



Species composition, distribution, and zonation patterns in the intertidal seaweed assemblages from Santo Antão, Cape Verde

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ABSTRACT

Intertidal communities have been extensively studied for decades. Many of these studies have focused on macroalgae, as they are key components of many rocky coastal ecosystems. Despite this, there are still regions of the world where there is a lack of knowledge of intertidal macroalgal communities. This is the case in some tropical regions, such as the Cape Verde archipelago, located on the tropical west coast of Africa. To contribute to the knowledge of the macroalgal communities of this region, during July 2022, we studied the distributional pattern and zonation of macroalgal communities along the rocky intertidal of Santo Antão Island, the northernmost island of the archipelago and the least studied. Using a nested design, we compared the macroalgal assemblages of six rocky shores along the entire coastline, including three sites per shore, and four quadrats per site and tidal level. We found 43 macroalgal species – 29 Rhodophyta, 12 Ochrophyta, 2 Chlorophyta – and one Cyanobacteria. The orders Ceramiales, Corallinales, and Gigartinales were the groups more represented, followed by Ectocarpales and Dictyotales. The upper intertidal was dominated by brown algae, while red algae dominated the middle intertidal. Green algae had a scarce presence in both tidal levels. Our results found no differences between the north and south of the island but between rocky shores and tidal levels. Our results provide for the first time comprehensive information on the seaweed community structure, zonation patterns, and a comparison of seaweed abundances in a vertical and horizontal gradient along the entire rocky shores of Santo Antão Island. In the face of the current climate change, our data can be the baseline for future work on algal communities in this region.

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1. Introduction

Uncovering biodiversity on Earth remains vital for effective conservation, planning, and sustainable development, particularly under current climate crises. Knowledge about biodiversity stays scarce and unevenly distributed worldwide (Costello, 2015; Freitas et al., 2021). While there are species still not formally described (Linnean shortfall), for most taxa, the global, regional, and even local geographic distributions are poorly understood or contain gaps (Whittaker et al., 2005; Bini et al., 2006). Without being known to science, many species are disappearing or shifting their distributions due to human-induced climate changes and loss of natural habitats (Burrows et al., 2011, 2014; Freitas et al., 2021). As such, the lack of knowledge on species, abundance, and

distribution may hamper conservation and even restoration plans (Adams et al., 2019). These shortfalls are even more dramatic in developing regions, often biodiversity-rich, where sustainable conservation actions urge.

The intertidal rocky shores are widely distributed along the world's coastlines. As heterogeneous environments, assemblages of algae and invertebrates can be found distributed at specific height levels from the low to the high tidal level (Araújo et al., 2005; Mieszkowska, 2021). These intertidal organisms often live close to their physiological tolerance limits, as they are subjected to extreme conditions such as temperature, desiccation, wave forces, or rapid fluctuations in salinity (Mieszkowska, 2021). As such, the biodiversity and ecology of intertidal species have been a worldwide topic of interest, making the intertidal rocky shores one of the best studied coastal ecosystems (Paine, 1974; Underwood, 2000). Indeed, global environmental change impacts on species distribution, biodiversity, or productivity can be observed in rocky intertidal ecosystems (Mieszkowska, 2021). Some of these changes may even go unnoticed before actual changes occur. Thus, databases of biological information providing a baseline

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for detecting the rate and extent of changes in the distribution and abundance of intertidal species become fundamental (Mieszowska, 2015). In this context, it is still crucial to collect data on species presence and abundance and build the baseline for monitoring the impact of climate change on intertidal communities, particularly in developing countries.

Macroalgae are important components of rocky shores, representing the dominant autotrophic biomass and playing a central structural and functional role (Lüning, 1990; Mineur et al., 2015). Many are foundation species, growing across substrates and forming extensive canopies (Scrosati et al., 2021). Globally, seaweeds' distribution and abundance are mainly determined by their tolerance to temperature (Chapman, 1987; Lüning, 1990). This makes them good indicators of ecosystem health, particularly under climate change (Baweja et al., 2016). Indeed, climate change is already shaping the species distribution, with cold-water species shifting poleward or in-depth and warm-water species expanding their range further north (Pecl et al., 2017). In temperate regions bordering subtropical/tropical zones, this redistribution of species may be even more drastic, and there may be changes in the community composition due to the poleward shift of subtropical and tropical species in a phenomenon called tropicalization and simplification (Vergés et al., 2019; Agostini et al., 2021). For example, in the temperate reefs of Australia and Japan the communities usually dominated by macroalgae are being replaced by coral communities (Tuckett et al., 2017; Agostini et al., 2021). This might also be the case in other transition zones, but the lack of information hampers the detection of these ecological processes.

Cape Verde ecoregion encompasses the Cape Verde archipelago, located in the West Africa Transition province within Tropical Atlantic Biogeographic Realm (Spalding et al., 2007). It limits the Lusitanian province, being the frontier between the Temperate and Tropical Atlantic Realms. Although this area is a tropical region, there are large areas without reef-building corals and mangroves. In addition, many of the seaweeds found in tropical West African extent far into the adjacent warm temperate region (Michanek, 1979; Lüning, 1990). Rocky reefs communities in Cape Verde consist of various organisms, including hermatypic corals, sponges, and seaweeds growing on the volcanic rock (Van der Land, 1993; Morri et al., 2000). The strong upwelling of the West African coast is responsible for the fact that, tropical species are not the dominant ones, and that North Africa is dominated by a marine flora highly related to that of southern Europe, called Lusitanian-African, which includes from Portugal to Mauritania and the Canary Islands, Madeira, and the Azores. Some studies have shown that the algal flora of Senegal lacks tropical species, and biogeographically there is a transition with more temperate algae in the north and an abrupt transition in species composition towards the southern regions (Lawson and John, 1987; Harper and Garbary, 1997).

The intertidal of Cape Verde has been largely overlooked, with only a few studies focused on the intertidal species (e.g. López et al., 2019; Vieira et al., 2020). Looking at seaweeds, there is even less knowledge: most information has been focused on the description of algal species (Otero-Schmitt, 1995a; Almada, 2015; Gabriel and Fredericq, 2019) or contributions to the biogeographical relationship of the seaweeds in the Macaronesian archipelagos (Gil-Rodríguez and Haroun, 1992; Haroun and Reine, 1993). Some studies have also focused on seaweed assemblages to identify spatial organization patterns of subtidal seaweeds in the Macaronesia archipelagos (Sangil et al., 2018), to study the benthic community structure (Freitas et al., 2019), or to determine the potential biotechnological applications in the Macaronesia seaweeds as key elements of the Blue Economy strategies in the region (Haroun et al., 2019). However, the composition of Cape Verde's

intertidal algal communities, their spatial distribution, and zonation are still unknown. Additionally, the few existing studies are biased toward the southern islands, making the northernmost islands almost unnoticed. This is the case of the Santo Antão island, which is the northernmost and more oceanic island, where very little is known about the structure of macroalgae assemblages. Due to the geographic location between the temperate and tropical Atlantic, climate change is expected to dramatically affect the algae communities of Santo Antão. Indeed, it has already been observed in other regions located in biogeographic transition zones (Tuckett et al., 2017; Agostini et al., 2021). This might be even more alarming in Santo Antão island, where there is increasing development, tourism, and demand for sources of income, most from artisanal fishing on shores (authors' personal observation). As such, gathering information on intertidal communities of algae is of fundamental importance to know the direction of possible changes. In this regard, this work aims to describe the diversity, distribution, and zonation patterns of intertidal macroalgae assemblages of Santo Antão island.

2. Material and methods

2.1. Study area

Santo Antão Island (Fig. 1) is the northernmost island of the Cape Verde archipelago, which is a small archipelago located ~500 Km west of the African coast of Senegal. It comprises ten islands and eight islets organized into two sets according to their position in relation to trade winds (Windward and Leeward) (Fig. 1) and is the southernmost of the archipelagos of the Macaronesian along with the archipelagos of Azores, Madeira, Salvages, and Canary Islands (Dash et al., 1976; Plesner et al., 2003). However, due to the tropical climate of Cape Verde and the biota present, the archipelago is considered an ecoregion within the West African Transition province of the Tropical Atlantic realm, not in the Macaronesian biogeographic region (Spalding et al., 2007). Cape Verde has a convergence of different water masses comprising the Cape Verde Frontal Zone System (Zenk et al., 1991; Fernandes et al., 2005) that, along with the strong downstream upwelling plume from the coast of Senegal and Mauritania, makes Cabo Verde waters highly productive (Aristegui et al., 2009; Hoepffner et al., 2014). The tidal regime is mostly semi-diurnal, and the amplitude of the tides varies from 0.5 m (neap tides) to 1.6 m (spring tide) (Alves et al., 2020). Water temperature typically ranges from 21.5 °C in March to 25 °C in November (Pérez-Rodríguez et al., 2001).

2.2. Seaweed surveys and data analysis

During the low tides of July 2022, six shores around the island were surveyed, three on the northern side and three on the south (Fig. 1). At each shore, the percentage cover of macroalgae was visually estimated using 50 x 50 cm quadrats. The sampling plan included three sites (30–50 m long) per shore separated by 50–80 m, and four quadrats per site and intertidal zone (upper and middle intertidal) ($n = 24$ quadrats per shore; $n = 12$ quadrats per intertidal zone). Sampling quadrats were haphazardly arranged within each site and level to obtain an appropriate representation of the seaweed assemblage at each shore. Raw data were used to obtain univariate estimates for seaweed total cover, richness, and diversity per shore. Univariate estimates between shores were compared by a partly nested permutational analysis of variance (PERMANOVA) based on Euclidean distances with *Zone* (fixed, two levels: north and south) and *Intertidal level* (fixed, two levels: upper and middle) as orthogonal factors; *Shore* and *Sites* within *Shore* were random factors

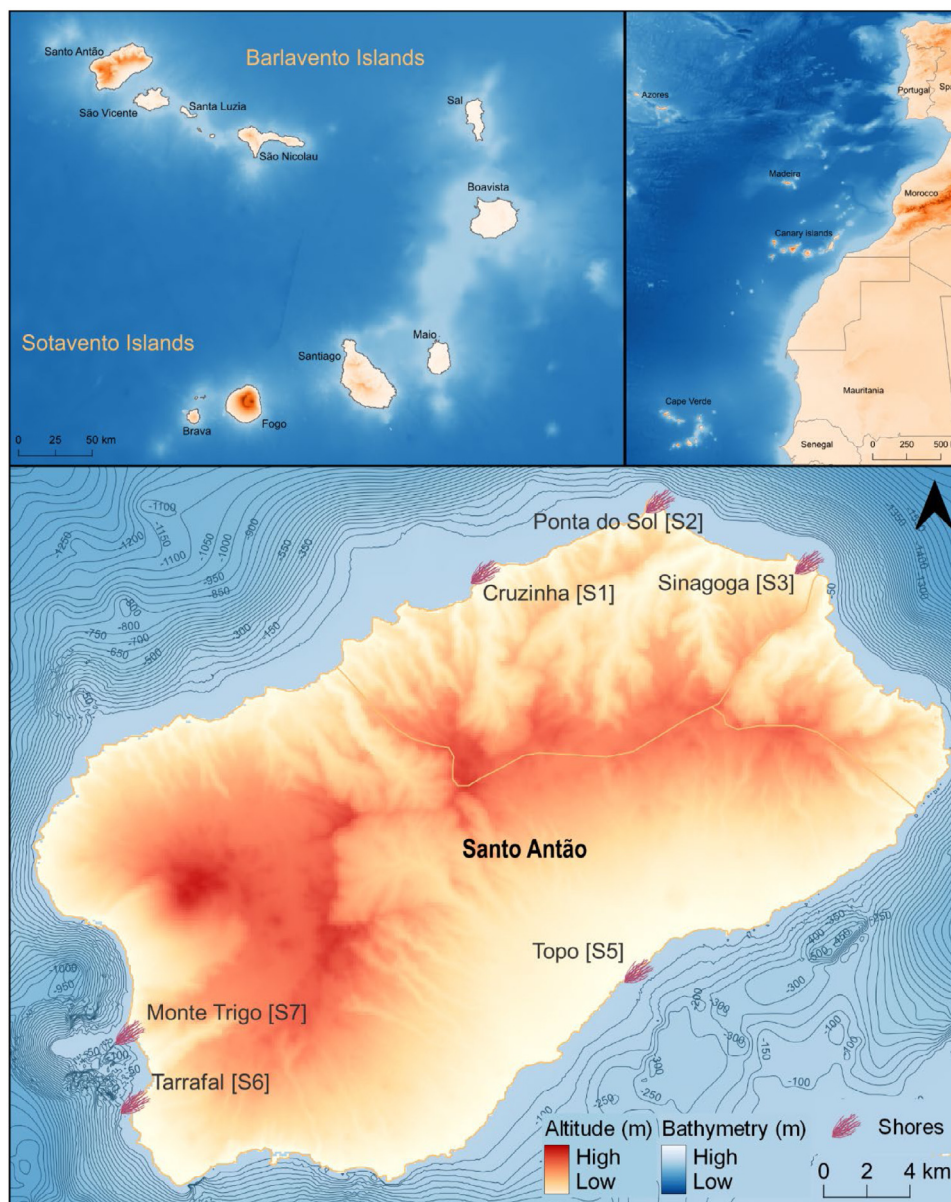


Fig. 1. Map showing the location of the seven intertidal rocky shores sampled.

nested on *Zone* (McArdle and Anderson, 2001). P -values (P) were estimated with an asymptotic permutation distribution. When there were less than 10 permutations, P -values were generated with the Monte Carlo method (Anderson and Robinson, 2003). PERMANOVA was also used to compare the structure of the seaweed assemblage at shores using Bray-Curtis (BC) similarities. Since PERMANOVA is sensitive to differences in multivariate dispersion among groups, the homogeneity of the within-group BC variation and the univariate variables was tested with the similarity-based multivariate extension of Levene's test implemented in the PERMDISP routine. BC similarities were based on fourth root transformed cover data to weigh down the contribution of quantitatively dominant species. All analyses were performed with PRIMER 7 (Clarke and Gorley, 2015b,a).

3. Results

3.1. Macroalgal community

We found 43 macroalgal species (29 Rhodophyta, 12 Ochrophyta, 2 Chlorophyta) and one Cyanobacteria. The orders Ceramiales, Corallinales, and Gigartinales were the groups more represented followed by Ectocarpales and Dictyotales. Most species were warm-temperate affinity (29), and only a few of them were tropical ones (15). The upper intertidal shore presented 26 species, three of which were upper-intertidal specific (*Calothrix crustacea*, *Digenea simplex*, and *Hydroclathrus clathratus*). Mid-intertidal presented 41 species, 18 of them only were found at this level (Table S1, Mat. Suppl.). While in the upper intertidal, the most abundant algae were brown (e.g., *Asteronema*

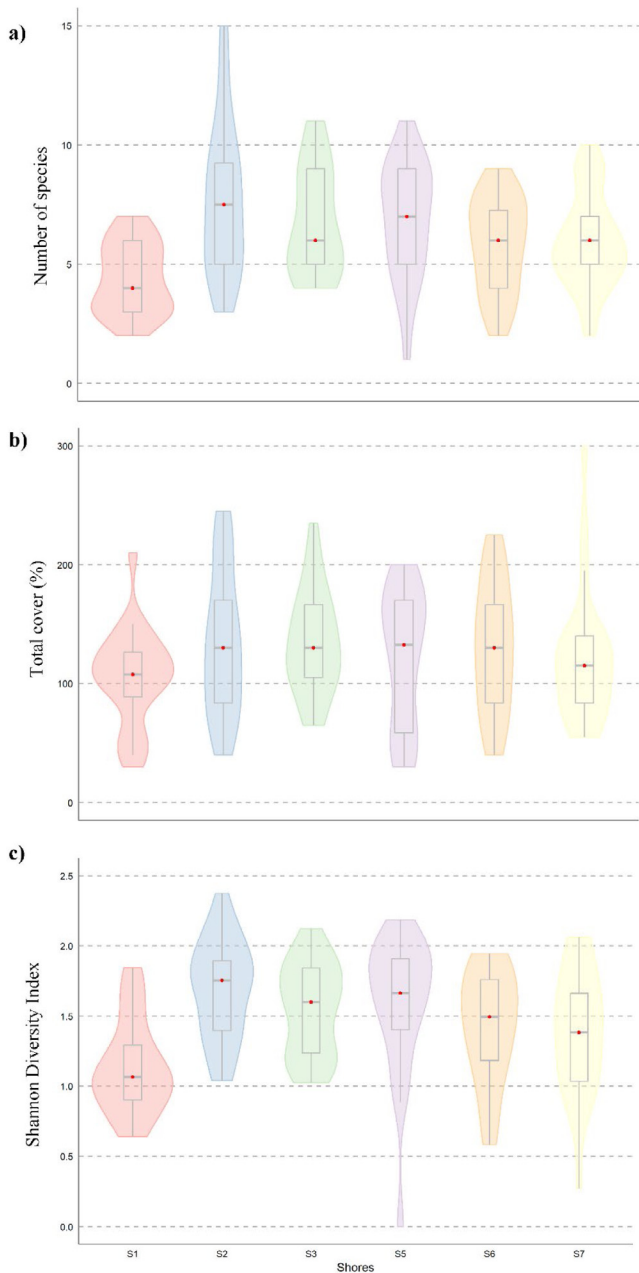


Fig. 2. Variation along shores on (a) number of species, (b) total cover, and (c) Shannon diversity Index. Values are means for each combination of site and tidal level at each shore (± 1 SE, $n = 3$ for sites and $n = 2$ for tidal level).

breviarticulatum, *Ralfsia verrucosa*, *Chonospora minima*), the middle intertidal was dominated by red algae, and green algae had a scarce presence in both tidal levels. *Palisada perforata*, *Hypnea spinella*, *Spyridia* spp., and *Laurencia* spp. were present at most sites in the middle intertidal together with *Sargassum vulgare*.

3.2. Spatial characterization

On average, the intertidal seaweed communities of Santo Antão had 6.26 ± 0.206 species per site ranging from a maximum of 15 species to a minimum of one species per quadrat (Fig. 2a). Overall, there were no significant differences in the number of species observed between the north and southern shores ($P = 0.931$; mean \pm SE = 6.21 ± 0.256 and 6.31 ± 0.324 , respectively).

However, PERMANOVA showed significant differences between intertidal levels across shores ($P = 0.039$). Accordingly, PERMANOVA found significant differences between intertidal levels ($P = 0.003$) and shores in the number of species ($P = 0.002$) (Table 1). Mid-intertidal had, on average, more species (7.76 ± 0.258), ranging from four to 15 species by quadrat. Upper intertidal had fewer species (on average 4.75 ± 0.200), ranging from one to nine species per quadrat. Curiously, Cruzinha (S1) and Ponta do Sol (S2) shores showed contrasting patterns in the number of species per quadrat, despite both being located on the northern side of the island. While Cruzinha was, on average, the shore with the least number of species per quadrat (4.42 ± 0.300), Ponta do Sol was the shore with the most species observed per quadrat (7.71 ± 0.647). The total cover of species was very similar on both the north and south sides of the island and between shores, and only were found significant differences in the total cover of species between intertidal zones across sites within shores ($P = 0.033$) (Fig. 2b).

A similar pattern to the total number of species was observed for Shannon diversity, with no significant differences between north and south, but between intertidal zones and shores ($P = 0.003$ and $P = 0.008$ respectively) (Fig. 2c). Overall, all shores showed a similar pattern of species both at upper and mid-levels. Upper intertidal was dominated by *Asteronema breviarticulatum*, *Ralfsia verrucosa* and *Chonospora minima* (Fig. 3) followed by *Jania* sp1., and *Lithophyllum incrustans*. Mid-intertidal showed higher abundances of each species than at the upper intertidal (Fig. 3). *Palisada perforata*, *Hypnea spinella*, *L. incrustans*, *R. verrucosa*, and *Sargassum vulgare* were the most abundant species in this intertidal zone, followed by *Spyridia filamentosa*, *Laurencia hybrida*, and *Jania* sp1.

The community composition and structure analyses indicated no significant differences between the north and south of the island. However, PERMANOVA showed significant differences between intertidal zones, shores, and sites ($P = 0.003$, $P = 0.0001$, and $P = 0.0001$, respectively) (Table 1). Differences between intertidal levels varied across shores and sites (Fig. S1, Mat. Suppl.). The significant differences found by PERMANOVA were illustrated in the two-dimensional PCOs plot (Fig. 4) where upper intertidal and mid-intertidal samples were separated along axis 1 (40.7% of total variation), from the right to the left respectively. *Asteronema breviarticulata* and *Chonospora minima*, the dominant species at the upper intertidal zone (Fig. 3), correlated with PCO1 (>0.4) and to the right side of the plot, whereas the mid-intertidal had more species correlated (Fig. 4), also evidencing higher diversity and equitability (Fig. 3). On the other hand, samples of the mid-intertidal are situated on the left side of the PCO, with a negative correlation of *Spyridia filamentosa*, *Hypnea spinella*, *Sargassum vulgare* or *Palisada perforata*, the most abundant species in the mid-intertidal. Along the axis PCO2 (13.8% of total variation), despite not being significant, there seems to be some distinction between north and south upper intertidal due to the presence of *Ralfsia verrucosa* at the north and *Jania* sp. at the south (Fig. 4).

4. Discussion

The fauna and flora assemblages of the tropical coast of West Africa have been largely unnoticed for decades, especially in remote regions like the Cape Verde archipelago. Although some studies have described the presence of many of the species reported here on rocky shores of other Cape Verde islands (e.g. Gil-Rodríguez and Haroun, 1992; Haroun and Reine, 1993; Prud'homme Van Reine et al., 2002, only a few of them provided information about seaweed assemblages and zonation patterns (Otero-Schmitt, 1995b; Almada, 2015). In this study, we provide for the first-time comprehensive information on the seaweed

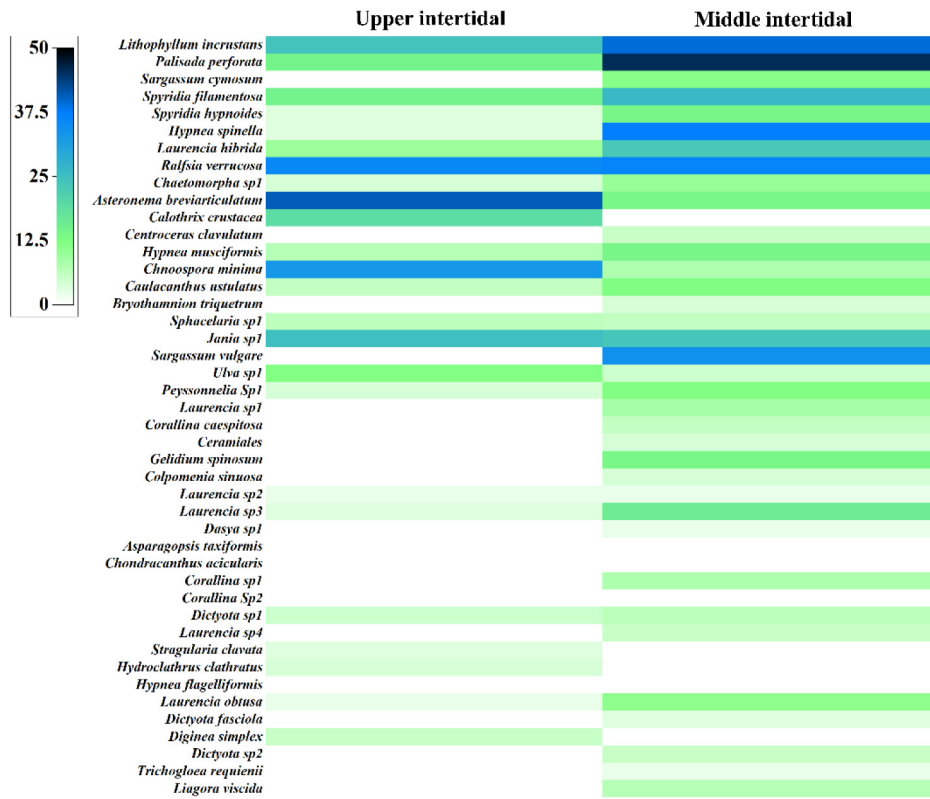


Fig. 3. Shade plot for the abundance of intertidal levels is represented by the shade of blue and green, from white (absent) to dark blue (most abundant). Colour shading scale within individual cells is linearly proportional to fourth-root transformed abundances. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

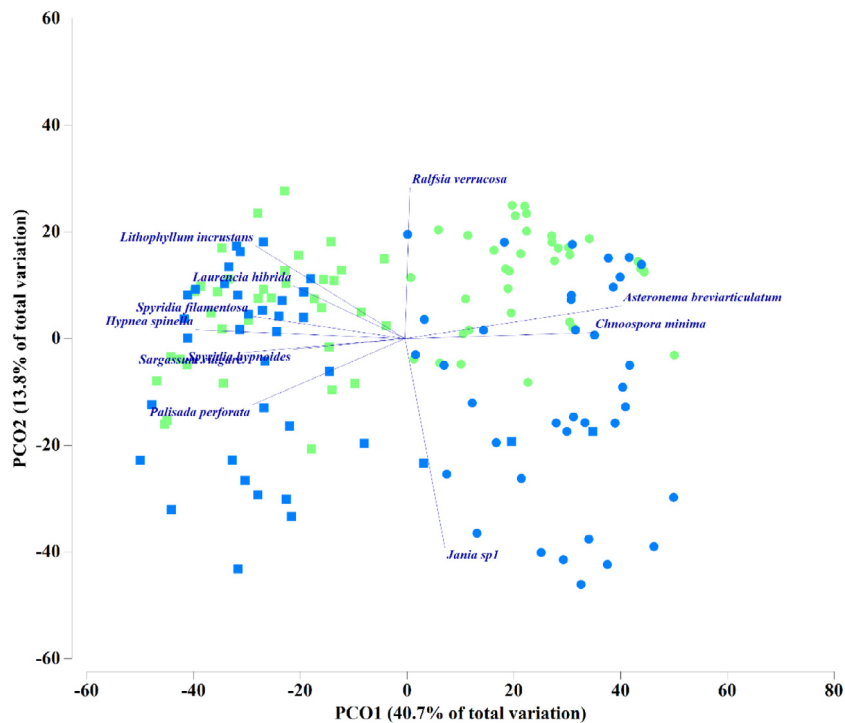


Fig. 4. Variation on the structure of the seaweed assemblages between the north (green) and south (blue) of the island, and between upper (circles) and medium (squares) intertidal levels. Overlay vectors are species whose cover has a Pearson correlation >0.4 with any axis; the length and direction of the vector indicate the relationship with the axes of the ordination. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Results of analyses of the permutational variance (PERMANOVA) for the effects of zonation (North vs. South), intertidal level (Upper vs. Middle), sampling location (Shore), and site within shore (Site) on the BC similarity index (BC similarity), species richness as the total number of species (S), seaweeds coverage (Total coverage), Shannon diversity (H'). MS, mean square; Pseudo-F = statistic analogous to F in ANOVA obtained with a permutation procedure (9999 permutations). *p < 0.05, **p < 0.01, ***p < 0.001.

Source	BC similarity			S		N		H'	
	df	MS	Pseudo-F	MS	Pseudo-F	MS	Pseudo-F	MS	Pseudo-F
Zo	1	16303	2.1344	0.34028	0.0087892	0.17361	4.89E-05	0.0034053	0.0029848
In	1	98180	14.898 **	327.01	49 **	1.71E+05	171.54 ***	6.5747	47.504 **
Sh(Zo)	4	7638.3	2.77 ***	38.715	8.3835 **	3553	0.97073	1.1409	6.4807 **
ZoxIn	1	4734.3	0.71838	3.6736	0.55047	3854.3	3.8779	0.097751	0.70628
Si(Sh(Zo))	12	2757.6	3.7929 ***	4.6181	1.7608	3660.1	3.0847 ***	0.17604	1.8061 †
InxSh(Zo)	4	6590.2	4.3643 ***	6.6736	3.5993 †	993.92	0.42514	0.1384	1.1419
InxSi(Sh(Zo))	12	1510	2.077 ***	1.8542	0.70697	2337.8	1.9703 †	0.12121	1.2435
Res	108	727.04		2.6227		1186.5		0.097472	
Total	143								

community structure, zonation patterns, and a comparison of seaweed abundances along a vertical and horizontal gradient for the entire Santo Antão Island's rocky shores. Given the current climate change scenario, the data we collected in this study could serve as a baseline for other future monitoring programs of algal communities in this region. The species composition found confirms the pattern already described for the West African region (Haroun and Reine, 1993; Harper and Garbary, 1997), with a predominance of warm-temperate species (29) and a few tropical ones (15). Most of the warm-temperate seaweeds were present in other Macaronesian archipelagos (Gil-Rodríguez and Haroun, 1992; Haroun and Reine, 1993; Prud'homme Van Reine et al., 2002; Neto et al., 2014). Species with tropical affinity were common to tropical regions such as the Caribbean Sea or Hawaii (Haroun and Reine, 1993). Many of these species have their southern range in this region which makes them susceptible to local extinction if water warming continues to increase (Burrows et al., 2020; Mieszowska et al., 2021). In other biogeographic boundaries between temperate and tropical zones, such as Western Australia, has been observed the loss of seaweeds and the expansion of corals in temperate reefs due to the effects of marine heatwaves in the last decades (Tuckett et al., 2017). Similar patterns are expected in seaweeds restricted to subtropical and tropical areas. Like other tropical ectotherms, they are at the greatest risk of extinction, due to their low tolerance to the upcoming warming, and limited acclimation ability (Nguyen et al., 2011).

In Santo Antão Island, we could not find different patterns between northern and southern shores neither in community structure nor in species richness, Shannon diversity index, and abundance. As expected, we found consistent differences between tidal levels. At all shores, the upper intertidal presented fewer species and diversity than the mid-intertidal. These differences between tidal levels have been well documented in several studies worldwide being the physiological stress the main factor controlling this distributional pattern (Lubchenco, 1980; Paine and Levin, 1981; Underwood et al., 1983; Paine, 1994; Underwood and Chapman, 1996; Underwood, 1999). The brown seaweeds *Asteronema breviararticulatum* and *Chnoospora minima* were the most abundant species in the upper intertidal at all shores. These species were found also on phycological studies of other islands in Cape Verde, always at wave-exposed sites, and considered relevant communities for the Cape Verde coastlines (Prud'homme Van Reine et al., 2002; Almada, 2015; Gabriel and Fredericq, 2019). On the contrary, red algae dominated the mid-intertidal, always accompanied by *Sargassum* spp., and showed more species and abundance than the upper intertidal. The dominant species were *Spyridia* spp., *Hypnea* spp., *Palisada perforata*,

and *Laurencia* spp. that occurred intermingled in the intertidal, forming a coarse algal turf with *Sargassum* spp. This algal pattern with the same species was observed on the island of Santiago, one of the southernmost islands of the archipelago (Almada, 2015). Floristic studies carried out on other islands of the Cape Verde archipelago had verified that *Laurencia sensu lato*, *Palisada perforata*, *Chnoospora minima*, and *Sargassum vulgare* together with crustose calcareous Rhodophyta, were the predominant species in the algal communities of the rocky coasts exposed or very exposed to waves (Otero-Schmitt, 1995a,b; Almada, 2015). Given the dominant character of algal turf throughout the rocky intertidal, articulated calcareous red algae (e.g., *Jania* sp1.) also played an important role in the formation of the dense mats. Calcareous and non-calcareous crustose algae also form an important part of the intertidal landscape, being very abundant in both the upper and middle intertidal.

Previous studies on the characterization of the algal communities of the Cape Verde archipelago described a species-poor intertidal. This is mostly due to their caespitose character and the high degree of sedimentation of the studied areas (Otero-Schmitt, 1995b). However, our results in Santo Antão Island showed a high diversity of species at both tide levels studied, similar to what had been observed in Santiago Island (Almada, 2015). A growing number of studies are showing that algal turf is often comprised of many species, contrary to what used to be assumed (Connell et al., 2014; Díaz-Tapia et al., 2021). According to the last seaweed checklist for the Cape Verde archipelago, a total of 372 species are listed, both intertidal and subtidal (Gabriel and Fredericq, 2019). Our study focused only on the intertidal, where 43 species were found only for the upper and middle intertidal. This study was conducted during the summer, as it is typically the optimal season to study the abundance and diversity of seaweeds owing to the life cycle of many species (Fulton et al., 2014), and due to better local oceanographic conditions to perform the fieldwork. Despite this, some species might not be observed, especially if they only occur at a given time of the year (Otero-Schmitt, 1995b). Furthermore, the wave exposure of the island and its intensity, with the narrow rocky shores combined with short tidal amplitude, hampered the sampling at the lower intertidal. Although studies to assess the seasonal variability of intertidal communities would be of great interest (Paine and Levin, 1981; Piñeiro-Corbeira et al., 2018; Barrientos et al., 2019), most of the species found are perennial (e.g. *Palisada perforata*, *Sargassum vulgare*). Given that perennial species can be found throughout the year, their monitoring is not limited to seasonal studies. Long-term monitoring of perennial species can be a useful tool for studying the impact of global change since changes in their distribution and abundance can be an indicator of global change (Piñeiro-Corbeira et al., 2016; Barrientos et al., 2020; Vale et al., 2021).

5. Conclusions

Detailed knowledge of the community structure in poorly known regions is fundamental for overcoming some of the conservation shortfalls. This is particularly important in transitional regions between temperate and tropical waters, where species from different biogeographic affinities may coexist, and are particularly vulnerable to climate change. Our study is the first spatial comprehensive assessment of intertidal seaweeds present on the poorly known island of Santo Antão. We found a high diversity of seaweeds distributed along the tidal zones of Santo Antão shores. The zonation patterns observed were consistent with those in other biogeographic transition areas, where longer monitoring programs already revealed compositional changes in the intertidal communities due to climate change. Therefore, assessments like this are of great interest to monitor changes in species distribution due to climate change impacts. In this study, we lay the groundwork for future monitoring of the intertidal macroalgal communities of the Cape Verde archipelago, particularly for the least studied island, Santo Antão.

CRedit authorship contribution statement

Cristina Piñeiro-Corbeira: Conceptualization, Methodology, Formal analysis, Visualization, Data curation, Writing – original draft, Writing – review & editing. **Francisco Arenas:** Conceptualization, Methodology, Writing – review & editing. **Marina Dolbeth:** Funding acquisition, Conceptualization, Methodology, Writing – review & editing. **Cândida G. Vale:** Formal analysis, Data curation, Visualization, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at <https://doi.org/10.1016/j.rsma.2023.102999>.

References

- Adams, V.M., Barnes, M., Pressey, R.L., 2019. Shortfalls in conservation evidence: Moving from ecological effects of interventions to policy evaluation. *One Earth* 1, 62–75.
- Agostini, S., Harvey, B.P., Milazzo, M., Wada, S., Kon, K., Floc'h, N., Komatsu, K., Kuroyama, M., Hall-Spencer, J.M., 2021. Simplification, not tropicalization, of temperate marine ecosystems under ocean warming and acidification. *Global Change Biol.* 00, 1–14.
- Almada, C.H.B.A., 2015. Estudio Florístico Y Ecológico de Las Algas Bentónicas Del Archipiélago de Cabo Verde. Universidad de Las Palmas de Gran Canaria.
- Alves, B., Angnuureng, D.B., Morand, P., Almar, R., 2020. A review on coastal erosion and flooding risks and best management practices in West Africa: what has been done and should be done. *J. Coast. Conservation* 24 (38).
- Anderson, M.J., Robinson, J., 2003. Generalized discriminant analysis based on distances. *Aust. N. Z. J. Stat.* 45, 301–318.
- Araújo, R., Bárbara, I., Sousa-Pinto, I., Quintino, V., 2005. Spatial variability of intertidal rocky shore assemblages in the northwest coast of Portugal. *Estuar. Coast. Shelf Sci.* 64, 658–670.
- Aristegui, J., Barton, E.D., Álvarez-Salgado, X.A., Santos, A.M.P., Figueiras, F.G., Kifani, S., Hernández-León, S., Mason, E., Machú, E., Demarcq, H., 2009. Sub-regional ecosystem variability in the canary current upwelling. *Prog. Oceanogr.* 83, 33–48.
- Barrientos, S., Barreiro, R., Cremades, J., Piñeiro-Corbeira, C., 2020. Setting the basis for a long-term monitoring network of intertidal seaweed assemblages in northwest Spain. *Mar. Environ. Res.* 160, 105039.
- Barrientos, S., Barreiro, R., Olmedo, M., Piñeiro-Corbeira, C., 2019. Can patch size and patch distance improve the recolonization of mussel-seed beds exploited for aquaculture? *Aquat. Conserv. Mar. Freshw. Ecosyst.* 29, 1897–1908.
- Baweja, P., Kumar, S., Sahoo, D., Levine, I., 2016. Chapter 3 - biology of seaweeds. In: Florence, J., Levine, I. (Eds.), *Seaweed in Health and Disease Prevention*. Academic Press, San Diego, pp. 41–106.
- Bini, L.M., Diniz-Filho, J.A.F., Rangel, T.F.L.V.B., Bastos, R.P., Pinto, M.P., 2006. Challenging wallacean and linnean shortfalls: knowledge gradients and conservation planning in a biodiversity hotspot. *Divers. Distrib.* 12, 475–482.
- Burrows, M.T., Hawkins, S.J., Moore, J.J., Adams, L., Sugden, H., Firth, L., Mieszowska, N., 2020. Global-scale species distributions predict temperature-related changes in species composition of rocky shore communities in Britain. *Global Change Biol.* 26, 2093–2105.
- Burrows, M.T., Schoeman, D.S., Buckley, L.B., Moore, P., Poloczanska, E.S., Brander, K.M., Brown, C., Bruno, J.F., Duarte, C.M., Halpern, B.S., Holding, J., Kappel, C.V., Kiessling, W., O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Schwing, F.B., Sydeman, W.J., Richardson, A.J., 2011. The pace of shifting climate in marine and terrestrial ecosystems. *Science* 334, 652–655.
- Burrows, M.T., Schoeman, D.S., Richardson, A.J., Molinos, J.G., Hoffmann, A., Buckley, L.B., Moore, P.J., Brown, C.J., Bruno, J.F., Duarte, C.M., Halpern, B.S., Hoegh-Guldberg, O., Kappel, C.V., Kiessling, W., O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Sydeman, W.J., Ferrier, S., Williams, K.J., Poloczanska, E.S., 2014. Geographical limits to species-range shifts are suggested by climate velocity. *Nature* 507, 492–495.
- Chapman, A.R.O., 1987. Population and community ecology of seaweeds. In: Blaxter, J.H.S., Southward, A.J. (Eds.), *Advances in Marine Biology*. Academic Press, pp. 1–161.
- Clarke, K.R., Gorley, R.N., 2015a. Getting Started with PRIMER V7, first ed. PRIMER-E, Plymouth.
- Clarke, K.R., Gorley, R.N., 2015b. PRIMER V7: User Manual/Tutorial, 1st edition. PRIMER-E, Plymouth.
- Connell, S.D., Foster, M.S., Airoidi, L., 2014. What are algal turfs? Towards a better description of turfs. *Mar. Ecol. Prog. Ser.* 495, 299–307.
- Costello, Mark J., 2015. Biodiversity: The known, unknown, and rates of extinction. *J. Curr. Biol.* 25, R368–R371.
- Dash, B.P., Ball, M.M., King, G.A., Butler, L.W., Rona, P.A., 1976. Geophysical investigation of the Cape Verde Archipelago. *J. Geophys. Res.* (1896–1977) 81, 5249–5259.
- Díaz-Tapia, P., Muñoz-Luque, L., Piñeiro-Corbeira, C., Maggs, C.A., 2021. Phylogenetic analyses of macaronesian turf-forming species reveal cryptic diversity and resolve stichothamnion in the vertebrata clade (Rhodomelaceae, Rhodophyta). *Eur. J. Phycol.* 444–454.
- Fernandes, J., Lazaro, C., Santos, A.M., Oliveira, P., 2005. Oceanographic Characterization of the Cape Verde Region using Multisensor Data. European Space Agency, (Special Publication) ESA SP.
- Freitas, R., Mendes, T.C., Almeida, C., Melo, T., Villaça, R.C., Noguchi, R., Floeter, S.R., Rangel, C.A., Ferreira, C.E.L., 2019. Reef fish and benthic community structures of the Santa Luzia Marine Reserve in the Cabo Verde islands, eastern central atlantic ocean. *Afr. J. Mar. Sci.* 41, 177–190.
- Freitas, T.M.d.S., Stropp, J., Calegari, B.B., Calatayud, J., De Marco Jr., P., Montag, L.F.d.A., Hortal, J., 2021. Quantifying shortfalls in the knowledge on Neotropical Auchenipteridae fishes. *Fish Fish.* 22, 87–104.

- Fulton, C., Depczynski, M., Holmes, T., Noble, M., Radford, B., Wernberg, T., Wilson, S., 2014. Sea temperature shapes seasonal fluctuations in seaweed biomass within the Ningaloo coral reef ecosystem. *Limnol. Oceanogr.* 59, 156–166.
- Gabriel, D., Fredericq, S., 2019. The marine macroalgae of Cabo Verde archipelago: An updated checklist. p. 36.
- Gil-Rodríguez, M.C., Haroun, R., 1992. *Laurencia Viridis* Sp. Nov. (Ceramiales, Rhodomelaceae) from the Macaronesian Archipelagos, Vol. 35. pp. 227–238.
- Haroun, R., Gil-Rodríguez, M.C., Neto, A.I., Machín-Sánchez, M., Viera-Rodríguez, M.A., 2019. A review of current uses and potential biotechnological applications of seaweeds from the macaronesian region (Central-East Atlantic Ocean). *J. Appl. Phycol.* 31, 3777–3790.
- Haroun, R.J., Reine, W.F.P.H.v., 1993. A biogeographical study of *Laurencia* and *Hypnea* species of the Macaronesian region.
- Harper, J.T., Garbary, D.J., 1997. Marine algae of northern Senegal: The flora and its biogeography. 40, pp. 129–138.
- Hoepffner, N., Djavidnia, S., Nykjaer, L., Derycke, P., 2014. Thermal infrared remote sensing and sea surface temperature of marine and coastal waters around Africa. In: Barale, V., Gade, M. (Eds.), *Remote Sensing of the African Seas*. Springer, Netherlands, Dordrecht, pp. 55–73.
- Van der Land, J., 1993. Marine biota of the cape verde islands. *Courier Forschungsinstitut Senckenberg* 159, 39–44.
- Lawson, G.W., John, D.M., 1987. The marine algae and coastal environment of tropical West Africa. *J. Cramer*.
- López, C., Reimer, J.D., Brito, A., Simón, D., Clemente, S., Hernández, M., 2019. Diversity of zoantharian species and their symbionts from the Macaronesian and Cape Verde ecoregions demonstrates their widespread distribution in the Atlantic ocean. *Coral Reefs* 38, 269–283.
- Lubchenco, J., 1980. Algal zonation in the new England rocky intertidal community : An experimental analysis. *Ecology* 61, 333–344.
- Lüning, K., 1990. *Seaweeds: Their Environment, Biogeography, and Ecophysiology*. Wiley.
- McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data: A comment on distance-based redundancy analysis. *Ecology* 82, 290–297.
- Michanek, G., 1979. Phytogeographic provinces and seaweed distribution. 22, pp. 375–392.
- Mieszkowska, N., 2015. Intertidal indicators of climate and global change. In: Letcher, T.M. (Ed.), *Climate Change*. Elsevier, Amsterdam, Netherlands, pp. 213–229.
- Mieszkowska, N., 2021. Chapter 22 - Intertidal indicators of climate and global change. In: Letcher, T.M. (Ed.), *Climate Change*, third ed. Elsevier, pp. 465–482.
- Mieszkowska, N., Burrows, M.T., Hawkins, S.J., Sugden, H., 2021. Impacts of pervasive climate change and extreme events on rocky intertidal communities: Evidence from long-term data. *Front. Mar. Sci.* 8.
- Mineur, F., Arenas, F., Assis, J., Davies, A.J., Engelen, A.H., Fernandes, F., Malta, E.-j., Thibaut, T., Van Nguyen, T., Vaz-Pinto, F., Vranken, S., Serrão, E.A., De Clerck, O., 2015. European seaweeds under pressure: Consequences for communities and ecosystem functioning. *J. Sea Res.* 98, 91–108.
- Morri, C., Cattaneo Vietti, R., Sartoni, C., Bianchi, C., 2000. Shallow Epibenthic Communities of Ilha Do Sal. Cape Verde Archipelago, Eastern Atlantic.
- Neto, A.I., Viera, M.A., Haroun, R., 2014. A synthetic overview of marine physiological studies in the macaronesian archipelagos. *Silva Lusitana* 22.
- Nguyen, K.D.T., Morley, S.A., Lai, C.-H., Clark, M.S., Tan, K.S., Bates, A.E., Peck, L.S., 2011. Upper temperature limits of tropical marine ectotherms: Global warming implications. *Plos One* 6, e29340.
- Otero-Schmitt, J., 1995a. The communities of *Laurencia* (Rhodomelaceae, Rhodophyta) at the Cape Verde islands.
- Otero-Schmitt, J., 1995b. Comunidades bentónicas marinas de las islas de Sal, San Vicente, Santiago, Fogo y Brava (Islas Cabo Verde). In: *Vieraea: Folia Scientiarum Biologicarum Canariensium*. pp. 1–11.
- Paine, R.T., 1974. Intertidal community structure. *Oecologia* 15, 93–120.
- Paine, R.T., 1994. Marine rocky shores and community ecology: An experimentalist's perspective. *Ecol. Inst.*
- Paine, R.T., Levin, S.A., 1981. Intertidal landscapes: disturbance and the dynamics of pattern. *Ecol. Monograph* 51, 145–178.
- Pecl, G.T., Araújo, M.B., Bell, J.D., Blanchard, J., Bonebrake, T.C., Chen, I.-C., Clark, T.D., Colwell, R.K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R.A., Griffis, R.B., Hobday, A.J., Janion-Scheepers, C., Jarzyna, M.A., Jennings, S., Lenoir, J., Linnetved, H.I., Martin, V.Y., McCormack, P.C., McDonald, J., Mitchell, N.J., Mustonen, T., Pandolfi, J.M., Pettolelli, N., Popova, E., Robinson, S.A., Scheffers, B.R., Shaw, J.D., Sorte, C.J.B., Strugnell, J.M., Sunday, J.M., Tuanmu, M.-N., Vergés, A., Villanueva, C., Wernberg, T., Wapstra, E., Williams, S.E., 2017. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science* 355, eaai9214.
- Pérez-Rodríguez, P., Pelegrí, J.L., Marrero-Díaz, A., 2001. Dynamical characteristics of the Cape Verde frontal zone. *Sci. Mar.* 65, 241–250.
- Piñeiro-Corbeira, C., Barreiro, R., Cremades, J., 2016. Decadal changes in the distribution of common intertidal seaweeds in galicia (NW iberia). *Mar. Environ. Res.* 113, 106–115.
- Piñeiro-Corbeira, C., Barrientos, S., Olmedo, M., Cremades, J., Barreiro, R., 2018. By-catch in no-fed aquaculture: exploiting mussel seed persistently and extensively disturbs the accompanying assemblage. *ICES J. Mar. Sci.* 75, 2213–2223.
- Plesner, S., Holm, P.M., Wilson, J.R., 2003. 40Ar–39Ar geochronology of Santo Antão, Cape Verde islands. *J. Volcanol. Geotherm. Res.* 120, 103–121.
- Prud'homme Van Reine, W., Haroun, R., Kostermans, L., 2002. Checklist on seaweeds in the atlantic ocean and in the cape verde archipelago.
- Sangil, C., Martins, G.M., Hernández, J.C., Alves, F., Neto, A.I., Ribeiro, C., León-Cisneros, K., Canning-Clode, J., Rosas-Alquicira, E., Mendoza, J.C., Tittley, I., Wallenstein, F., Couto, R.P., Kaufmann, M., 2018. Shallow subtidal macroalgae in the north-eastern atlantic archipelagos (Macaronesian region): A spatial approach to community structure. *Eur. J. Phycol.* 53, 83–98.
- Scrosati, R.A., Catalán, A.M., Valdívila, N., 2021. Macroalgal canopies reduce beta diversity in intertidal communities. *Botanica Marina*.
- Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A., Robertson, J., 2007. Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *BioScience* 57, 573–583.
- Tuckett, C.A., de Bettignies, T., Fromont, J., Wernberg, T., 2017. Expansion of corals on temperate reefs: direct and indirect effects of marine heatwaves. *Coral Reefs* 36, 947–956.
- Underwood, A.J., 1999. Physical disturbances and their direct effect on an indirect effect: Responses of an intertidal assemblage to a severe storm. *J. Exp. Mar. Biol. Ecol.* 232, 125–140.
- Underwood, A.J., 2000. Experimental ecology of rocky intertidal habitats: what are we learning? *J. Exp. Mar. Biol. Ecol.* 250, 51–76.
- Underwood, A.J., Chapman, M.G., 1996. Scales of spatial patterns of distribution of intertidal invertebrates. *Oecologia* 107, 212–224.
- Underwood, A.J., Denley, E.J., Moran, M.J., 1983. Experimental analyses of the structure and dynamics of mid-shore rocky intertidal communities in new south Wales. *Oecologia* 56, 202–219.
- Vale, C.G., Arenas, F., Barreiro, R., Piñeiro-Corbeira, C., 2021. Understanding the local drivers of beta-diversity patterns under climate change: The case of seaweed communities in galicia. *North West Iber. Peninsula. Diversity Distributions* 27, 1696–1705.
- Vergés, A., McCosker, E., Mayer-Pinto, M., Coleman, M.A., Wernberg, T., Ainsworth, T., Steinberg, P.D., Williams, G., 2019. Tropicalisation of temperate reefs: Implications for ecosystem functions and management actions. *Funct. Ecol.*
- Vieira, C., Henriques, F., D'hondt, S., Neto, A., Almada, C.H., Kaufmann, M., Sansón, M., Sangil, C., Clerck, O.D., 2020. *Lobophora* (dictyotales) species richness, ecology and biogeography across the north-eastern atlantic archipelagos and description of two new Species1. *J. Phycol.* 56, 346–357.
- Whittaker, R.J., Araújo, M.B., Jepson, P., Ladle, R.J., Watson, J.E.M., Willis, K.J., 2005. Conservation biogeography: assessment and prospect. *Divers. Distrib.* 11, 3–23.
- Zenk, W., Klein, B., Schroder, M., 1991. Cape verde frontal zone. *Deep Sea Res. Part A Oceanogr. Res. Pap.* 38, S505–S530.