2. *Ocean Science Discussions*, pp.1-32.

Marchini, A., Ragazzola, F., Vasapollo, C., Castelli, A., Cerrati, G., & Gazzola, F. et al. (2019). Intertidal Mediterranean Coralline Algae Habitat Is Expecting a Shift Toward a Reduced Growth and a Simplified Associated Fauna Under Climate Change.

Martínez, B., Viejo, R., Carreño, F. and Aranda, S., 2012. Habitat distribution models for intertidal seaweeds: responses to climatic and non-climatic drivers. *Journal of Biogeography*, 39(10), pp.1877-1890.

Rivadeneira, M., Thiel, M., González, E., & Haye, P. (2010). An inverse latitudinal gradient of diversity of peracarid crustaceans along the Pacific Coast of South America: out of the deep south. *Global Ecology And Biogeography*, *20*(3), 437-448.

Robin South, G., 1987. Biogeography of the benthic marine algae of the North Atlantic Ocean—an overview. *Helgoländer Meeresuntersuchungen*, 41(3), pp.273-282.

Sepkoski, J., 1988. Alpha, beta, or gamma: where does all the diversity go?. *Paleobiology*, 14(3), pp.221-234.

Smit, A., Bolton, J. and Anderson, R., 2017. Seaweeds in Two Oceans: Beta-Diversity. *Frontiers in Marine Science*, 4.

Spalding, M., Fox, H., Allen, G., Davidson, N., Ferdaña, Z., Finlayson, M., Halpern, B., Jorge, M., Lombana, A., Lourie, S., Martin, K., McManus, E., Molnar, J., Recchia, C. and Robertson, J., 2007. Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas. *BioScience*, 57(7), pp.573-583.

Thiel, M. (2002). The zoogeography of algae-associated peracarids along the Pacific coast of Chile. *Journal Of Biogeography*, *29*(8), 999-1008.

Willig, M., Kaufman, D., & Stevens, R. (2003). Latitudinal Gradients of Biodiversity: Pattern, Process, Scale, and Synthesis. *Annual Review Of Ecology, Evolution, And Systematics*, *34*(1), 273-309.

Zacharias, M. and Roff, J., 2001. Explanations of patterns of intertidal diversity at regional scales. *Journal of Biogeography*, 28(4), pp.471-483.