INSTITUTO UNIVERSITÁRIO
CIÊNCIAS PSICOLÓGICAS, SOCIAIS E DA VIDA

REDEFINITION OF THE CIRCALITTORAL ZONE AND ITS ASSEMBLAGES FROM AZORES INSULAR SHELVES THROUGH VIDEO SURVEY

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Tese submetida como requisito parcial para a obtenção do grau de:

MESTRE EM BIOLOGIA MARINHA E CONSERVAÇÃO

2019

Dissertação de Mestrado realizada sob a orientação de Pedro Afonso e Fernando Tempera, apresentada no ISPA – Instituto Universitário para obtenção de grau de Mestre na especialidade de Biologia Marinha e Conservação

ACKNOWLEDGEMENTS

I would like to thank my supervisors, Fernando Tempera and Pedro Afonso, for the guidance and teaching.

I would like to thank my master professor, Emanuel Gonçalves, for guidance, mostly regarding thesis writing schedules.

I would like to thank the institute, Instituto Superior de Psicologia Aplicada, for the master opportunity.

I would like to acknowledge some professors who had a positive footprint on my learning process as professor Ana Rita Luís and professor Leonor Galhardo.

I would like to thank DOP/Uaç for the thesis experience and learning.

I would like to thank all the people that were always so willing to help on every thesis issue, including Meri Billan, David Figueras, António Godinho, Diya Das, Gonçalo Graça, Jordi Blasco, Ricardo Medeiros and Mara Schmiing.

At last, I would like to acknowledge my parents for all the support and inspiration they gave me.

RESUMO

Os oceanos enfrentam uma crise de perda de biodiversidade graças ao crescimento das atividades humanas e das alterações climáticas, enquanto o conhecimento do ambiente marinho e destes impactos continua escasso. Tal conhecimento reflete-se no circalitoral das plataformas insulares dos Açores e nas correspondentes comunidades, alvo do nosso estudo que teve como objetivo descrevê-los através da: (i) identificação dos padrões verticais baseado nas comunidades existentes, (ii) investigação da sua interação com importantes descritores ambientais, e (iii) comparação das comunidades com os biótopos estabelecidos pela EUNIS. A diversidade de morfotipos foi apurada por "drop down" câmaras colocadas de 50 a 200 m de profundidade em três ilhas do arquipélago e, posteriormente, estudada quanto à sua distribuição aos níveis individual e da comunidade. Os resultados apoiam a redefinição do circalitoral para os Açores. Aos 80 m, a luz que chega ao fundo marca o início da dominância de bioconstruções coralinas e comunidades faunísticas eretas. A partir dos 110 m a insuficiente luz seleciona apenas comunidades animais. Começando pelo circalitoral inferior, esponjas dominam até ca. 140 m enquanto os corais negros alcançam o circalitoral profundo, hidrodinamicamente estável permitindo a subsistência de uma mistura de esponjas e gorgónias frágeis dos ca. 140 m aos 200 m. Porém, a definição dos limites desta sub-zona deverá ser refinada com base na influente estabilidade térmica. A maioria dos biótopos identificados representa VMEs não contemplados na EUNIS, evidenciando a importância do conhecimento proveniente destes e de outros estudos para ações de conservação das plataformas insulares dos Açores e, possívelmente de outros arquipélagos da Macaronésia.

Palavras-chave: circalitoral, zonação, mapeamento de habitats, VMEs.

ABSTRACT

Oceans face a biodiversity loss crisis as human activities and climate change increase while knowledge of the marine environment and those impacts is still lagging behind. This includes the circalittoral zone and communities of the Azores insular shelves which this work aimed at describing through (i) identifying its vertical patterns based on its assemblages, (ii) investigating its relationships with key environmental descriptors, and (iii) critically compare it with the established EUNIS biotopes. Morphological species diversity was investigated through drop down cameras deployed at 50 to 200 m on three islands across the archipelago, and the distribution range of morphotypes assessed at the individual and assemblage levels. Results support a redefinition of the circalittoral zone for the Azores islands and its distinct sub-zones. Seabed light marks the transition to the coralligenous bioconstructions and erect fauna communities of the upper circalittoral at 80 m. As light gets sparser, only animal communities subsist below 110 m. This includes the lower circalittoral, dominated by sponges down to ca. 140 m and by black coral gardens extending to the more hydrodynamically stable deep circalittoral with a mix of fragile sponges and gorgonians from ca. 140 m to 200 m. Future studies could aim at refining the deep circalittoral limits based on thermal stability. Most of the identified biotopes represent VMEs which are not contemplated in the current EUNIS classification, highlighting the importance of these and other recent studies for knowledge-based conservation actions of the insular circalittoral of the Azores and, possibly, other Macaronesian archipelagoes.

Key word: circalittoral, zonation, habitat mapping, VMEs.

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1 – INTRODUCTION

1.1 – MARINE HABITAT CLASSIFICATION AND MAPPING

From the shore to the deep seabed, there is a clear zonation of communities associated to the influence of several environmental factors which vary according to that increase in depth. These environmental factors include substrate type, temperature, salinity and hydrodynamic conditions which primarily characterize each marine habitat according to the hierarchical EUNIS (European Nature Information System) habitat classification, the most comprehensive classification system nowadays (David W. Connor et al., 2004; Davies et al., 2004; UKSeaMap, 2010; Wahl, 2009). Initially, the EUNIS classification based its marine environment section on the JNCC Marine Habitat Classification for Britain and Ireland, by Connor et al., 2004, and, since then, effort was done to incorporate more classifications and to increase the geographical cover of the European seas, leading to a more comprehensive system (Galparsoro et al., 2012). It currently covers the northeast Atlantic and Mediterranean while it does not apply to most of the marine habitats of the Atlantic coast of southern Europe and of the biogeographical distinct Macaronesia islands (Evans et al., 2016; Galparsoro et al., 2012).

A consistent and comprehensive classification system allows for the development of habitat maps at a broad scale since it enables both (i) a standardized interpretation of the raw data to build up maps and (ii) comparability between maps arisen from different sources (Cameron & Askew, 2011). Likewise, the European Marine Observation and Data Network (EMODnet) developed a consistent broadscale European map, EUSeaMap, of physical habitats based on the comprehensive EUNIS classification system (EMODnet, n.d.). These maps aim to be the bases for posterior long-term sustainable use and management of the marine environment and its resources (Blue Growth) as well as for protection of the marine environment (mostly of vulnerable habitats), demanded by current European directives as the Marine Strategy Framework Directive (MSFD) and by the research and innovation roadmap for climate services mainly developed by Horizon 2020 (Cameron & Askew, 2011; EMODnet, 2016; Galparsoro et al., 2012; Peran et al., 2016; Street et al., 2015).

Hence, there's a pressing need to continue identifying and mapping Macaronesian seabed biotopes through understanding the influence of environmental factors and the arisen assemblages characterizing the particular zonation pattern.

1.1.1 – BIOLOGICAL ZONES: CIRCALITTORAL ZONE

In compliance with the EUNIS classification, the circalittoral zone (level 2) stands for a portion of the sublittoral zone, following the infralittoral, which tends to extend until the end of the continental shelf (followed by the bathyal), on both hard and soft bottoms. This zone is marked by the dominance of animal communities, although Algae are still present in the upper portion, and by communities dominated by a diversity of species, instead of a single species dominance. Such community structure, strikingly different from the single algal species dominated infralittoral, is strongly influenced by the interaction of several environmental factors – mostly, light, wave action, substrate type, tidal currents, thermal stability and salinity – which further split the broad circalittoral into two main sub-zones: the shallow circalittoral and the deep circalittoral (encompassing biotopes at level 3, A4 and A5) (David W. Connor et al., 2004; Monteiro et al., 2011; Wahl, 2009).

The shallow circalittoral is a layer mostly marked by the amount of light that reaches the seabed (from all the above mentioned) since it represents the minimum limit for the performance of photosynthetic activity by erect macro-algae, hence, controlling their distribution. The upper shallow circalittoral starts at a depth where seagrass and green macrophyte are absent whilst brown macroalgae as Fucales, Laminariales (one of the last macrophyte algae to disappear), Desmarestiales and Sporochnales, alongside Rhodophyta (not referring to encrusting calcareous) can still occur. Nevertheless, the characteristic communities of this layer are the communities of coralligenous crustose or loose lying red algae; and faunal communities. Formed by encrusting coralline algae or Rhodolith (Maerl beds), this coralligenous habitat builders are abundant in the upper circalittoral where they provide structure and biomass that increases the flora and fauna (as sponges) associated. However, they are not so abundant in the lower circalittoral. Thus, the lower circalittoral starts at the depth at which the seabed light allows the presence of sparse red crustose algae (without foliose Algae) in biotopes dominated by animal communities. This layer extends until the lower depth limit of multicellular photosynthetic forms (including red encrusting coralligenous Algae), as rariphotic (rarus = scarce, according to Baldwin et al., 2018) depths are reached, delineating the inferior limit of the lower circalittoral (Amorim et al., 2015; Baldwin et al., 2018; Bekkby et al., 2017; David W Connor et al., 2004; EMODnet, 2016; EUSeaMap, n.d.-a; Evans et al., 2016; Monteiro et al., 2011; Vasquez et al., 2015).

The transition from the later sub-zone to the further rariphotic deep circalittoral, or offshore circalittoral, lies at the maximum depth at which the seabed is disturbed by swell (wave base). In absence of light and wave action influence, the deep circalittoral zone is typified by stable conditions – reflected by the lack of both physical disturbance and rapid changes in salinity and temperature –, and by tidal currents being its dominant feature. Consequently, this zone allows for the dominance of erect, fragile and large-bodied epifauna like arborescent octocorals, branching stony corals and erect branching or laminar sponges (in absence of algae species) until the end of the continental shelf, around 200 m (boundary with the upper bathyal) (Althaus et al., 2013; Baldwin et al., 2018; Bo et al., 2011; Clark et al., 2015; David W Connor et al., 2004; David W. Connor et al., 2004; EUSeaMap, n.d.-b; Evans et al., 2016; UKSeaMap, 2010).

Regarding the substrate type, rocky bottoms are usually restricted to the shallow circalittoral zone while the several types of sediment bottoms spread from the circalittoral to the offshore circalittoral, which can be explained by the tectonics, erosion and hydrodynamics of the continental shelf (David W Connor et al., 2004; David W. Connor et al., 2004; Harris, 2012).

Therefore, the variables often used in the literature as proxies to determine the thresholds of these two main layers are (1) light penetration and (2) wave base. However, the other variables mentioned in the beginning of the section may be used as proxies, as it is the case for temperature, instead of wave base, to define the boundary between the layers or other variables as sedimentation for suspension feeders, pressure and dissolved oxygen (Baldwin et al., 2018; Lesser et al., 2009; Vasquez et al., 2015).

Both limits, and communities, vary according to the specific abiotic variables of a habitat which are influenced by conditions as turbidity, due to dissolved organic pigments and suspended matter, latitude, climate and currents (David W. Connor et al., 2004; EUSeaMap, n.d.-a; Hartnoll, 1998). Likewise, EMODnet has worked on refining the boundaries between each biological zone for the European seas considering the specific environmental variables of each region (Populus et al., 2017).

1.1.2 – VULNERABLE MARINE ECOSYSTEMS (VMES)

As already mentioned, in the past decades, there was urgent need to halt biodiversity loss mainly due to increasing destructive fishing activities which led to identification and further protection of vulnerable marine ecosystems (VMEs) – communities susceptible to disturbance from human activities, especially fishing, and that are slow or unable to recover from that impinged disturbance (F Enrichetti et al., 2019; Thompson et al., 2016).

Owing to their complex three-dimensional structure, linked to important functionality but also fragility, algal and animal forests are likely to constitute vulnerable ecosystems (Bekkby et al., 2017; Francesco Enrichetti et al., 2019). These include seagrass meadows, kelp and macroalgal forests, coralligenous (including maërl) beds, coral gardens, sponge aggregations, areas with gorgonian forests and various deep-sea habitats as seamounts, canyons, coral gardens and hydrothermal vents. Additionally, these ecosystems have an important representation in the North-East Atlantic Ocean and Mediterranean Sea and most of the ones occurring at shelf depths can be found at the circalittoral zone (Bekkby et al., 2017; EUSeaMap, n.d.-a, n.d.-b; Evans et al., 2016; Tempera et al., 2013).

Adding to their functionality and vulnerability, these ecosystems provide important ecological services as carbon storage (Bekkby et al., 2017). Thus, the pressing need to identify and protect these ecosystems requires detailed documentation of their biological traits together with the bottom fishing footprint on those areas in order to ensure fishing grounds do not match areas where VMEs occur or are likely to occur (F Enrichetti et al., 2019; Thompson et al., 2016). This identification process has been done by directives as the MSFD based on habitat maps using the EUNIS habitat classification's common language to ensure a common direction of VMEs protection and/or restoration between member states (Allee et al., 2000; Bekkby et al., 2017; F Enrichetti et al., 2019; Galparsoro et al., 2012).

1.2 – THE AZORES

The Azores is a mid-north Atlantic archipelago composed of nine islands scattered across an extent of 617 km between the latitudes 39° 44' N – 36° 55' N and longitudes 31° 15' W – 25° 00' W. They are located on the Azorean Microplate in the junction between the Eurasian, North-American and African plates as well as at the northern edge of the North Atlantic Subtropical Gyre. The archipelago is divided in three groups of islands: Flores and Corvo in the Western group; Faial, Pico, São Jorge, Graciosa and Terceira in the Central group; São Miguel and Santa Maria in the Eastern group, together with several rocks and reefs known as the Formigas islets (at northeast of Santa Maria). The Azores belong to the Macaronesia biogeographical zone as well as the Madeira archipelago (Portugal), Cape Verde (Cape Verde) and the Canary Islands (Spain) (Amorim et al., 2015; Ojamaa, 2015; Tempera et al., 2013; Wallenstein, Neto, Alvaro, & Santos, 2008; Wallenstein, Neto, Alvaro, & Tittley, 2008).

The islands have a volcanic origin which explains their narrow shelves (from a few hundred meters to a few kilometers) and flanks reaching 1000 m depth at ca. 200 m offshore (Amorim et al., 2015; Ojamaa, 2015; Tempera et al., 2013; Wallenstein, Neto, Alvaro, & Tittley, 2008). Being in a low vortex activity area, currents represent the main source of water dynamic and temperature variability (Amorim et al., 2015; Bashmachnikov et al., 2004; Ojamaa, 2015; Tempera et al., 2013; Wallenstein, Neto, Alvaro, & Tittley, 2008). These currents also maintain Azorean waters at an average temperature of 17 – 23 ºC. The combination of shore geomorphology, continental shelf and wave dynamics provide an environment for a wide variety of fauna and flora communities to develop very differently when compared to those of the mainland Europe (Wallenstein, Neto, Alvaro, & Tittley, 2008).

Apart from the islands, the Azorean Plateau is marked by its rich topography owing to the 400 seamounts, fracture zones, hydrothermal vents and deep coral reefs (Amorim et al., 2015; Ojamaa, 2015).

The archipelago's water column and seafloor surrounding the islands are under Portugal's marine jurisdiction (the Azores Exclusive Economic Zone, EEZ) and its ecosystems are exploited by some key economic activities as commercial fishing (mainly artisanal longline, handline and pole-and-line), tourism and marine traffic, followed by sand dredging (Abecasis et al., 2015; Tempera et al., 2013).

Previous efforts inventoried the biotopes of the Azores shelves and suggested new Macaronesian habitat types to the EUNIS Habitat Classification (see Tempera et al., 2013). This compilation includes 81 habitats which constitute previously undescribed assemblages (Tempera et al., 2013).

Among those, some were particularly typical of the circalittoral zone. These included hard bottom circalittoral biogenic beds (maërl and *Neopycnodonte cochlear*), hydrarian gardens (*Polyplumaria flabellata*) and sponge aggregations. Plus, it included biotopes of mono-specific aggregations of *Nemertesia ramosa* or *Antipathes subpinnata* – the sole black coral garden found at circalittoral depths (de Matos et al., 2014; Gomes-Pereira et al., 2012; Tempera et al., 2013).

Nevertheless, the habitat inventory still reflected the lack of data regarding these faunal communities of the circalittoral zone on the habitat descriptions (Tempera et al., 2013). Additionally, these habitats seem to constitute VMEs. Regarding the Azores islands cold-water coral gardens are already considered VMEs but mostly at deep-sea depths (Bekkby et al., 2017; Pham et al., 2015).

The lack of descriptive and geographical coverage data and the distinctness of the proposed biotopes from the EUNIS ones strongly underlined the need to consistently and comprehensively survey the circalittoral biotopes of the continental shelves of the Azores Islands. This will allow further identification and mapping of the Azorean circalittoral biotopes which will constitute essential data for biotope assessment and decision-making regarding their protection (F Enrichetti et al., 2019; Galparsoro et al., 2012; Tempera et al., 2013; Thompson et al., 2016).

The present work aimed to survey the circalittoral biotopes, from 50 m to 200 m, of the Azores Islands' shelves in order to (i) find the thresholds defining this zone, based on the existing literature, (ii) describe the assemblages found and (iii) compare them to the established EUNIS habitats. For that, benthic habitats were video surveyed in order to investigate the morphological species and the associated substrate, which is highly applied nowadays as a quicker, low cost and non-capture or invasive method (Bo et al., 2014; Marzloff et al., 2018; Piazzi et al., 2019; Schönberg et al., 2014). Additionally, the presence/absence and abundance data were analyzed together with environmental predictor variables, which is a recommended approach according to EMODnet (Populus et al., 2017).

2 – MATERIALS AND METHODS

Underwater videos collected from several scientific projects which sampled the insular shelves from the Azores islands were used in order to investigate the circalittoral benthic species distribution, at an archipelago scale, on hard and mixed substrates.

2.1 – STUDY AREA

The Azores archipelago comprises nine volcanic islands scattered across three groups on the mid-north Atlantic Ocean (Fig. 1). The western group sits on the American plate and is separated by the Mid-Atlantic Ridge from the central and eastern groups which sit on the southwestern-most end of the Eurasian plate (Amorim et al., 2017; Viveiros et al., 2017). The islands are surrounded by narrow shelves which make up a total area of 1500 km^2. An estimate from Vasquez et al., 2017, suggests that half is composed of rocks and a third composed of mixed sediment (Vasquez et al., 2015).

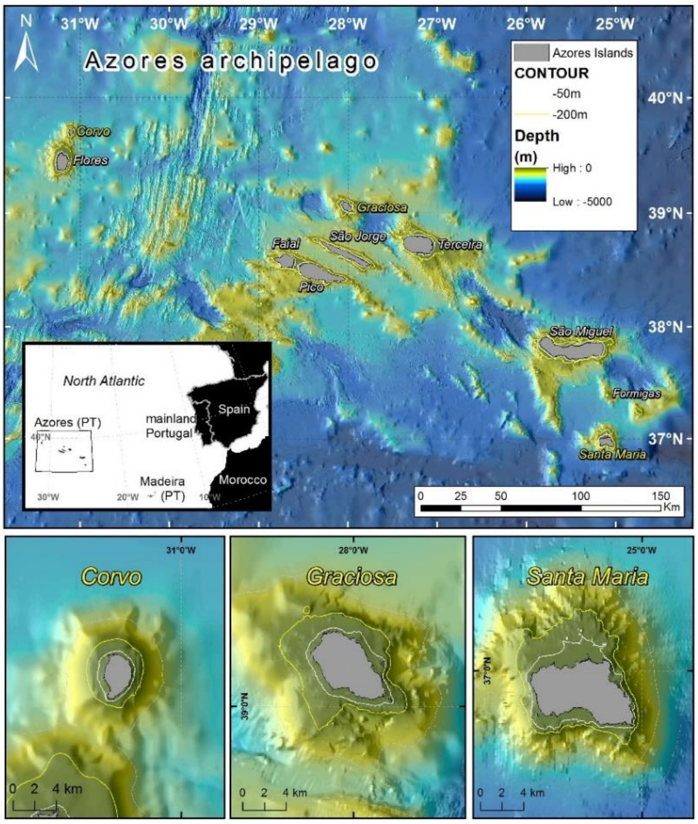


Figure 1. Location of the Azores islands (up) with a close view of (bottom, left to right) Corvo, Graciosa and Santa Maria islands. Sampling area is encompassed between both solid lines contouring the islands.

From this, the shelf area of an island per group was sampled. Starting from Corvo island, it is the smallest and western most island of the archipelago (on the American plate) where the insular shelf ranges between 39º45'30" – 39º39'0" N and 31º10'0" – 31º3'30" W; Graciosa, from the central group, comprises the northern most island, located on the Terceira Rift, and presents a shelf area encompassed between 39º8'30" – 38º58'0" N and 28º7'0" – 27º54'30" W; and Santa Maria, the most eastern and southern island located below this rift, with a shelf area ranging from 37º5'30" – 38º54'0" N and 25º13'0" – 24º59'30" W (retrieved from nautical charts of the hydrographic institute).

2.2 – SURVEYS

Several scientific projects regarding the mapping and description of the continental shelves' biotopes of the islands Corvo (western group), Graciosa (central group) and Santa Maria (eastern group) were performed during the summers of 2016, 2017 and 2018 (BALA project on August and September, 2016 and on June, 2017; Blue Azores expedition and PLATMAR – unpublished data – on June, August and September, 2018). We chose to analyse rocky and mixed substrates benthic circalittoral habitats. The islands Corvo and Santa Maria had data collected both in 2016 and 2018 while Graciosa was only sampled in 2017.

A RUV (remote underwater video) structure was specifically developed for benthic habitat video surveying. This comprised a stainless-steel structure holding a light and a waterproof housing containing a battery-operated video camera (Fig. 2) (Zarco-Perello & Enríquez, 2019). To ensure a vertical position (and easy visual location), a float was holding the structure by a rope while another rope was connecting the camera edge of the structure to a stone. Depending on the mission, the system was deployed with a GoPro3+ or a GitUp2 which was mounted at a distance of 85 cm (Graciosa survey 2017), 95 cm (Corvo and Santa Maria surveys 2018) or 2 m (Corvo and Santa Maria survey 2016) from the seafloor and was oriented with an angle varying between 45º and 90º to the seafloor.

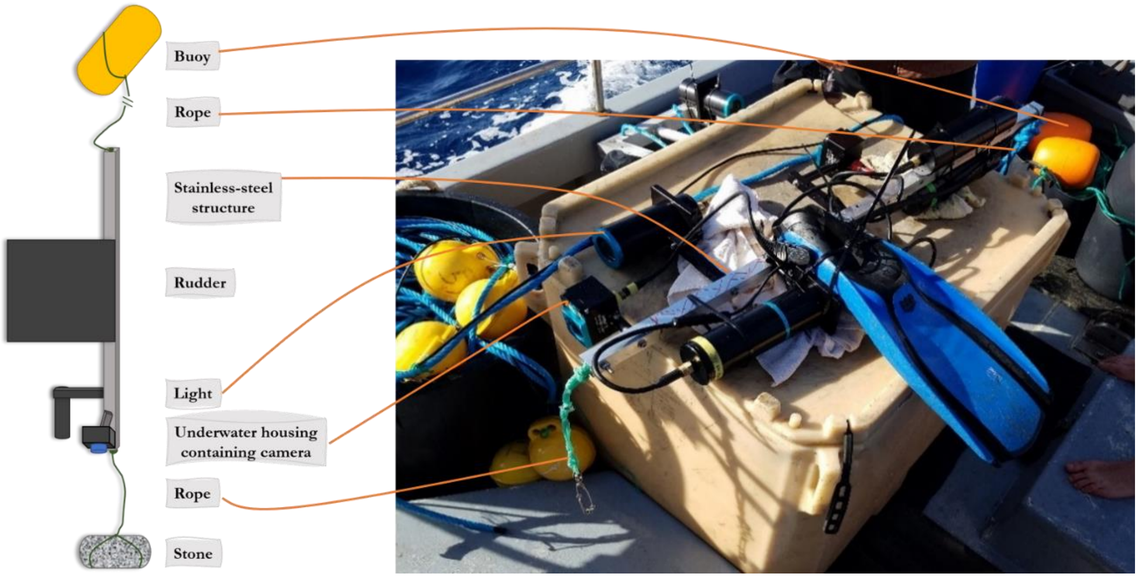


Figure 2. Illustration of the RUV system. (left) a representation of the standard system used; (right) example of a more complex system used during Blue Azores expedition in 2018. This comprised other components, as a Top Camera used to have a wider perspective of the habitats analyzed.

The RUV was deployed from a boat in several stations per island in every sector direction following perpendicular lines to the coast (radials) (Fig. 3). In each of those radials, the RUV was deployed at six different depths: 50, 80, 110, 140, 170 and 200 m. All deployments were done in consecutive days in a given island/year.

Whenever echosounder revealed the required depth, the structure would be deployed, manually or by a winch, followed by the annotation of the GPS coordinates. The RUV was then dropped down to the seafloor from a few seconds to minutes and hauled back. From the moment of bottom, the camera would usually describe some rotation. Also, the boat was left to drift while the RUV was on the sea bottom, typically covering a distance between 5 and 10 meters.

As in PLATMAR long video transects were performed and encompassed various sampling depths, the moments (few seconds to minutes) matching those depths were determined using the programme ArcGIS.

GPS coordinates corresponded to the boat position.

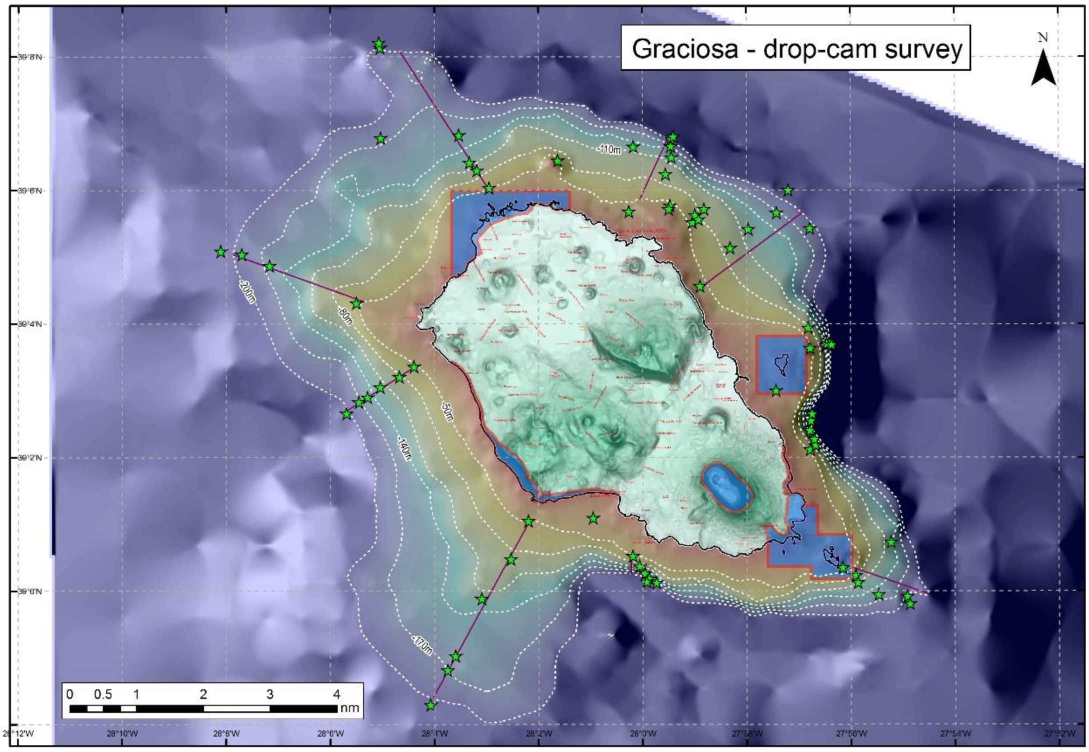


Figure 3. Illustration of the sampled stations (stars) along radials (lines) in the Graciosa Island survey in 2017. Blue boxes represent marine protected areas (MPAs).

2.3 – VIDEO ANALYSIS

2.3.1 – PRE-PROCESSING: DATA GATHERING AND CLEANING

After each expedition, all videos were stored as MP4 files and an Excel file created to contain all the metadata of the videos. These files comprised video ID, date, time, island, radial/site/area, GPS, depth and overall bottom type. Prior to video analysis, we checked if all videos had the correspondent GPS and time data so that all data could be used in the same analysis or if there was a need for some modifications. Thus, all usable data from all video parts (since each video could contain several drop videos) of the several projects was compiled in a new Excel file, such as the time range of each useful parts.

2.3.2 – POST-PROCESSING

In order to associate the videos to their position and time information compiled in the previous step, we chose to use the programme OFOP (Ocean Floor Observation Protocol). The first step lied on making a _posi file (a .txt file for OFOP to recognize the coordinates, in decimal degrees, for each moment of the video) with the coordinates and the time for each video. Then, the programme would smooth and spline the GPS data given in the posi file creating a file with GPS coordinates for each second of video. By overlaying the GPS and time data on the video, the programme enabled the desired annotation combined with the georeferenced data.

All videos were fully screened several times.

2.3.3 – ANNOTATION

Organisms observed on the videos were annotated in an Excel spreadsheet as morphotypes. Reliable taxonomical identification was deemed impossible because image quality was insufficient to show diagnostic details and knowledge of the circalittoral fauna of the Azores is still incomplete.

Identified biota were mostly sessile and vagile benthic organisms including algae, echinoderms, polychaetes, bryozoans, sponges, bivalves, cnidarians that were grouped into morphological types using criteria like broad taxa, prominence and size (a proxy of vulnerability to physical damage) and external features like colour and shape.

Annotation typically started by the observer noting down substrate characteristics and summarizing the list of organisms observed during the first overall view of the bottom, which generally lasted less than a minute depending on the time spent at bottom and the camera drift and rotation rate.

After this initial list, the first appearance of every morphotype (and species) would be noted down and the list of occurring species would be updated as species disappeared throughout the transect or their abundance changed.

The abundance scale comprised seven levels representing the number of individuals or percentage of coverage, which were consistent with the SACFOR scale (Tab. 1).

Table 1. Description of the abundance scale levels and the correspondent SACFOR level. Coverage was used for most of the levels as it was easier to apply at sampling all organisms on the videos.

Abundance levels	Density/Coverage	SACFOR level
1	1 or ≤ 1%	Rare (R)
2	unclear if there is one or two occurrences	Rare (R)
3	2% – 15%	Occasional (O)
4	16% – 25%	Frequent (F)
5	26% – 50%	Common (C)
6	51% – 65%	Abundant (A)
7	>65%	Superabundant (S)

Sampling morphotypes, i.e., morphological types, not only requires less effort than sampling species and generates less classification errors (some taxonomic groups cannot be identified without samples) as it can reveal important features of the habitats the organisms were found on (Althaus et al., 2013; Bertolino et al., 2013; Bo et al., 2014; Marzloff et al., 2018; Piazzi et al., 2019; Schönberg et al., 2014). For that, guidance was derived from morphotype guides as *CATAMI Classification Scheme for scoring marine biota and substrata in underwater imagery*, Althaus et al., (2013), for the general organisms; on Schöenberg and Fromont, 2014 for a larger range of sponges morphotypes; and two Azorean guides: the *Image Catalogue of Cold Water Corals of the Azores (Northeast Atlantic)* by Department of Oceanography and Fisheries, Centre of IMAR of the University of the Azores V.2, 2012 and *Sponge Catalogue of the Azores (Northeast Atlantic)* V. 0.02, IMAR-DOP/UAç 2012. All morphotypes and species were organized according to their taxonomical relationship based on the website WoRMS (http://marinespecies.org/).

The substrate type, was also based on CATAMI, Althaus et al. (2013), and two categories were used: rocky – substrate totally or predominantly composed of rock as long as the sediment layer didn't interfere with its colonization by rocky organisms; or mixed substrate – substrate in which sediment can compose >50% of the substrate, containing some boulders, cobbles or concretions (as in "Substrate: Unconsolidated (soft): Pebble / gravel", "Consolidated (hard): Cobbles" and "Consolidated (hard): Boulders", CATAMI, Althaus et al., 2014).

2.4 – PRE-STATISTICAL ANALYSES

2.4.1 – RAW AND COMPOSITIONAL DATA

Raw data comprised the one obtained through video annotation (2.3.3). A table with the relative frequency of occurrence of each morphotype per depth stratum per island and a histogram of the number of observations per depth strata were produced in order to provide an overall view of the data collected.

In order to produce community samples containing sufficient compositional information, raw observations were aggregated by 10 m depth classes. A median abundance score was computed per depth class for each morphotype from the semi-quantitative data. Morphotypes that did not attain an abundance at least 0.1 in at least one depth stratum were excluded from the analysis. Henceforth, depth strata were used as samples while morphotypes represented variables. Depth strata was taken as a morphotype quantitative assemblage (median semi-quantitative scores).

2.4.2 – ENVIRONMENTAL DESCRIPTORS

In addition to the compositional data, three environmental variables were used as descriptors of the stations: Depth, Seabed PAR (Photosynthetically Available Radiation) and Wave Base.

Depth was obtained for each station during the survey or, in the case of long transects, derived from the best bathymetry available for the area. This comprised multibeam bathymetry at 20m resolution for the islands of Santa Maria and Flores; and a 100m-resolution grid extracted from the EMODNET Bathymetry portal for Graciosa. Replaced by a grid interpolated from nautical chart isobaths and significant bathymetry points in a sector of the island where the EMODNET grid presented a major vertical bias.

Seabed PAR represents the amount of radiation that reaches the seabed. It was computed using climatologic PAR and KdPAR information extracted from the EMODNET Seabed Habitats portal and the best depth estimate for each observation point.

The Wave Base represents the maximum depth at which swell action impinges the seabed. It was computed using climatological wave data modelled under project EasyCo.

Concordant with EUSeaMap, the quotient of wave length and depth, defined as wave base ratio, was adopted.

2.5 – STATISTICAL ANALYSES

This section tackles two analyses: (i) an initial one where the thresholds that delimit the Azorean circalittoral partitions (biological zones) are investigated based on morphotype distribution patterns, and (ii) a subsequent multivariate analysis aiming to investigate whether the vertical partitions hence delimited enclose distinct species assemblages.

2.5.1 – EXPLORATORY ANALYSIS OF MORPHOTYPES DISTRIBUTION PATTERNS: DEFINING PARTITIONS THRESHOLDS

2.5.1.1 – MORPHOTYPES' RANGES PER VARIABLE

For each variable, all morphotypes (except for those present at one sole value) were represented in a 'high-low-close' graph using the maximum and minimum values of their distribution along the variable, referring to the raw data. Morphotypes' resulting distributions were ordered by their first appearance (from here until 3.1.3, included). This representation aimed to find groupings of morphotypes and variable-induced thresholds that could reflect the influence of the variables on the organisms.

2.5.1.2 – TRANSITION POINTS PER VARIABLE

In order to better visualize variable-induced thresholds, those associated to the disappearance and appearance of a notable number of organisms along an abiotic variable, horizontal stacked bar graphs were produced. For that purpose, the starts and ends of the distributional data of the morphotypes' ranges were organized in levels created for each variable: depth was organized by 10 m strata, seabed PAR by levels of 0.1 mol. phot. m^{-2} d^{-1} and exponential (10^{x}) and wave base ratio by WBR = 0.1.

2.5.1.3 – OPTIMAL DEPTHS

The last two relative abundance levels of the scale (6 and 7) were obtained from the raw data and used to plot aggregations (the highest abundance level) of each morphotype along the three abiotic variables studied, in 'high-low-close' graphs.

Unlike the previous topics, the morphotypes distributions were ordered according to their average value since that is the most probable value where the aggregations can be found.

2.5.2 – MULTIVARIATE ANALYSIS: ASSESSING THE DISTINCTNESS OF PARTITIONS' ASSEMBLAGES

A Hierarchical Clustering analysis (HC) followed by an Analysis of Similarities (ANOSIM) were performed to identify statistically significant groups of samples characterized by similar morphotype composition. Similarity Percentage (SIMPER) was then performed to assess which morphotypes explained the similarity between each groups' samples and the dissimilarities between the groups. All analyses were performed on the statistical package PRIMER based on Clarke & Gorley, 2006, *PRIMERv6 User Manual Tutorial* and on Yim & Ramdeen, 2015, *Hierarchical Cluster Analysis Comparison of Three Linkage Measures and Application to Psychological Data* for the HC.

A Bray-Curtis similarity matrix was computed from the semi-quantitative (abundance) compositional data mentioned above. There was no need to perform any data transformation.

2.5.2.1 – SORTING OF THE BIOLOGICAL ASSEMBLAGES (HC)

A hierarchical clustering of the samples was performed using the Bray-Curtis similarity matrix and a Group Average linkage. The latter option was used since it provides a more accurate evaluation of the distance between clusters (compared to single and complete linkage) through averaging all distance values between pairs of samples from different clusters. A cut-off was added to the dendrogram in order to mark the ideal stopping point of grouping the samples.

2.5.2.2 – ASSESSING THE SIGNIFICANCE OF THE ASSEMBLAGES' GROUPS PRODUCED (ANOSIM)

A factor "Depth Groups" was created by grouping the samples according to the resulting clusters from the cut-off point. Then, a one-way ANOSIM analysis was performed on the aggregation factor, through the similarity matrix, with maximum of 999 permutations (providing a significance level of $p<0.1\%$).

2.5.2.3 – MORPHOTYPES CHARACTERIZING BIOLOGICAL ZONES (SIMPER)

A one-way SIMPER analysis was applied to the factor using the raw data matrix and the Bray-Curtis similarity measure. A 90% cut-off was used meaning that the results list only the variables most contributing to the group until the cumulative percentage of contribution reached 90%. Only morphotypes contributing with percentages of order of magnitude ≥ 1 were used to explain the similarity within group and between each pair of groups.

3 – RESULTS

3.1 – EXPLORATORY ANALYSIS OF MORPHOTYPES DISTRIBUTION PATTERNS: DEFINING PARTITIONS THRESHOLDS

3.1.0 – Raw Data Analysis

Occurrences predominate in Santa Maria Island, mostly at [-40, -50[; [-70, -80[; [-80, -90[; [-100, -110[; [-110, -120[; [-130, -140[and [-140, -150[depth strata (Tab. 2). Corvo island has more occurrences at [-50, -60[; [-60, -70[; [-90, -100[; [-120, -130[; -170, -180[and [-200,-210[depth strata and Graciosa is the island with less occurrences, being the only island with occurrences at [-210, -220[m. Only some depths present occurrences for the three islands: from -60 m to -80 m, at [-120, -130[, at [-150, -160[and from -170 to -190 m.

Table 2. Relative Frequency of Occurrences per Sampled Depth Strata per Island.

DEPTH STRATA	CORVO	GRACIOSA	SANTA MARIA
[-40,-50[	0.00	0.02	0.98
[-50,-60[	0.71	0.00	0.29
[-60,-70[	0.76	0.04	0.20
[-70,-80[	0.04	0.01	0.95
[-80,-90[	0.05	0.03	0.92
[-90,-100[	0.91	0.00	0.09
[-100,-110[	0.18	0.00	0.82
[-110,-120[	0.00	0.00	1.00
[-120,-130[	0.50	0.29	0.21
[-130,-140[	0.00	0.00	1.00
[-140,-150[	0.00	0.00	1.00
[-150,-160[	0.34	0.06	0.60
[-160,-170[	0.36	0.00	0.64
[-170,-180[	0.67	0.02	0.32
[-180,-190[	0.35	0.04	0.62
[-190,-200[	0.33	0.00	0.67
[-200,-210[	0.79	0.00	0.21
[-210,-220[	0.00	1.00	0.00

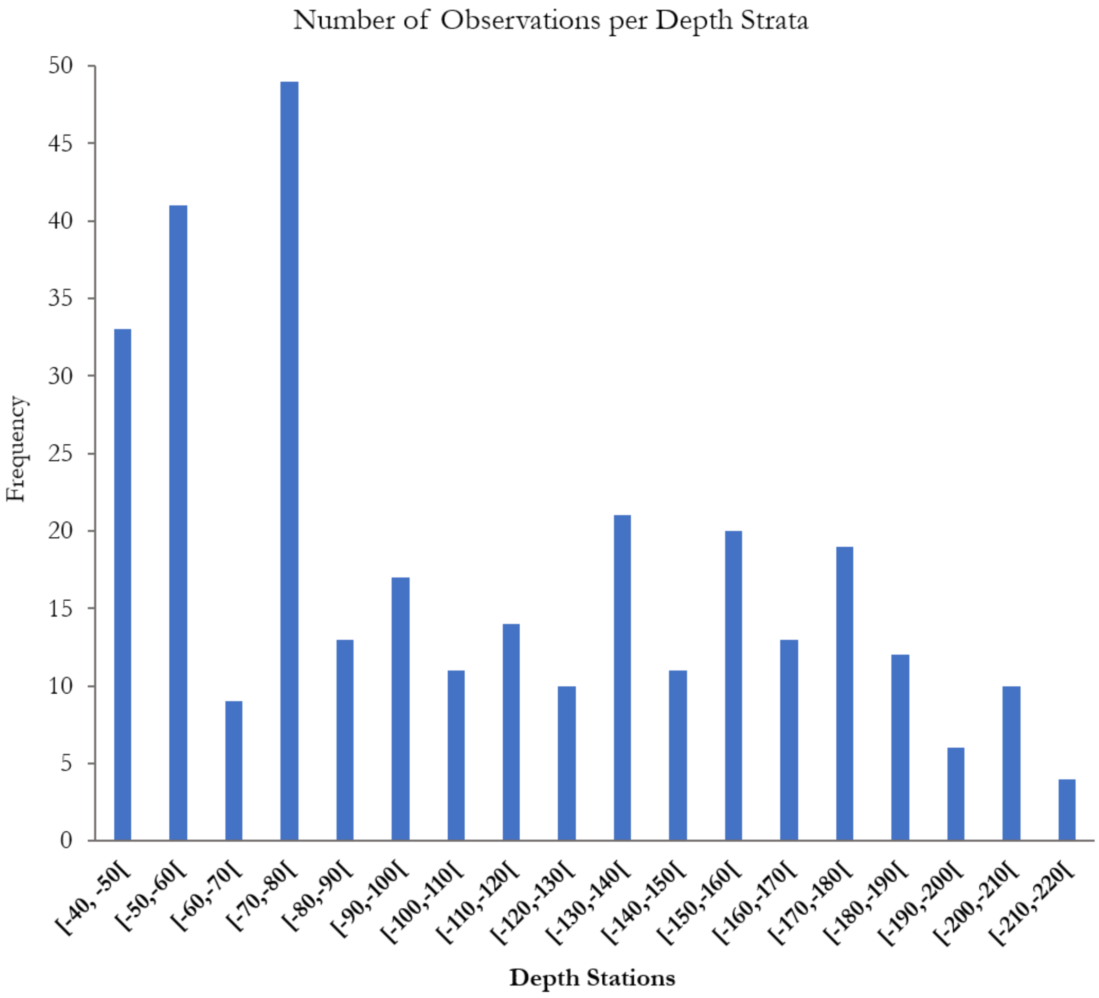
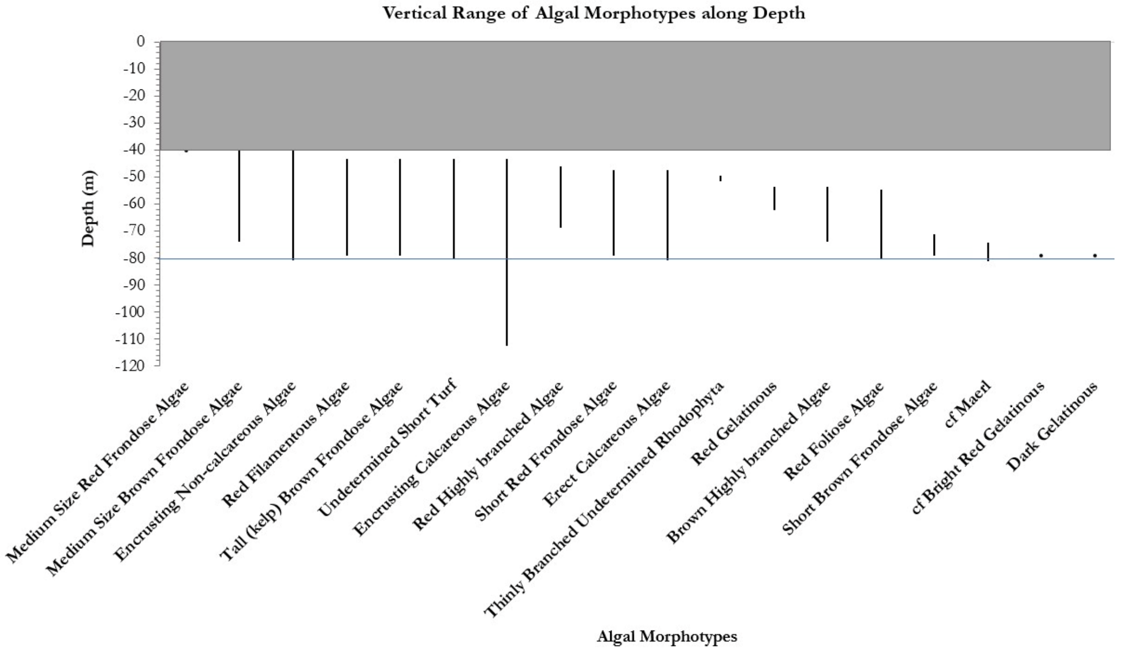


Figure 4. Overall number of observations per 10 m depth stratum.

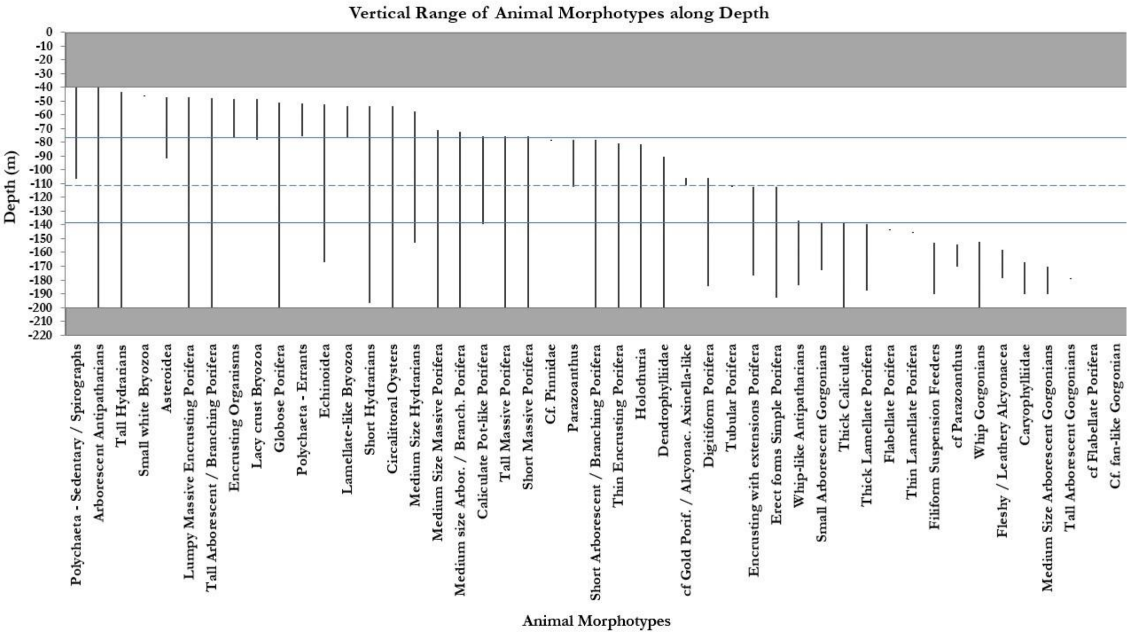
The histogram presented in Fig. 4 shows a disproportionate number of samples in the -40, -50 and -70 m depth strata. The depths -130, -150 and -170 m have around 20 observations while all the other depths range from ~5 to ~15 observations. The -190 m and -210 m strata are the least sampled ones.

3.1.1 – MORPHOTYPES' DISTRIBUTION RANGES & TRANSITIONS

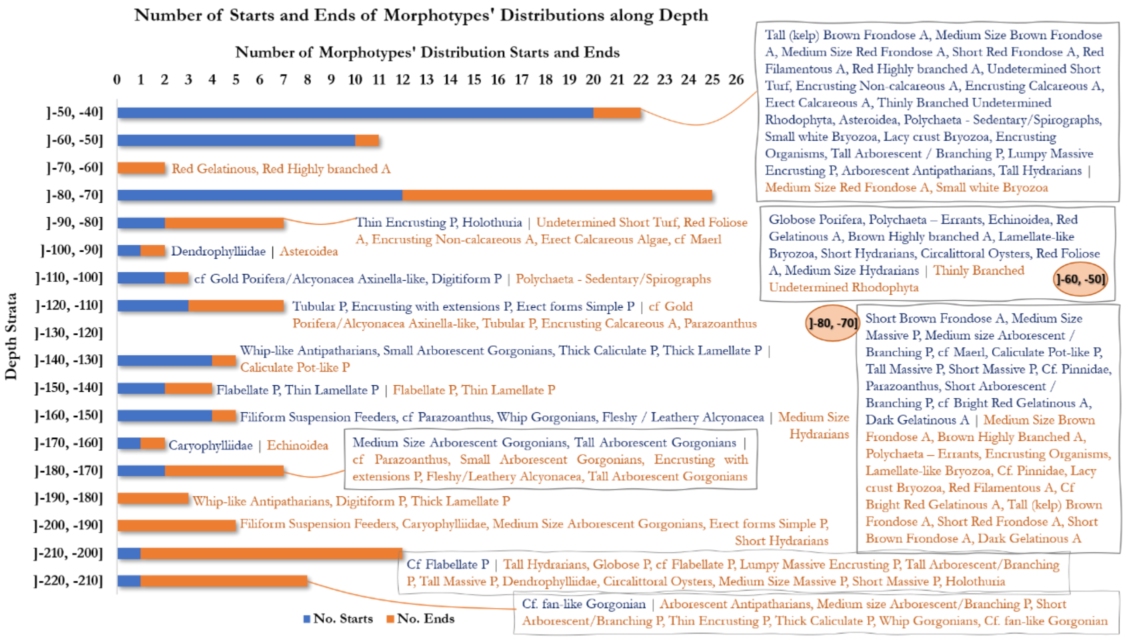
Depth



(a)



(b)



(c)

Figure 5. Morphotypes' distribution along depth illustrated by morphotypes ranges (a,b) and by the number of morphotypes appearing (start) and disappearing (end) per depth stratum (c). (a,b) Solid blue lines represent more likely biological thresholds than those represented by dashed ones, discussed in the text. Depths in the grey areas (> -50m and < -200m) were scarcely sampled and beyond the sampling scope so no distribution interpretations are sanctioned. (c) The morphotypes which make up the bars are written next to them in the correspondent color. 'A' is the abbreviation of 'Algae' and 'P' of 'Porifera'. Orange curve lines connect descriptions to bars except for the descriptions of]-60, -50] and]-80, -70] which are indicated by an orange circle instead. Nor this nor the boxes represent any sort of highlighting of the information (applicable to the following figures).

The plots of the morphotypes distributions (Fig. 5) demonstrate how the occurrence of most species is restricted to more or less limited depth ranges and highlights how multiple species appear or disappear at similar depths (biological zones' thresholds).

The majority of erect sciaphilic algal morphotypes disappeared around -80 m (Fig. 5a), including tall (kelp) brown frondose Algae and red foliose Algae (Fig. 5c). Only encrusting calcareous algae subsisted down to 110 m depth. A few animal morphotypes (e.g., lacy crust bryozoans, errant polychaetes) seemed to be restricted to these shallower depths as well.

A second group of organisms appears between the first depth and -110 m (sole dashed line of Fig. 5b) and includes some suspension feeders with a broad vertical range as thin encrusting and digitiform Porifera, Holothuria and Dendrophyllidae. Alongside, a group of organisms disappears, around 110 m depth, including encrusting calcareous Algae, Asteroidea (seastars), *Parazoanthus* and cf. gold Porifera/Alcyonacea Axinella-like.

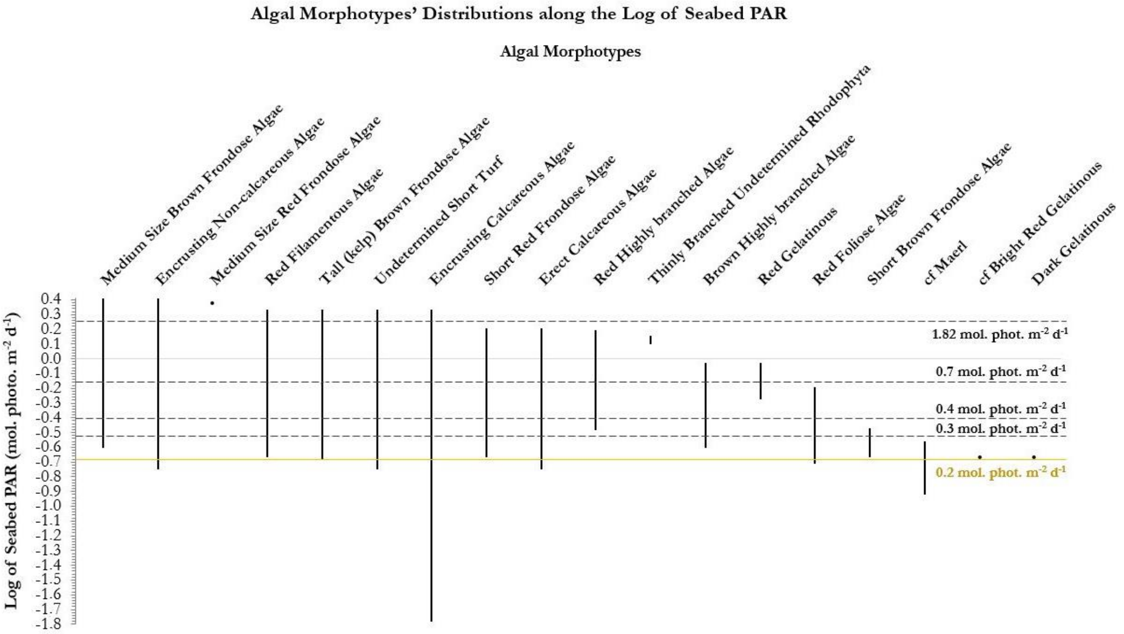
Around -140 m, after the appearance of encrusting with extensions and erect simple forms Porifera (around 110 m depth), a group of organisms dominated by erect Porifera and Alcyonacea appears, including those presenting fragile forms as medium size arborescent gorgonians, thick caliculate and lamellate Porifera, whip-like Antipatharia and gorgonians; alongside the scleractinian Caryophylliidae. These tend to disappear until -190 m, though thick caliculate Porifera and whip gorgonians extend past -200 m. Additionally, some organisms that showed particularly broad vertical distributions, as arborescent and massive Porifera, encrusting Porifera, circalittoral oysters, Holothuria and Dendrophylliidae, extended until this depth.

Although a great number of organisms appears at]-60, -40] m as well as a notable number disappears around]-220, -170] m (Fig. 5c), only at]-80, -70] m a great number of both disappearances and appearances is verified. This level makes up the largest bar length of all the plot and includes disappearances of, mostly, erect algal morphotypes (e.g., tall (kelp) brown frondose algae, again, but not red foliose algae) alongside the appearance of erect suspension feeders, mostly sponges.

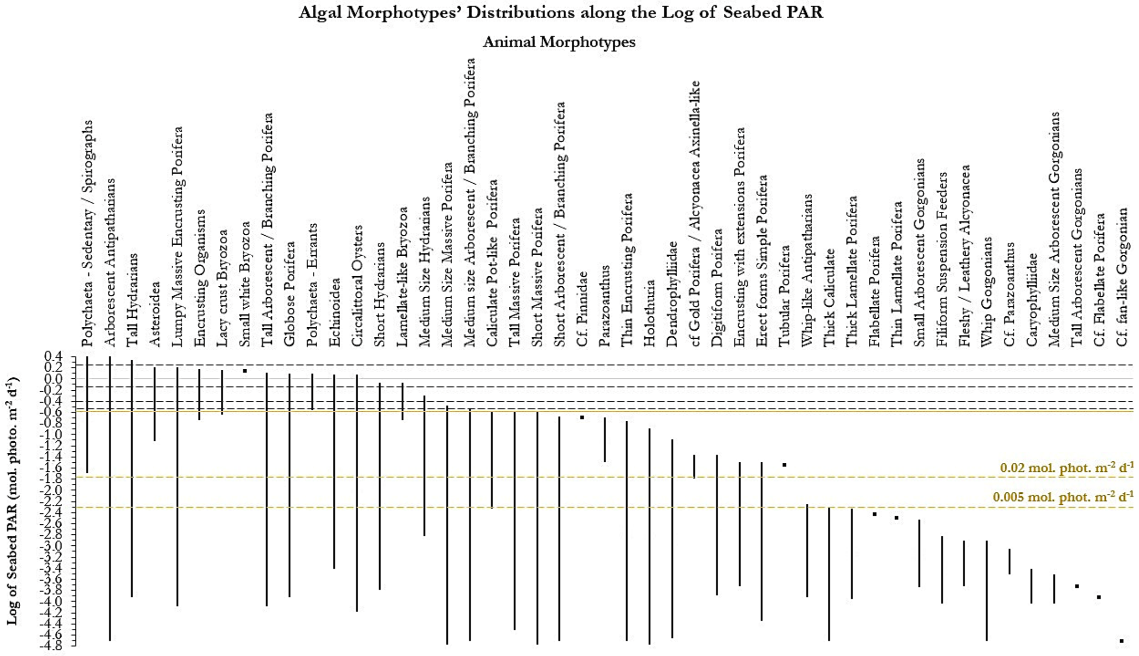
Hereafter, only animal morphotypes appear and disappear (except for the algal ones disappearing at]-90, -80] m and]-120, -110] m), mostly sponge ones, and the number of starts and ends seems less dissimilar until]-180, -170] m. From there, the number of ends surpasses the number of starts and there are, again, starts and ends composed of only suspension feeders: mainly erect Porifera and hard gorgonians.

Light at Seabed

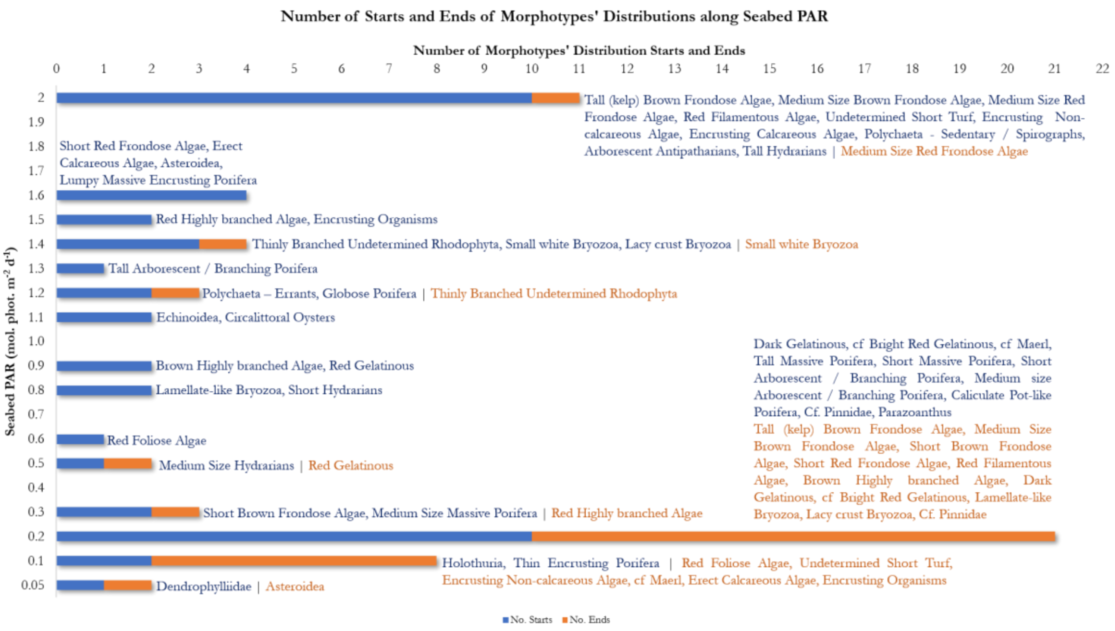
Representing organisms' distribution range by PAR level permits investigating the vertical location of light-induced thresholds such as the lower infralittoral/shallow circalittoral transition.



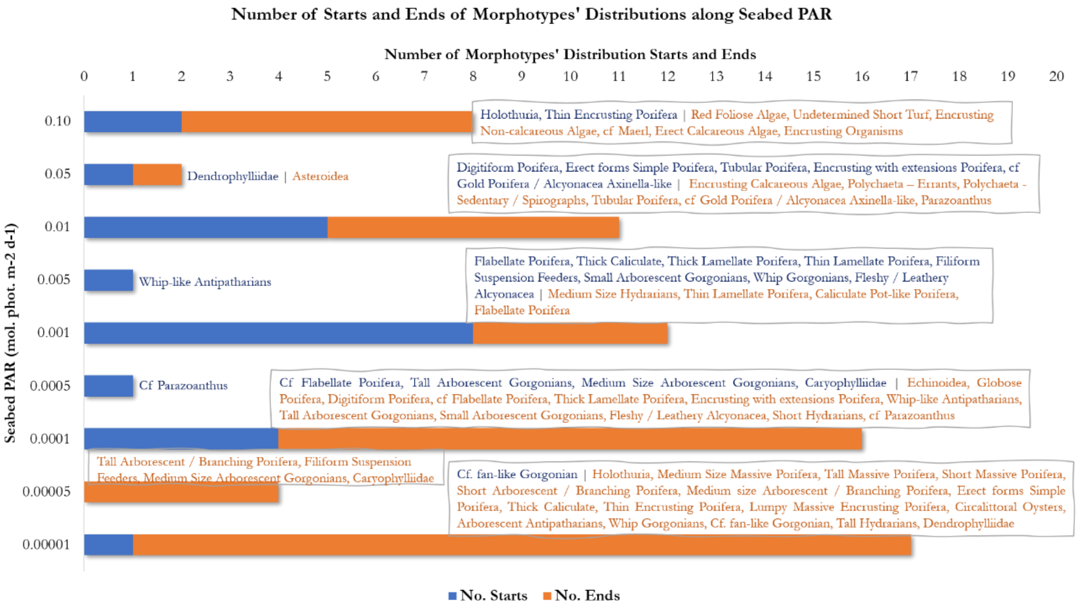
(a)



(b)



(c)



(d)

Figure 6. Morphotypes' distribution range along a light gradient (PAR) at the seabed illustrated by morphotypes ranges (a,b) and by the number of morphotypes appearing (start) and disappearing (end) at each level of PAR at the seabed (c,d). (a,b) Morphotypes are distributed across the logarithm of seabed PAR. Dashed black lines represent various PAR-based thresholds: upper black dashed line at y=0.26 corresponds to 1.82 mol. phot. m^{-2} d^{-1}, the boundary used for the Mediterranean, followed by y=-0.15, corresponding to 0.7 mol. phot. m^{-2} d^{-1}, the threshold used for Arctic (excluding Iceland), Iberia, Biscay, Macaronesia (IBM), Greater North Sea and Celtic Seas (GNCS); at y=-0.40 corresponds to 0.4 mol. phot. m^{-2} d^{-1}, the Azores Islands threshold; and the lower, at y=-0.52, to 0.3 mol. phot. m^{-2} d^{-1}, the one for Canary Islands. Dashed yellow lines represent probable threshold values for the present distribution. (c,d) transition graphs with seabed PAR organized by 0.1 PAR levels (c) and by exponential values (10^x) and their intermediate value, starting at 0.01 PAR (d). Morphotypes which make up the bars are written next to them in the correspondent color.

The plots of the morphotypes distributions (Fig. 6) illustrate, once more, the occurrence of most species is restricted to more or less limited light ranges and highlights how multiple species appear or disappear at similar light levels, possibly delineating biological zones' thresholds.

Horizontal dashed black lines indicate the literature-based thresholds marking the end of the infralittoral zone and the beginning of the upper circalittoral for several regions defined based on seabed PAR. However, these values don't seem to be associated to a notable number of organisms appearing and disappearing (Fig. 6a, b, c) at those levels (transition values) that build up a specific group.

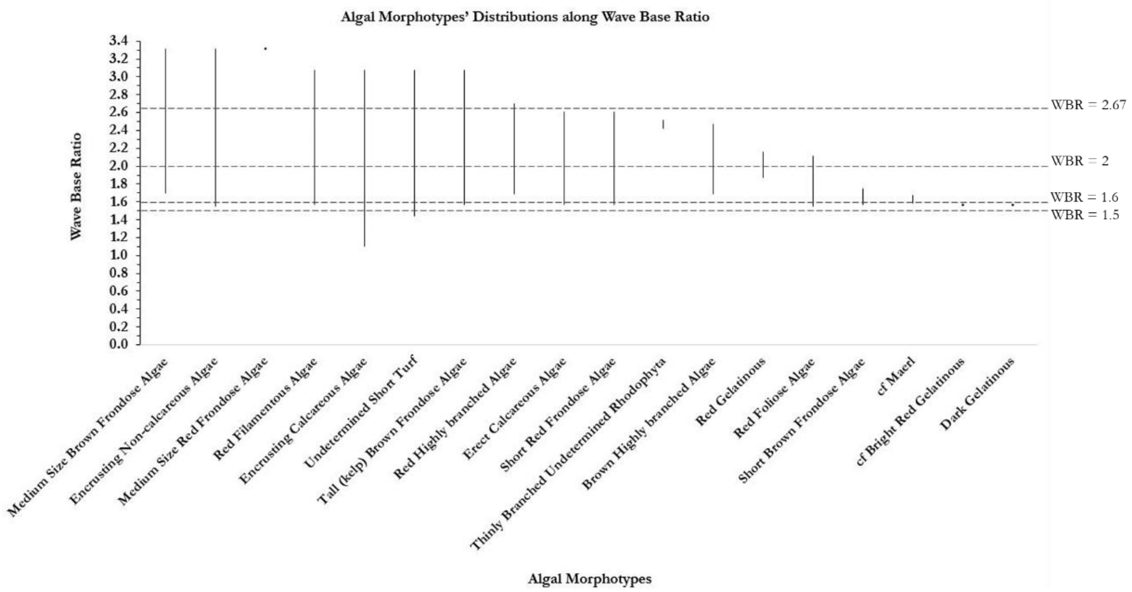
Until 0.2 mol. phot. m^{-2} d^{-1}, few algal species disappear compared to the great number of appearances (Fig. 6a, c). At that value, however, most sciaphilic algae disappear, including tall (kelp) brown frondose algae but not red foliose algae (disappearing right below it), alongside animals belonging to Bryozoa and Polychaeta. Hereafter, encrusting non-calcareous and calcareous algae (including cf maërl) persist but only the later extends until 0.02 mol. phot. m^{-2} d^{-1}. Additionally, only animal morphotypes, specifically, erect Porifera, appear at this value (Fig. 6 b, c, d). Together with the ones appearing thereafter until 0.02 mol. phot. m^{-2} d^{-1}, a group of suspension feeders with erect arborescent forms prevails, including short arborescent/branching Porifera, *Parazoanthus*, thin encrusting Porifera, Holothuria, Dendrophylliidae, cf Gold Porifera/Alcyonacea and digitiform Porifera.

Following the disappearance of morphotypes such as Asteroidea, *Parazoanthus*, cf Gold Porifera/Alcyonacea and encrusting calcareous algae, an animal-dominated group of organisms remains nearly unchanged until around 0.005 mol. phot. m^{-2} d^{-1}, $y=-2.3$ (Fig. 6 b, d). From this point on, numerous morphotypes appear in sequence and displaying fragile forms, including, again, erect Porifera and arborescent gorgonians. Of those, only whip gorgonians and thick caliculate Porifera alongside some long range morphotypes extend until the last light values for the seabed, as described in the previous topic.

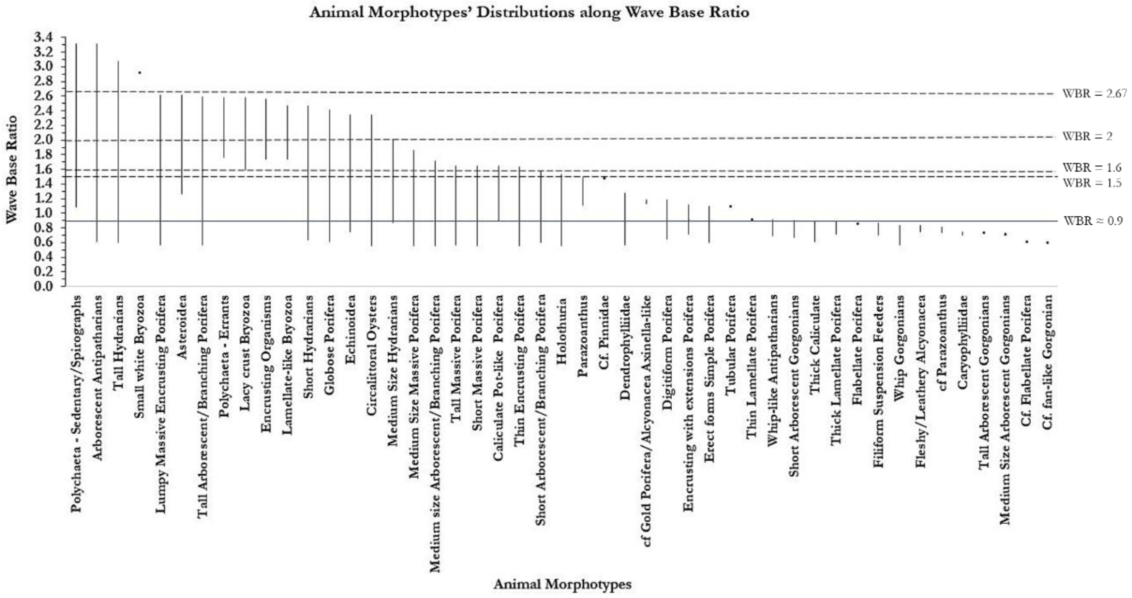
The greatest number of morphotypes appearances lies both at 2 mol. phot. m^{-2} d^{-1} and 0.2 mol. phot. m^{-2} d^{-1} while the largest number of disappearances lies below 0.0005 mol. phot. m^{-2} d^{-1} ($y<-3.3$), followed by 0.2 mol. phot. m^{-2} d^{-1} (Fig. 6). Yet, at seabed PAR equal to 0.2 mol. phot. m^{-2} d^{-1}, major numbers of appearances and disappearances are combined, forming the widest bar length of all levels (Fig. 6c).

Wave Base

Representing the organisms' distribution range along a wave base ratio gradient permits investigating the vertical location of swell-induced thresholds such as the transition from the (lower) shallow circalittoral zone to the deep circalittoral zone.



(a)



(b)

(c)

Figure 7. Morphotypes' distribution range along a wave base ratio gradient represented by morphotypes ranges (a,b) and by the number of morphotypes appearing (start) and disappearing (end) at each wave base ratio level (c). Dashed black lines indicate the wave base ratio (WBR) for various regions: at y=2.6 the threshold for the Iberian Peninsula, at y=2 for GNCS, at y=1.6 representing a depth of 80 m for Azores Islands and Bay of Biscay, from Santander to La Coruña) and at y=1.5 also for Bay of Biscay, from the French coast until Santander. Solid line represents probable threshold value for the present distribution. (c) transition graph with WBR organized by 0.1 levels. Morphotypes which make up the bars are written next to them in the correspondent color. Again, the circles indicate the level those organisms are associated to.

The plots of the morphotypes distributions (Fig. 7) hardly illustrate the occurrence of numerous species is restricted to more or less limited wave base ratio ranges as well as they don't seem to highlight multiple species appearances or disappearances at similar wave base ratio levels.

The number of organisms appearing across the wave base ratio does not seem to change significantly, i.e. numerous organisms don't seem to be restricted to particular levels (Fig. 7c), except for WBR = 0.8, eventually, where fragile organisms appear, including diverse erect sponges and whip gorgonians. In contrast, the number of disappearances seemed more concentrated at WBR = 1.5 and below WBR = 0.8. The first included mostly erect algae and associated Bryozoa, while after WBR = 0.8, diverse groups of animals disappear, including long range (Fig. 7b) arborescent antipatharians, Echinoidea and lumpy Porifera; and those restricted to lower values, as fragile gorgonians and sponges. Despite WBR = 1.5, no other previously established threshold (dashed lines at Fig. 7a & b) displayed prominent numbers of appearances and disappearances of organisms.

From the algal dominated levels, solely encrusting calcareous algae and spirographs extend until around WBR = 1.1 and, henceforth, only animal organisms persist. Right below, at WBR = 1.0, erect and tubular Porifera join other suspension feeders as erect massive and arborescent Porifera, hidrarians, *Holothuria* and Dendrophylliidae (Fig. 7b, c). Around WBR = 0.9, fragile Porifera and Alcyonacea morphotypes dominate, such as lamellate and caliculate Porifera and diverse gorgonians. Both animal stages were restricted to considerably smaller ranges compared to those of organisms as algae, hydrarians, massive and arborescent Porifera, circalittoral oysters and Echinodermata.

3.2 – MULTIVARIATE ANALYSIS: ASSESSING THE DISTINCTNESS OF PARTITIONS' ASSEMBLAGES

3.2.1 – SORTING OF THE BIOLOGICAL ASSEMBLAGES (HC)

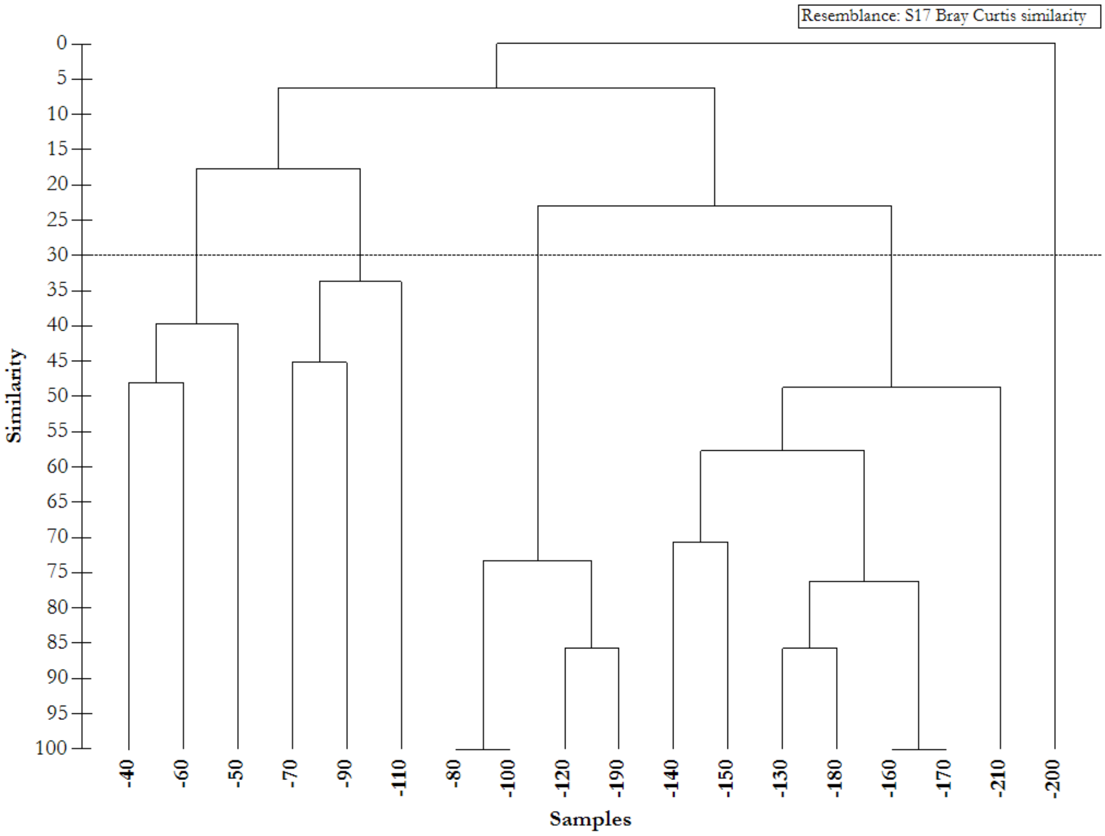


Figure 8. Dendrogram hierarchically clustering biological assemblages (each depth) of combined data by a 10 m depth interval. Dashed black line indicates cut-off point. Clustering method: Group Average. Similarity index: Bray-Curtis.

The sorting of the assemblages (samples) aimed to assess the similarity between them in order to produce clusters (Fig. 8) that, possibly, represented different communities (and, thus, reflected different biological zones). For that purpose, a 30% similarity was chosen as the cut-off point and so four major groups arose alongside a sole sample (-200 m). The first group combines the shallowest assemblages/samples of this work: -60, -50, -40; the second, some of the following in the depth profile: -110, -90, -70; the third a heterogenous group: -190, -120, -100, -80; and the fourth most of the deepest assemblages: -210, -180, -170, -160, -150, -140, -130. These groups constitute the factor "Depth Groups". Furthermore, the deepest assemblages display higher similarity levels compared to the other groups, including 2 pairs with 100% similarity (-100 and -80; -170 and -160).

3.2.2 – ASSESSING THE SIGNIFICANCE OF THE ASSEMBLAGES' GROUPS PRODUCED (ANOSIM)

The ANOSIM statistical test, R, meant to test if the groups' biological assemblages (created in 3.2.1) differed significantly so that it could be statistically proven they constitute different communities.

The ANOSIM test allowed rejecting the null hypothesis that there are no differences between the biological assemblages of the four groups due to the very large R value of 0.9 (close to 1: all dissimilarities between assemblages of different groups are larger than any dissimilarity among samples within either group), at a significance level of $p<0.001$. Additionally, all pairs of groups proved to be greatly dissimilar by displaying R values equal or higher than 0.88, with $p<0.05$ (except for pair 1 & 2, $p<0.1$, which is not relevant as the R value is preferred for this analysis over the p value).

3.2.3 – Morphotypes characterizing biological zones (SIMPER)

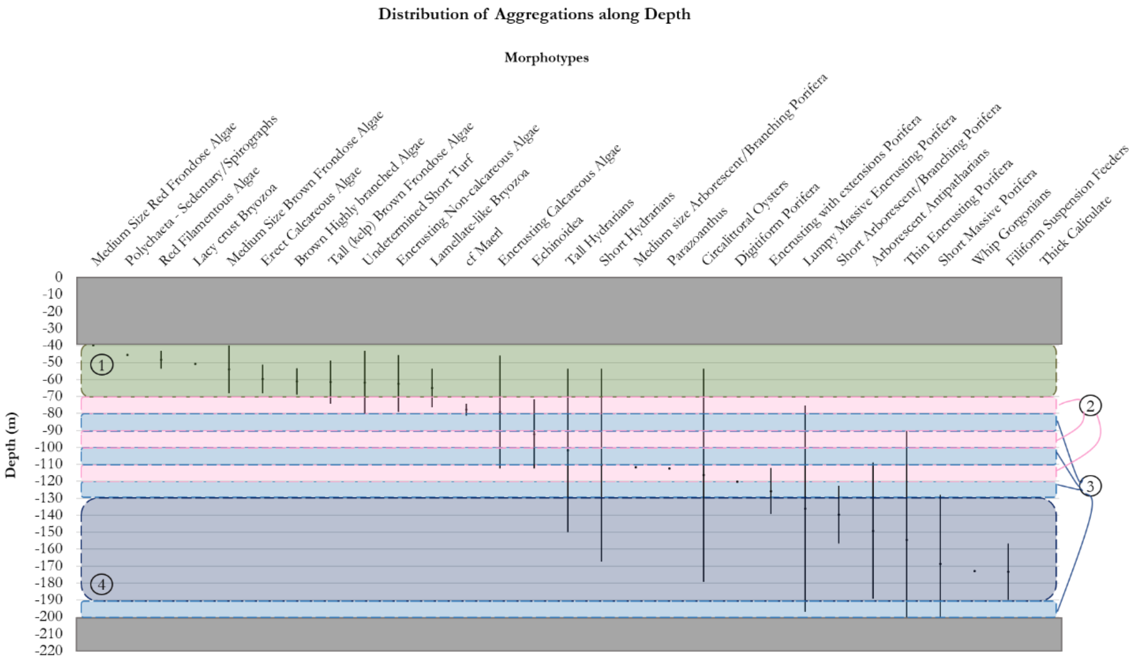


Figure 9. Optimal depths for each morphotype illustrated by the range of aggregations (classes 6 and 7 of the relative abundance scale) along depth. The vertical lines represent the depths at which aggregations of a given morphotype are likely to be found, given the maximum and the minimum depths of its distribution. The colored blocks contoured by dashed lines (from up to down): green, pink, light blue and dark blue, indicate the depth strata composing each group of assemblages and illustrates the SIMPER results. Gray areas represent non-surveyed depths.

A one-way SIMPER analysis enabled discriminating which morphotypes mostly characterized each group of biological assemblages as well as how much was their contribution to both the group similarity and the dissimilarity between pairs of groups. The SIMPER outcome was compared with the optimal depth ranges of the morphotypes (depths at which the morphotypes are highly abundant), so that the communities could be better assessed as they are mostly defined by characteristic species (those that are abundant or conspicuous in the community).

Out of the four groups, the last two showed high average similarities (within group) and the first two groups didn't present very low average similarities (around 42 and 38%). Plus, the dissimilarity between pairs of groups was always greater than 70%. The first group was mainly characterized by erect medium size brown frondose algae followed by erect and encrusting calcareous algae which were highly abundant alongside other morphotypes of erect sciaphilic algae, including kelp and undetermined short turf, non-calcareous encrusting algae and animals, including Bryozoa, hydrarians and circalittoral oysters (Fig. 9). The second was mostly defined by the abundant encrusting calcareous algae and Echinoidea, together with other abundant animals as encrusting sponges, including lumpy and thin, circalittoral oysters and arborescent sponges and cnidaria. These were also accompanied by kelp and short turf, at upper depths. The third group included similar assemblages to the previous one (without erect algae), for upper depths, while, in lower depths, algae were no longer present and encrusting Porifera together with short erect Porifera and circalittoral oysters were the most abundant invertebrates. The fourth group was characterized by abundant lumpy and thin encrusting Porifera followed by the also abundant whip gorgonians, circalittoral oysters, various erect sponge forms, arborescent antipatharians and hydrarians.

Regarding the optimal depth ranges alone, animal morphotypes outnumbered algae morphotypes and had wider distributions. However, aggregations were present throughout the whole range of depths with wider ranges belonging to encrusting calcareous algae, circalittoral oysters, tall and short hydrarians, lumpy massive and thin encrusting Porifera, short massive Porifera and arborescent Antipatharia.

4 – DISCUSSION

4.1 – Circalittoral Limits

For all abiotic variables used, morphotypes' distributions reflected the existence of levels that separated groups of organisms, distinct in their biological characteristics. These characteristics referred, mostly, to either broad taxa (sciaphilic algae and suspension feeders) or morphological traits (as prominence, size and fragility). Thus, those segregating values found potentially represented biological zones thresholds. However, distinction must be done between these and both high values (on the top of the plots) associated to a lot of morphotypes' appearances and low values (on the bottom of the plots) associated to a great number of morphotypes' disappearances. Such values did not present significant numbers of both appearances and disappearances of morphotypes' distributions with different biological characteristics and were biased by sampling range and number of observations from 190 m.

Before the depth-wise profile analysis of the thresholds, it is important to underline some species characterizing the circalittoral zone (Angiolillo & Canese, 2018; Bertolino et al., 2013; de Matos et al., 2014; EUSeaMap, n.d.-a, n.d.-b; Piazzi et al., 2019; Tempera et al., 2013) were present not only as morphotypes with large ranges of distribution but also with large ranges of aggregations, mainly on the broad circalittoral zone. These include encrusting calcareous Algae, circalittoral oysters, tall and short hydrarians, lumpy massive and thin encrusting Porifera, short massive Porifera and arborescent antipatharians.

On a vertical profile, the amount of light reaching the seabed seemed to be the first environmental factor to induce a great segregation of organisms. From the morphotypes ranges along the seabed PAR gradient (Fig. 6), most erect sciaphilic algae disappeared around 0.2 mol. phot. m^{-2} d^{-1} which included kelp but not red foliose algae (disappeared right below the value) and preceded crustose algae and faunal communities. This is coherent with the literature's description for the transition infralittoral/shallow circalittoral. The literature thresholds, however, were not associated to a notable number of morphotypes appearances and disappearances nor were they consistent with the typical characteristics of this transition of biological zones. Thus, this work showed the boundary between the lower infralittoral and the upper shallow circalittoral for Azores Islands must lie at 0.2 mol. phot. m^{-2} d^{-1}, around 80 m depth, instead of at 0.4 mol. phot. m^{-2} d^{-1} as defined by EUSeaMap 2017 (Populus et al., 2017). Among all the literature thresholds, the other Macaronesia archipelago, the Canary Islands, holds the closest value to the present one (seabed PAR = 0.3 mol. phot. m^{-2} d^{-1}), which should be expected since they're located in the same biogeographical zone (Populus et al., 2017).

Additionally, wave base ratio also highlighted a transition value around WBR = 1.5, which coincides with the seabed light one, possibly, contributing for the evidence of this upper limit depths.

Following the disappearance of encrusting calcareous algae alongside Asteroidea, *Parazoanthus* and cf Gold Porifera/Alcyonacea, around 0.02 mol. phot. m^{-2} d^{-1}, an animal-dominated group of organisms remains nearly unchanged until around 0.005 mol. phot. m^{-2} d^{-1} (Fig. 6). Although not as conspicuous as the previously mentioned light boundary, this succession coincides with the literature's description of the lower shallow circalittoral: beginning at a depth at which a further reduction of seabed light does not allow for aggregations of encrusting calcareous algae to persist, and faunal communities prevail (EUSeaMap, n.d.-a; Evans et al., 2016). As so, the threshold between the upper and lower shallow circalittoral for the Azorean Islands should be found at a depth exposed to an amount of light of 0.02 mol. phot. m^{-2} d^{-1}, around 113 m depth.

While not strongly supported by light at the seabed or wave base, opposing the predictions (Evans et al., 2016; Populus et al., 2017), the morphotypes distributions seemed to highlight a transition around 140 m depth and WBR = 0.8 (Fig. 5 & 7). As wave base impinges negligible disturbance to the seabed at half of the wavelength, which would match values around WBR = 2 (by the wave base ratio formula: quotient of wavelength and depth) (Populus et al., 2017; Thurman & Trujillo, 1999), the potential transition level WBR = 0.8 cannot be considered (<<WBR=2) as a boundary value. Thus, the inherent stability resulting from the negligible effect of wave action didn't lead to fragile erect morphotypes to thrive, as laminar forms, opposing to simple and massive forms (associated to sedimentation) (Althaus et al., 2013; Clark et al., 2015; EUSeaMap, n.d.-b; Populus et al., 2017).

Such results could have arisen due to the enhanced thermal stability predicted to characterize the deep circalittoral zone (Bekkby et al., 2017; Boavida et al., 2016; EUSeaMap, n.d.-b; Evans et al., 2016; Kazanidis et al., 2019; Populus et al., 2017). This stability was predicted for the Azores islands to be around 150 m, after the maximum depths of the mix layer in winter (Amorim et al., 2017). Yet, this topic should be further addressed by distributing the morphotypes along a temperature gradient as should statistical modeling (GLMs) of all the variables be used to grasp the true extent of the variables' relationship to the morphotypes' distributional patterns.

Thus, from the present study, the Azorean broad circalittoral zone must extend from around -80 m to -200 m. The upper limit of the circalittoral zone, or the transition from the infralittoral zone to the circalittoral zone, was strongly evident (at 0.2 mol. phot. m^{-2} d^{-1}, ~80 m depth) by light at the seabed and, possibly, wave base. Light attenuation also highlighted the transition from the upper to the lower layer of the circalittoral zone (~0.02 mol. phot. m^{-2} d^{-1}, ~113 m), although not so accurately (and supported by key morphotypes). The threshold between lower shallow circalittoral/deep circalittoral was evident not by a variable value but by the distribution of a key group of species (WBR = 0.8 or 140 m depth) (Populus et al., 2017). Finally, as the inferior limit of the deep circalittoral zone is greatly defined by the end of the continental shelf and this shelf end for the Azores islands lies around 200 m (Chiocci et al., 2013; Peran et al., 2016; Quartau et al., 2015), such depth and topography were considered to mark the lower limit of the deep circalittoral (which was not proven by this work as sampling range did not enable that) and, thus, of the broad circalittoral zone. This limit coincides with the threshold for the GNCS (Greater North Sea and Celtic Seas) regions (Populus et al., 2017) but should be investigated in future studies based on upper slope community surveys.

4.2 – DISTINCT CIRCALITTORAL ASSEMBLAGES

4.2.1 – DESCRIPTION OF THE ARISEN BIOLOGICAL ASSEMBLAGES

All groups of biological assemblages were proven to be strongly distinct (very high R values) with great dissimilarity between the groups of communities and great similarity within each of the two deepest groups of communities, based on characterizing species. The lower similarities within each of the two shallowest groups of communities may be explained by: (i) the distinct algal morphotypes occurring at each sample (except for those they have in common) together with the sole appearance of animal morphotypes (as hydrarians) at -50 m sample; and (ii) by the transitional depths encompassed by the second group, from an algal dominated lower infralittoral community (present until the sample -70 m) to an animal-dominated upper shallow circalittoral community (including -90 and -110 m). Despite these lower similarities, the resulting assemblages greatly depicted different biological zones.

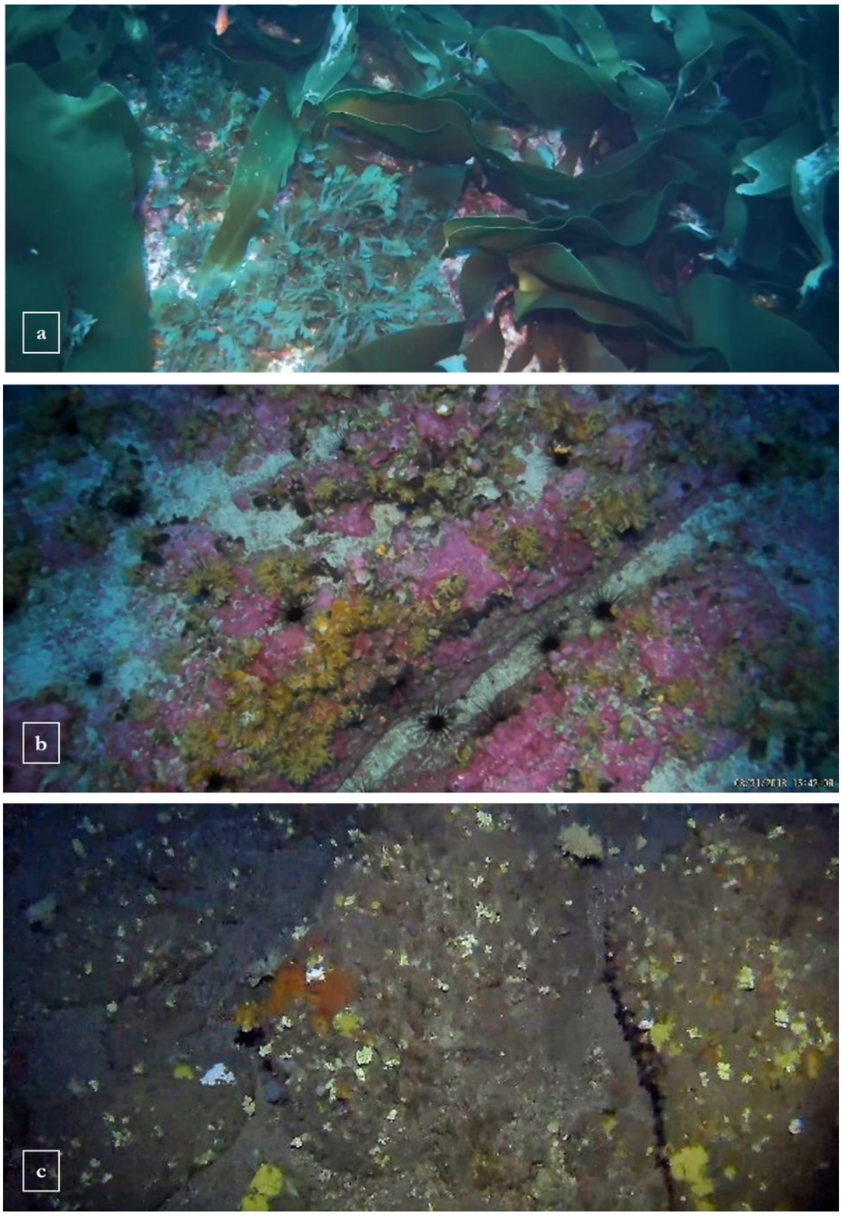
In order to describe those bionomic zones, emphasis was placed on community analysis while species analysis was also taken in account since it showed to be compliant with the community output. This approach enhances the community composition spectrum and the comparability with EUNIS habitat classification (following topic), which also considers some less abundant species.

The first layer (or group of assemblages), between 40 and ~70 m depth, illustrated typical assemblages of the infralittoral zone, specifically, the lower infralittoral, as it was dominated by dense erect medium size and tall brown frondose (kelp) algae (holding aggregations of the lacy crust bryozoan epibiont on the fronds) associated with short turf, of mostly red algae, articulated Rhodophyta and an understory of non-calcareous and calcareous encrusting algae. Moreover, some assemblages of dense circalittoral oysters and encrusting calcareous algae with sparse *Laminaria* were also present at this layer on irregular rocky bottoms (GRA 23 12h14 & SMA 04 17h22) (Davies et al., 2004; Tempera et al., 2013).

Those communities associated to dense kelp extended only few meters below on the upper portion of the second layer (Tempera et al., 2013). Hereafter, kelp tended to only grow sparsely (Fig. 9 & 5) until ~79 m where crustose Rhodophyta dominated alongside animals as sea urchins, lumpy encrusting sponges and circalittoral oysters. Then, between ~80 m and ~113 m depth, these abundant algal bioconstructions on hard substrate built up a calcareous bioherm, together with circalittoral oysters, inhabited by abundant faunal communities which comprise the most striking biological characteristics of the upper shallow circalittoral. The faunal community resembles the later mentioned but also includes other abundant invertebrates as thin encrusting sponges and arborescent cnidaria (including both antipatharians and scleractinians), alongside occurrences of arborescent sponges, sea stars and holothurians. Thus, a complex and highly diverse three-dimensional benthic community is created and illustrates two levels of a typical coralligenous assemblage stratification towards the open water: (i) one encompassing encrusting algae (habitat builders) and invertebrates, as encrusting and erect sponges and urchins (bioeroders), and other (ii), an upper layer, including large arborescent sponges and cnidarians (in absence of gorgonians) (Ballesteros, 2006; Museo Friulano di Storia Naturale, 2009; Piazzi et al., 2019). Additionally, the present assemblage differs from the typical coralligenous ones abundant in gorgonians in upper depths of the Mediterranean Sea and resembles the deep assemblages on outcrops of the Apulian continental shelf and of the North Adriatic (Piazzi et al., 2019).

These three-dimensional bioconstruction communities also characterize the upper depths of the third layer as this broad layer holds the transition from communities where algae are still present to exclusively faunal communities (typical of the lower and deep circalittoral zones (Evans et al., 2016; Populus et al., 2017)). The later ones are present at lower depths, characterized by abundant encrusting and erect sponges, mostly arborescent and massive, with an understory of short hydrarians. In these communities of sponge aggregations, sponges not only represent the most characteristic species as they have main roles in structuring the habitat (e.g., through bioerosion and sediment consolidation) and enhancing biodiversity (by creating space for new organisms) (Bekkby et al., 2017; EUNIS, n.d.). Thus, combining the absence of aggregations of crustose algae from ~113 m (illustrated at the exploratory analysis) and the abundance of sponge communities typical of the lower circalittoral, from ~110 m to ~130 m, these outcomes strongly indicate the lower shallow circalittoral should be comprehended between ~113 m and ~130 m (EUSeaMap, n.d.-a).

Similar communities to the sponge aggregations extend from ~130 m to ~190 m although with abundant arborescent black corals, alongside occurring gorgonians, being the most striking features of the communities. Like sponges, anthozoans constitute important habitat engineers creating highly biodiverse three-dimensional habitats by providing feeding opportunities, spawning and nursery areas. As such anthozoans aggregated on these deep circalittoral depths, they likely formed cold-water coral gardens, as those of *Antipathella subpinnata* at the Azores Islands. However, the present biotope was dominated by monospecific aggregations of *Antipathes furcata,* from -189 m to -109 m, associated to the abundant encrusting sponges, short erect sponges, circalittoral oysters and sparse tall hydrarians (Fig. 10). A similar pattern was verified at several Mediterranean areas where *A. furcata* formed sparse colonies together with other coral species from 100 m to 200 m (Angiolillo & Canese, 2018). While arborescent antipatharians formed aggregations along a wide depth range, some characteristic species appeared across this zone: around 140 m erect fragile sponge forms preceded the gorgonians at around 160 m from which only whip gorgonians formed aggregations at 173 m alongside encrusting and erect sponges (Bekkby et al., 2017; Bertolino et al., 2013; Bo et al., 2012; Tempera et al., 2013). Thus, if the description of the deep circalittoral is considered, such bionomic zone may be upper limited by the appearance of these gorgonian and fragile sponge species (Evans et al., 2016).



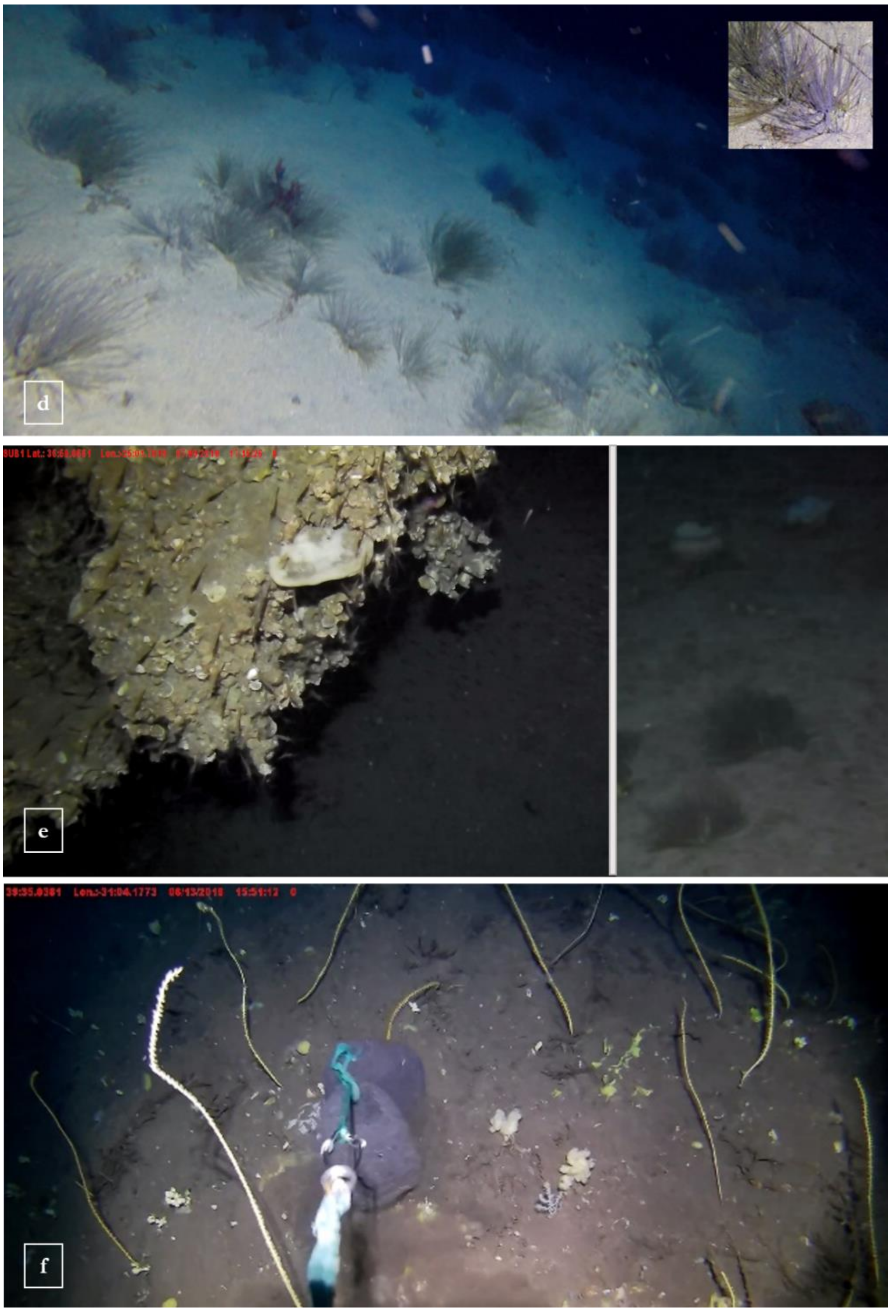


Figure 10. Illustration of some biotopes of the broad circalittoral biological zones. (a) dense kelp with *M. membranacea* and medium size brown algae as *Z. tournefortii* and red algae at -51 m on Santa Maria Island; (b) crustose community with arborescent sponges, Parazoanthus, sea urchins and circalittoral oysters between -113 and -100 m on Santa Maria Island; (c) sponge community: mostly encrusting and short arborescent with also tall arborescent, at -123 m on Graciosa Island; (d) *A. furcata*, possibly two different morphotypes or in association with tall hydrarians as *Nemertesia* aff. *antennina*, at -154 m on Santa Maria, and close up of *A. furcata* with fishing line; (e) (left) lamellate white sponge on rock possibly accompanied by circalittoral oysters and shrimps at -163 m and (right) two caliculate tall sponges alongside *A. furcata* at -140 m on Santa Maria Island; (f) Whip (cf. *V. flagellum*) and small arborescent gorgonians and erect arborescent and encrusting sponges at -173 m on Corvo Island.

4.2.2 – COMPARING THE ASSEMBLAGES WITH EUNIS HABITATS AND WITH HABITATS LATELY PROPOSED TO BE ADDED TO THE CLASSIFICATION

The first zone (belonging to the lower infralittoral) was coherent with three habitats described in Tempera et al. (2013): *Zonaria tournefortii* on exposed deep infralittoral rock (EUNIS habitat type: A3.15_PT11), Deep infralittoral *Laminaria ochroleuca* kelp forests (EUNIS Habitat Type: A3.11_PT02) and Sparse lower infralittoral *Laminaria ochroleuca* (EUNIS habitat type: A3.11_PT03). However, the depth range for the habitat dominated by *Zonaria tournefortii* was much shallower than that verified at the present work. Regarding the counterparts at the current EUNIS classification, it resembled the Mediterranean biotope A4.268 - Association with *Laminaria ochroleuca* and, somehow, A3.11 - Kelp with cushion fauna and/or foliose red seaweeds, however, these showed a different kelp abundance, species composition, and depth range from the present work's biotopes (EUNIS, n.d.; Tempera et al., 2013).

These habitats extended to the upper layer of the second zone and preceded the main biotope of this zone (upper shallow circalittoral). This biotope is broadly similar to the EUNIS habitat A4.21 - Echinoderms and crustose communities on circalittoral rock, particularly A4.214 - Faunal and algal crusts on exposed to moderately wave-exposed circalittoral rock, yet, it differs in the community composition as important and abundant species as circalittoral oysters are not present and its exposure conditions do not allow the development of erect morphotypes except for few species as *Alcyonium digitatum*. The coralline bioconstructions and associated faunal communities are most coherent with the proposed biotope description for Circalittoral oyster *Neopycnodonte cochlear* beds on high energy rocks and cobbles (EUNIS Habitat Type: A5.6_PT01) from Tempera et al. (2013) and the Mediterranean A4.26 Marmara coralligenous communities moderately exposed circalittoral rock. However, the range of this biotope is not represented at Tempera et al. (2013) for it reports a distribution from 60 to 150 m. On the other hand, it resembles the interval of depths reported for the Mediterranean, between 20-30 and 100-120 m (Ballesteros, 2006; European Red List of Habitats, n.d.-a, n.d.-d; Tempera et al., 2013).

These communities extended until the upper half of the third group of assemblages from where another biotope thrived and resembled mostly the Sponge garden and sparse tall hydrarians on mixed substrate (EUNIS habitat type: A4.13_PT07) and EUNIS habitat A4.12 Sponge communities on lower circalittoral rock. However, some important features of this assemblage aren't contemplated at the EUNIS habitat description as the dominant encrusting sponges, the understory of hydrozoans and the sparse occurrence of tall hydrarians as *Polyplumaria flabellata*. In contrast, these features are represented at A4.13_PT07, except for the hydrarian 'carpet', across a coincident depth range (EUNIS, n.d.; Tempera et al., 2013).

In the last zone subsist assemblages which resemble gardens already reported for the Azores Islands: *Antipathella subpinnata* gardens on deep circalittoral rock (EUNIS Habitat Type: A4.13_PT04) and *Polyplumaria flabellata* gardens (EUNIS habitat type: A4.13_PT03). Yet, the dominant species in the present study was the black coral *Antipathes furcata* and the sparse occurrence of *Nemertesia* aff. *antennina* was not contemplated. The late feature is contemplated in a not so similar biotope: *Nemertesia* aff. *antennina*, *Lytocarpia myriophyllum* and digitate sponges on sediment (EUNIS Habitat Type: A4.13_PT06). The EUNIS habitat A4.27 Communities of Mediterranean lower circalittoral rock also notably illustrates the present biotope though it shows the same limitations as above described for the Azores ones (Bekkby et al., 2017; Bo et al., 2012; European Red List of Habitats, n.d.-b; Tempera et al., 2013).

The other assemblage occurring at this zone resembles the most the Azorean proposed biotope *Viminella flagellum* and *Polyplumaria flabellata* on circalittoral mixed substrate (EUNIS habitat type: A5.45_PT01), with no EUNIS habitat previously contemplating this assemblage. The whip gorgonian species, *Viminella flagellum* dominates (although the present assemblage lacks the other dominant species, *P. flabellate*), associated with arborescent gorgonians, erect arborescent (and other forms as tubular and thick lamellate) and encrusting sponges at hard bottoms of coincident depths ranges. The sponge fauna, however, was also dominant at this work's assemblage (Tempera et al., 2013).

The assessment of these assemblages made possible answering one of the driving questions of this work: the circalittoral of the Azores Islands is not adequately represented at the current circalittoral habitats compiled at the EUNIS habitat classification. This outcome could be explained by the lack of representation a subtropical Archipelago could have by having its biotopes compared to data collected mostly from northern Europe and Mediterranean shores and shelves. Moreover, it was not completely reflected in the Azorean proposed habitats, although the resemblance was high. Divergences were patent in some dominant and associated species, depth ranges and locations found. For instance, the first report of biotopes dominated by *Antipathes furcata* contrasting with the previously reported *Antipathella* sp. biotopes.

4.2.3 – POTENTIAL VULNERABLE MARINE ECOSYSTEMS

The community analysis revealed the presence of several habitats dominated by habitat builders that potentially represent on-shelf VMEs. These include kelp and macroalgal forests in the lower infralittoral; coralligenous assemblages in the upper circalittoral; sponge aggregations and coral gardens in the lower circalittoral and deep circalittoral, with gorgonians in the latter one. In all those communities, characteristic species formed aggregations (sciaphilic Algae, crustose Algae, erect sponges, antipatharians and gorgonians, between others) which produced three-dimensional structure habitats mostly provided by arborescent morphotypes. Due to their prominence from the substrate, habitat builders may be easily impacted by bottom-tending fishing gear used on island shelves, such as demersal fishing with longlines, pole-and-hand and handline fishing – which is already verified for organisms as black corals, scleractinians including Dendrophylliidae and gorgonian corals as *V. flagellum* (at island slopes and seamounts) (Sampaio et al., 2012). Despite the fishery impact, various other pressures may occur, including climate change and sand dredging (Abecasis et al., 2015; Bekkby et al., 2017; Piazzi et al., 2019). In addition, the characteristic and habitat builder species above-mentioned often recover slowly from disturbances or do not recover at all (Enrichetti et al., 2019). By combining all this information, it is possible to identify potential VMEs from the broad circalittoral zone at the shelves of the Azores islands.

All these communities are still poorly studied (Bekkby et al., 2017; European Red List of Habitats, n.d.-b, n.d.-c; Piazzi et al., 2019) and information like this represents the first step into grasping their biological traits, health state, threats and the services they deliver. Together with their geographical distribution, this knowledge makes up the basis for directives as the MSFD (Willaert et al., 2019).

Additionally, the presence and abundance of encrusting sponges as well as erect branching invertebrates as *Parazoanthus*, may reflect a higher influence of sedimentation occurring at certain communities from the infralittoral abundant in short turf until these upper shallow circalittoral depths (Piazzi et al., 2019). Further studies could be conducted on investigating the impact of some human pressures acting at these insular shelves as sand dredging.

5 – CONCLUSION

This work allowed preliminarily assessing the circalittoral of the Azores islands as the bottom-up and top-down approaches (David W. Connor et al., 2004) lead to: the (i) delineation of the thresholds between infralittoral/circalittoral (around 80 m depth) and upper shallow circalittoral/lower shallow circalittoral (close to 113 m) and (i) definition of the communities characterizing those biological zones – a succession from algae dominated communities to faunal ones. Although the boundary between upper shallow circalittoral/lower shallow circalittoral was not as evident as the above one and requires further future assessment, the major conditions characterizing the lower shallow circalittoral were verified at both analyses which pointed out a range of depths this sub-zone would likely be found at. On the other hand, the deep circalittoral zone was solely evident from the patterns reflected by the assemblages as wave base was already negligible at those depths. In this regard, future studies are required to efficiently define the boundaries delineating all sub-zones of the broad circalittoral zone so that decision-making is guided by reliable information.

Further knowledge was provided regarding the Azores Islands shelves biotopes as this assessment highlighted the occurrence of the proposed assemblages at other not reported Azorean locations (other than at Formigas Bank, Faial-Pico channel, Condor Seamount and Açor Bank, the most frequent ones) and to enrich the diversity of habitats described for the Archipelago (as intermediate biotopes were described).

Particular emphasis should be given to the assemblages found as they comprise sessile or vagile and filter feeder species which are prone to be more vulnerable to water quality and physical impact stemming from fisheries and other economic activities at these shelves (Abecasis et al., 2015; Clark et al., 2015).

Despite the relatively cheap non-invasive low technology used for sampling, a great amount of data was produced that permitted answering the driving questions of this project and increased the knowledge regarding a poorly-sampled bionomic zone of the Azores island shelves. Nonetheless, data accuracy was curtailed by variations in the sampling approach that should be addressed before future quantitative sampling is conducted. The duration and distance covered in each station should be standardized and represent at least 1 minute of bottom time. A system to scale objects on the seabed imagery should be implemented as well as a system that permits precisely geoposition the observations on the seabed, which were so far assumed to be occurring directly downwards from the boat at surface.

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| STATE OF THE ART |

ANNEX

MARINE HABITAT CLASSIFICATION AND MAPPING

The present knowledge regarding the oceans' biodiversity of this "Blue Planet" is still far from being vast (Brown et al., 2011; Galparsoro et al., 2012; Tittensor et al., 2010).

Marine research lead to the conclusion that most of species diversity is found at benthos instead of at the pelagic zone (Gray, 1997). Likewise, between all the diversity levels, habitat diversity showed to be the most suitable concept to sample biodiversity since a habitat is easier to define as it has clearer boundaries (Brown et al., 2011; Gray, 1997). However, the scarce knowledge regarding benthic habitats, namely, their local extent, geographical scope, functioning and status (by qualitative descriptors as biological diversity and seafloor integrity) has been attributed to the low adequacy of seabed survey methods of the last decades, presenting similar quality to the land ones, and a lack of global acknowledge of the oceans as a main source of services including global functioning (Brown et al., 2011; Connor, 2005; Galparsoro et al., 2012; Gray, 1997).

Recently, several human activities turned into critical anthropogenic threats to the marine environment as fishing, aquaculture, mining, maritime transport, sediment discharges, sand extraction, pollution (e.g.: litter), introduction of invasive species, eutrophication, and climate change. These are responsible for serious damage to seabed ecosystems and for the reduction of benthic biodiversity and ecosystem functioning (Allee et al., 2000; Galparsoro et al., 2012; Gray, 1997; Vasquez et al., 2015; Willaert et al., 2019). Additionally, the scientific community has acknowledged the crucial ecological role of the oceans, mainly, the marine and coastal ecosystem services delivered (direct or indirectly) to humanity, as provisioning (e.g.: food), regulating and maintenance (e.g.: climate regulation) and cultural (e.g.: physical interactions with ecosystems) services (Tittensor et al., 2010; Willaert et al., 2019).

Hence, conservation and management could no longer be based on species approaches but rather on ecosystem ones which led to the urgent need to expand the understanding of the global marine diversity (from local to global scale). The inventory and classification of ecosystems demanded a scientific, comprehensive, unambiguous and easily understood (with no need for detailed technical knowledge) framework for classification of habitats, providing habitat descriptions to report habitat data in a comparable way. This framework together with habitat mapping would, thus, lead to a more comprehensive and consistent large-scale database suitable for long-term use and management of the marine environment and its resources (Allee et al., 2000; Connor, 2005; Davies et al., 2004; Galparsoro et al., 2012; Moss, 2008; Vasquez et al., 2015).

In Europe, numerous national habitat type classification systems were produced but they lacked the required similarity so that habitats could be reported at a European scale. As so, work on the inventory of major importance biotopes began by the CORINE (Coordination of Information on the Environment) project of the European Commission, in the mid-1980s. Due to the continuous work, the CORINE biotope types arose and was succeeded by the Palaearctic habitat classification. By re-structuring and re-defining these previous classifications, the European Nature Information System (EUNIS) produced the most comprehensive classification system aiming to cover all European habitat types (Galparsoro et al., 2012; Moss, 2008).

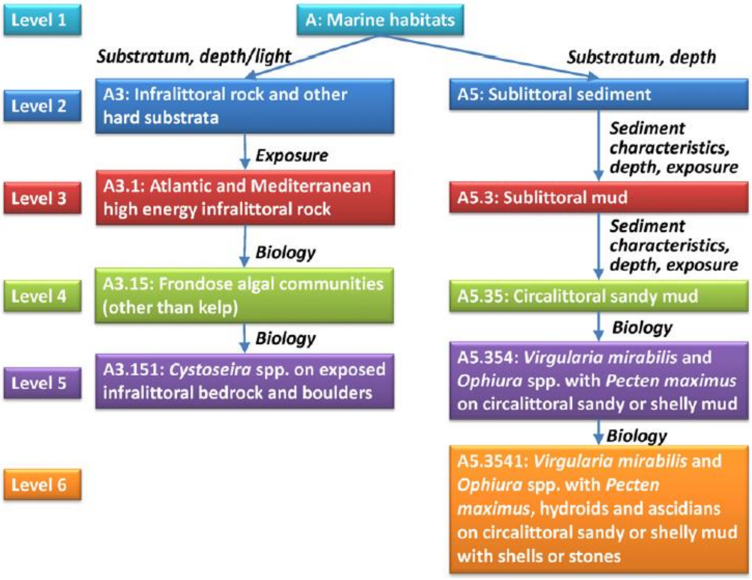


Figure 1. Illustration of the EUNIS hierarchy and the criteria used at each level of the classification through two examples. Retrieved from Galparsoro et al., (2012).

The EUNIS habitat classification comprises a hierarchical classification with reference habitat types for Europe alongside their descriptions (Fig. 1). It includes marine, freshwater and terrestrial habitats described through a common and easily understood language (not only for those who constructed the habitat maps or scientists in general but also resource managers and all other stakeholders) while presenting both objective and scientifically based content (with clear definitions and principles). This system should be comprehensive, yet, specific enough to be applicable at several hierarchical levels of complexity as well as flexible enough to add new information while keeping the required stability to support other systems. These not only enable habitat data to be reported and referenced in a comparable way as it enables national classifications to persist and to be relatable at an international scale. Thus, even if different habitat systems would be adopted by distinct legislations, they could all be interrelated and, therefore, allow achievement of a consensus among different parties (Allee et al., 2000; Galparsoro et al., 2012; Moss, 2008).

Until recently, the marine section of the classification covered the Atlantic, Baltic, Black Sea and Mediterranean Sea, partially (at level 3 of the classification) (Evans, 2013; Evans et al., 2016; Moss, 2008). However, with increasing available information (especially through mapping projects) together with experience using the EUNIS classification and the exclusion of most of southern Europe's Atlantic coast and the Macaronesia Islands highlighted the need for revising the classification. This led to the MeshAtlantic (Mapping European Seabed Habitat Maps in the Atlantic area) project action plan to assess the EUNIS classification system's applicability and effectiveness, on 2012 (Evans, 2013; Evans et al., 2016; Galparsoro et al., 2012; Tempera et al., 2013). By verifying the classification required improvements, the MeshAtlantic project set the goal to compile new habitat proposals for areas insufficiently represented by the classification, remarkably the Atlantic Area (INTERREG). For that compilation, habitats are to be defined and characterized, which can be fulfilled through habitat mapping (Galparsoro et al., 2012; Tempera et al., 2013).

The EUNIS habitat classification has also been used by marine mapping projects as Balance, MESH and EUSeaMap; and by directives as the Marine Strategy Framework Directive (MSFT) from where it based its 'predominant habitat types'. Hence, producing maps regarding bathymetry alongside geomorphologic and biological features of habitats based on the EUNIS classification would lead to a harmonized and consistent interpretation of the European habitats across the regional seas. These maps constitute the basis for the implementation of EU directives as MSFD (aiming to protect and/or restore the European Seas, to ensure sustainable human activities and to provide safe, clean, healthy and productive seas) and Habitats Directive (HD) (Galparsoro et al., 2012; Vasquez et al., 2015). As directives explicitly demanded for (multi-resolution) full spatial coverage of European seafloor, habitats have been surveyed through multiple techniques as single- and multi-beam sonar, LiDAR, grab sampling and other physical groundtruthing. However, such specific direct sampling methods showed to be impractical to be applied at the European seas due to the associated high costs and resources and time-consuming methodologies. On the other hand, these problems can be minimized if a broadscale approach is adopted instead. Assuming the environmental factors at the seabed and water column (geological as substrate type and oceanographic as water motion) greatly affect benthic communities, they can be considered proxies of these communities (composition and distribution) and be used to produce integrated maps regarding the physical characteristics of the seabed. In 2000, Roff et al. designed this mapping approach which turns environmental factors (as light penetration and water motion) data layers into ecologically relevant broad biological zones (as photic or aphotic and exposed or sheltered, respectively) based on a hierarchical classification to allow overlaying them in a map through Geographical Information System (GIS). Finally, this procedure would generate specific benthic "seascapes" as "Photic-Exposed-Gravel". Such cost-effective approach based on marine environmental data poses less concerns as it relies on existing information and derives maps of a greater spatial scope, having the only disadvantage of providing maps with less detail (Andersen et al., 2018; Vasquez et al., 2015).

Recently, this concept of mapping seabed habitats using marine environmental data was adopted worldwide but especially by Australia and Europe. Among several initiatives, EUSeaMap project successfully extended the broad-scale habitat mapping to the western Mediterranean basin by harmonizing the MESH seabed habitat maps with the BALANCE project ones (Andersen et al., 2018; Vasquez et al., 2015). Additionally, MeshAtlantic project (from 2010 to 2013) further extended the geographic coverage of the method by including four areas around Ireland, the Bay of Biscay, the Iberian Peninsula and the Azores Islands. At last, EMODnet Seabed Habitat formed the EUSeaMap 2016 comprising the areas covered by the mapping initiatives MeshAtlantic and EUSeaMap but updating it to extend to unmapped areas, namely, the Norwegian Sea, the Canary Islands, the Adriatic Sea, the Central and Eastern Mediterranean and the Black Sea. Thus, all the previous efforts gave rise to the comprehensive pan-European seabed habitat map EUSeaMap 2016 alongside its biologically-relevant categories (Andersen et al., 2018).

Through EUSeaMap 2016, biologically relevant thresholds between the biological zones (littoral, sublittoral, circalittoral, bathyal and abyssal) obtained from the predictors can be derived and subsequently matched to EUNIS habitat types. This correspondence step is likely to be conclusive since the physical and hydrological factors of the mapping project were obtained from the abiotic variables of the EUNIS classification system, the primary descriptors of its habitats through an hierarchical structure (Connor, 2005; Davies et al., 2004; Populus et al., 2017; UKSeaMap, 2010; Wahl, 2009).

BIOLOGICAL ZONES: THE CIRCALITTORAL

The circalittoral zone (at level 2) is a biological zone located at the sublittoral zone of the EUNIS classification (preceded by the infralittoral zone) which tends to extend until the end of the continental shelf (followed by the bathyal). The circalittoral is marked by the interaction of several environmental factors, mostly, light, wave action, substrate type, tidal currents, thermal stability and salinity. These factors strongly influence the communities to be strikingly different from the single algal species dominated communities at the infralittoral zone. It is, thus, dominated by animal communities, though algae are still present and can be abundant in the upper portion of the zone, and is characterized by domination of a diversity of species. Furthermore, the different communities associated to the abiotic variables split the circalittoral into two main sub-zones: the circalittoral or shallow circalittoral and the deep or offshore circalittoral (at level 3, encompassing biotopes at A4 and A5) (Connor, 2005; David W Connor et al., 2004; Monteiro et al., 2011; Wahl, 2009).

Before the efforts to revise and improve the classification, the circalittoral was mostly described by the JNCC Marine Habitat Classification for Britain and Ireland, by Connor et al. (2004) (Galparsoro et al., 2012). Compliant with this classification, the depth marking the beginning of the circalittoral zone is not fixed as it directly depends on (and is mostly affected by) the intensity of light reaching the seabed which, in turn, depends on its attenuation by factors as concentration of dissolved organic pigments and suspended matter (building up water turbidity, abundant in coastal waters) (David W Connor et al., 2004; Davies et al., 2004; Hartnoll, 1998). Nevertheless, the circalittoral zone usually extends from -5 m to -20 or - 50 m and is described as an immersed seabed under mesophotic, mesothermal, mesohaline or stenohaline conditions alongside moderately variable wave action. From -20 or -40 m to -80 or -100 m (or even -200 m) lies the circalittoral offshore, an immersed and aphotic layer with stable wave action, salinity and thermal stability, leaving tidal currents as its major factor. The circalittoral zone can be split in upper circalittoral and lower circalittoral. The upper circalittoral, conventionally starts at a depth where the light reaching the seabed represents 1% of surface illumination, which matches the critical depth for growth of kelp species. Thus, only sparse foliose algae persist, of all erect algae (kelp are absent), in this first layer dominated by animal communities. These foliose algae disappear as the lower circalittoral is reached. This layer usually starts at a depth with 0.1% surface illumination (their critical depth), were encrusting coralligenous algae can be found in depths dominated by faunal communities (Fig. 2) (David W Connor et al., 2004; Davies et al., 2004; Hartnoll, 1998).

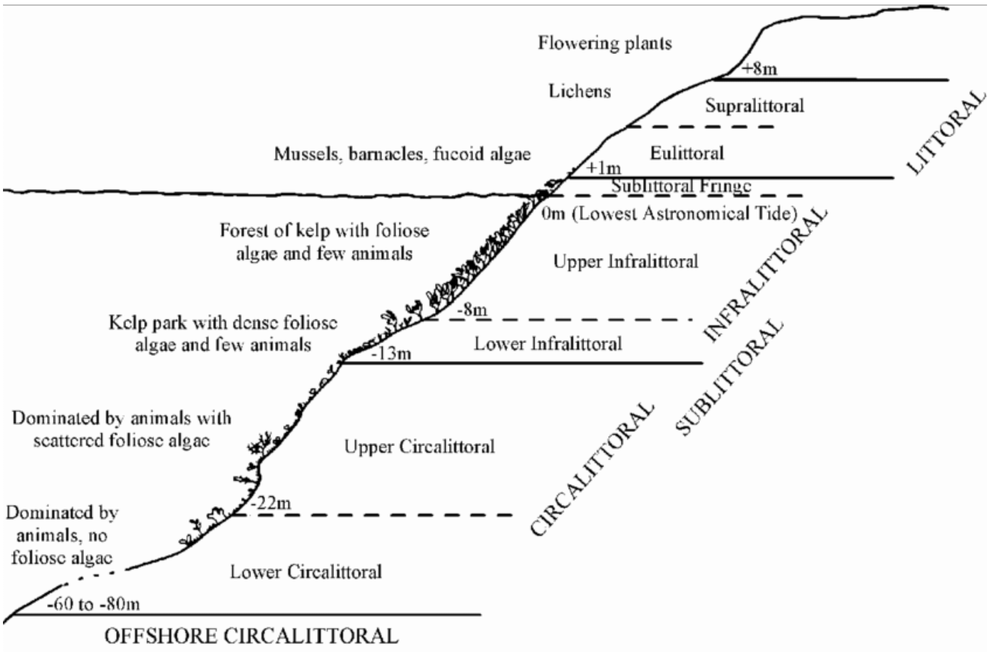


Figure 2. Depth-wise profile of a rocky shore displaying the biological zones (heights and depths characteristic of south-west Britain). Retrieved from: Connor et al., 2004.

At the present, after all the information added and the classification revised, the circalittoral zone still maintains its original characteristics although with some important changes (Tab. 1). The circalittoral or shallow circalittoral, as an animal dominated community, not only allows for a low frequency of foliose algae but for brown and red algae (sciaphilic macroalgae including the foliose algae) to be present and eventually grow to dominant proportions (in absence of vascular plants and green algae) (Evans et al., 2016; Populus et al., 2017). Extending from the infralittoral, brown algae can comprise Fucales, Laminariales (one of the last macrophyte algae to disappear), Desmarestiales and Sporochnales while red algae are represented by erect and encrusting Rhodophyta (EUSeaMap, n.d.-a). From the later, encrusting coralligenous algae (on hard substrates) and rhodoliths or maërl (also living or dead coralline algae but loose lying and forming masses on shell gravel with coarse sand) can aggregate to form a bioconstruction of red algae that gives structure to algae and animals (both sciaphilic) as sponges, corals, bryozoans and tunicates. These communities are most often built by encrusting rhodophytes as *Lithophyllum* sp. and *Mesophyllum* sp. which create concretions through deposition of a "cement" over diverse grounds (as rock debris, animal remains and waste of various origins) that support several levels of benthic animals. From base up, sub-base level fauna is composed by borers and interstitial fauna (living on borrows and cavities of the concretion) followed by base level with small sciaphilic species taking refuge by upper levels' fauna (the following). The intermediate level is occupied by epibionts as sponges and cnidarians, e.g. *Alcyonium* sp., and polychaeta while the upper level includes large gorgonians, erect sponges and cnidarians as *Parazoanthus* sp.. The resulting coralligenous assemblages represent characteristic communities of the upper circalittoral layer (Ballesteros, 2006; Bekkby et al., 2017; EUSeaMap, n.d.-a).

As light becomes an even more limiting factor to multicellular algae in the depths below, the lower circalittoral is a 'rariphotic' layer marked by the absence of the above-mentioned sciaphilic algae and by occurrence of not dominant coralligenous assemblages (Ballesteros, 2006; Bekkby et al., 2017; EUSeaMap, n.d.-a; Museo Friulano di Storia Naturale, 2009). The offshore or deep circalittoral (or even deep shelf) starts at a depth right below the maximum range of wave action disturbance of the seabed (wave base) and is a further rariphotic zone with so few light reaching the seabed that photosynthetic activity is no longer performed. Such stable conditions lead to few variation in temperature and salinity which, all together, provide suitable habitats for large, erect, fragile, epifauna to dominate (EUSeaMap, n.d.-b; Evans et al., 2016). Fragility is a biological characteristic which can be assigned to the high probability of a species to break when under physical disturbance (e.g. water motion or fishing gear), in contrast to robust (e.g. leathery) (Clark et al., 2015; Tillin & Tyler-Walters, 2014). This characteristic is reflected on species morphological traits as being large or erect as well as on living position and mobility traits including being sedentary or surface-living species. Thus, fragile species that can be found at this layer may comprise growth forms as arborescent octocorals, gorgonian fans, thicket-forming stony corals, branching stony corals, erect branching sponges – all which can reflect habitats lacking sedimentation – and laminar sponges – may inform about prevailing currents (Althaus et al., 2013; Baldwin et al., 2018; Clark et al., 2015). Eventually, if tall arborescent gorgonians represent one or more conspicuous species providing three-dimensional structural habitat alongside black corals, mostly, cold-water coral (CWC) gardens may be found at these depths (Bekkby et al., 2017; Roberts & Cairns, 2014).

Both limits, and communities, vary according to the specific abiotic variables of a habitat which are influenced by conditions as turbidity, due to dissolved organic pigments and suspended matter, latitude, climate and currents (David W Connor et al., 2004; EUSeaMap, n.d.-a; Hartnoll, 1998). Likewise, EMODnet considered the specific environmental variables of each location to produce different thresholds for the several European regions (Populus et al., 2017).

Regarding the substrate type, hard substrates are usually restricted to the circalittoral layer while soft substrates spread from the circalittoral to the offshore circalittoral, which can be explained by the tectonics, erosion and hydrodynamics of the continental shelf (David W Connor et al., 2004; DAVID W. CONNOR et al., 2004; Harris, 2012).

Therefore, the variables used in most of the literature as proxies to determine the thresholds of these two main layers are (1) light penetration and (2) wave base. However, the other variables mentioned in the beginning of the section may be used as proxies, as it is the case for temperature, instead of wave base, to define the boundary between the layers or other variables as sedimentation for suspension feeders, pressure and dissolved oxygen (Baldwin et al., 2018; Lesser et al., 2009; Vasquez et al., 2015).

Table 1. Illustration of the characteristic species of the biotopes of the circalittoral as well as the main factors and species marking the transitions between biological zones. It was based on levels 3 and 4 of the EUNIS habitat classification, Populus et al. (2007), Vasquez et al., 2015 and Ramos et al., 2016.

INFRALITTORAL				
Characteristic Species	Abundant photosynthetic green algae as foliose, filamentous and frondose macro-algae			
Main Transition Factor	**Light Penetration on the seabed**			
Transition Marking Species	**Sparse or abundant brown and red macrophyte algae (e.g. foliose algae); Crustose algae and faunal communities**			
CIRCALITTORAL				
Substrate Type	**Rock – Bedrock and Boulders**			
Energy	**High**	**Moderate**	**Low**	**Features**
Wave Exposure	**Extremely exposed, Very exposed, Exposed**	**Exposed, Moderately exposed**	**Sheltered, Very sheltered**	**Wave-sheltered**
Tidal streams	**Very strong, Strong** **Other features: Tide-swept**	**Moderately strong, Weak**	**Weak** **Very weak**	**Weak** **Very weak**
Biotopes	**A4.1** (one main biotope) Hydroid *Tubularia indivisa* dense 'carpet' Barnacle *Balanus crenatus* *Alcyonium digitatum* (on rocky outcrops) Sponges: *Pachymatisma johnstonia*, *Halichondria panicea*, *Esperiopsis fucorum* and *Myxilla incrustans*	**A4.2** (three main biotopes) **A4.21** Echinoderms (starfish *Asterias rubens*, brittlestar *Ophiothrix fragilis* and sea urchin *Echinus esculentus*) Fauna (isolated clumps of hydroids *Nemertesia antennina* and *Abietinaria abietina*, *Alcyonium digitatum*, anemone *Urticina felina* and cup coral *Caryophyllia smithii*) Crustose communities (red encrusting algae); other (polychaete *Pomatoceros triqueter* and the top shell *Calliostoma zizphinum*)	**A4.3** (one main biotope) Encrusting red algae Brachiopods (*Neocrania anomala*) Ascidians (*Ciona intestinalis, Ascidia mentula*)	**A4.7** (two main biotopes) **A4.71** [Caves and overhanging rock] Sponges *Dercitus bucklandi*, Anemones *Parazoanthus spp.* Cup corals *Caryophyllia inornatus*, *Hoplangia durotrix*

		A4.22 *Sabellaria* reefs (dense crusts of polychaete *Sabellaria spinulosa*)		**A4.722** [artificial substrata: discarded fishing nets or scrap metal on muddy sediment plains] ++*Ascidiella aspersa*
		A4.24 circalittoral mussel beds (++ mussels *Mytilus edulis* or *Musculus discors* 'carpeting' the underlying substrata)		**A4.721** [moderately wave-exposed, moderately strong to weak tidal streams steel wrecks] ++*Alcyonium digitatum*, *Metridium Senile*

Substrate Type	**Sediment**					
Sub-substrate type	**Coarse Sediment**	**Fine Sand**	**Muddy Sand**	**Sandy Mud**	**Fine Mud**	**Coarse Sediment**
Biotopes (one main per sediment type)	**A5.14** robust infaunal polychaetes mobile crustacea and bivalves sea cucumber (*Neopentadactyla*) *Branchiostoma lanceolatum*	**A5.25** wide range of echinoderms (may include *Echinocyamus pusillus*) polychaetes bivalves	**A5.26** variety of polychaetes bivalves as *Abra alba, Nucula nitidosa* echinoderms as *Amphiura spp, Ophiura spp.*, *Astropecten irregularis*	**A5.35** Sea pens *Virgularia mirabilis* brittlestars *Amphiura spp.* polychaetes *Lagis koreni, Owenia fusiformis* bivalves as *Mysella bidentate, Abra spp.*	**A5.36** *V. mirabilis, Pennatula phosphorea* anemone *Cerianthus lloydii, Amphiura spp.* burrowing megafaunal as *Nephrops norvegicus*	**A5.44** wide range of polychaetes, bivalves, echinoderms and burrowing anemones as *Cerianthus lloydii* hard substrata on the surface epifaunal species as *Nemertesia spp, Hydrallmania falcata*

Main Transition Factor	**Reduced/null effect of Wave Base (wave action on seafloor)**
Transition Marking Species	**Sparse fauna tolerant to physical disturbance**

<table>
<tr><th colspan="6">DEEP CIRCALITTORAL</th></tr>
<tr><th>Substrate Type</th><th>Coarse Sediment</th><th>Sand</th><th>Mud</th><th>Mixed Sediments</th><th>Coral Reefs</th></tr>
<tr><td>Biotopes (one main per sediment type)</td><td>A5.15
robust infaunal polychaete and bivalve species; ≈mixed sediment may have juvenile <i>Modiolus modiolus</i></td><td>A5.27
diverse range of polychaetes, amphipods, bivalves and echinoderms</td><td>A5.37
dominated by polychaetes and bivalves such as <i>Thyasira spp.</i>, echinoderms and foraminifera</td><td>A5.45
high number of infaunal polychaete and bivalve species; ≈coarse sediment and populations of <i>Modiolus modiolus</i> may develop</td><td>A5.63
<i>Lophelia pertusa</i>
sponges, polychaete worms, echinoderms (starfish, sea urchins, brittle stars) and bryozoans (sea mats)</td></tr>
<tr><td colspan="3">Main Transition Factor</td><td colspan="3">End of continental shelf</td></tr>
<tr><td colspan="6">Bathyal</td></tr>
</table>

MESOPHOTIC ZONE: A CURRENT DISCUSSION OF THE TROPICAL "CIRCALITTORAL"?

Contemporaneous to the definition improvement of the circalittoral zone, at tropical locations, the term mesophotic or *twilight* zone arose due to evidence regarding non-degraded reefs deeper than 30 m (in contrast to the damaged shallower counterparts, <20m). This zone was defined as a belt of low light depths (at the lower photic zone), usually ranging from 30-40 m to 150-200 m, beyond the traditional scuba limits that comprises coral ecosystems dominated by light-dependent zooxanthellate corals, azooxanthellate scleractinian corals, macroalgae and sponges (Baldwin et al., 2018; Bo et al., 2011; Corriero et al., 2019; Lesser et al., 2009; Lindfield et al., 2016; Rocha et al., 2018). With light being the dominant abiotic feature, these mesophotic coral ecosystems (MCEs) usually lie at the deep fore reef zone (Fig. 3) where they find protection from strong wave action and stable temperature conditions (Lesser et al., 2009).

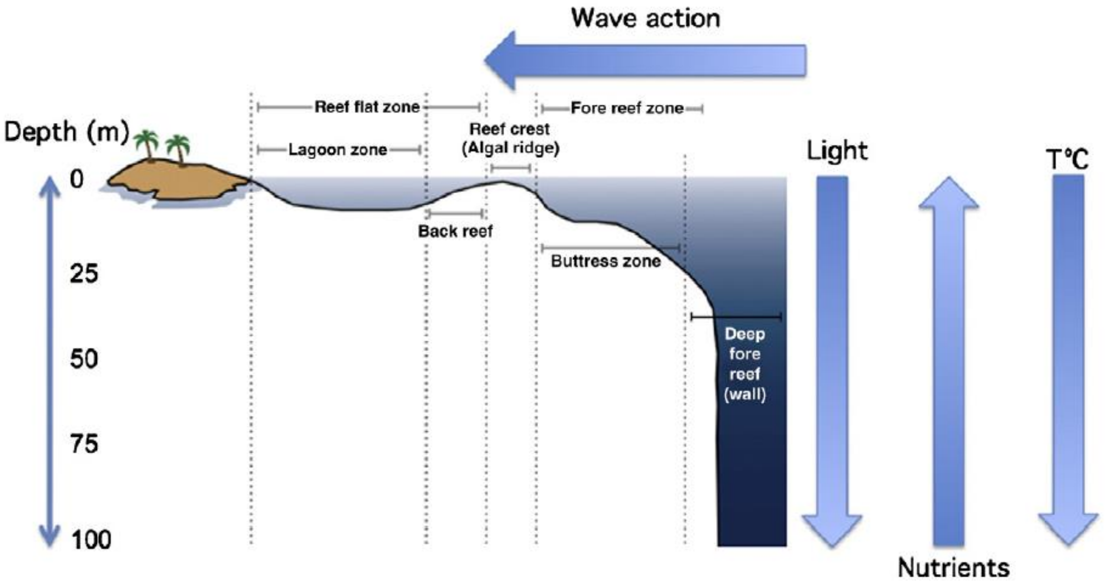


Figure 3. Zonation of the coral reef from shallow reefs to mesophotic depths. Blue arrows represent gradients of light, nutrients and temperature. Retrieved from Lesser et al., 2009.

Two years ago, Baldwin et al., extended the MCEs' geographical range to "tropical and some higher latitudes" and described a demersal rariphotic zone between ~130 m to 309 m, based on faunal breaks (Fig. 4), receiving less irradiation compared to the mesophotic but above the aphotic zone (still adopting the above-mentioned mesophotic range) (Baldwin et al., 2018). Last year, the first mesophotic coral reef was described for the Mediterranean Sea (a temperate region) built by scleractinian corallites cemented by calcified polychaeta tubes and in association to aggregates of *Neopycnodonte cochlear* (an oyster species occurring at the circalittoral zone (European Red List of Habitats, n.d.-c; Tempera et al., 2013)) (Corriero et al., 2019). Finally, Enrichetti et al. (2019), stated mesophotic environments consisted on vulnerable habitats of three-dimensional animal forests on biogenic and rocky reefs occurring at both tropical and temperate environments. These receive less than 3% of the surface irradiance which include the previously established 1% threshold for the disappearance of kelp, marking the infralittoral/circalittoral threshold (Amorim et al., 2015; EUSeaMap, n.d.-a; Evans et al., 2016). The major linkage to the zonation adopted by the EUNIS habitat classification was made through the delineation of the range of these mesophotic environments: from the circalittoral and offshore circalittoral to the upper bathyal of this classification (Francesco Enrichetti et al., 2019).

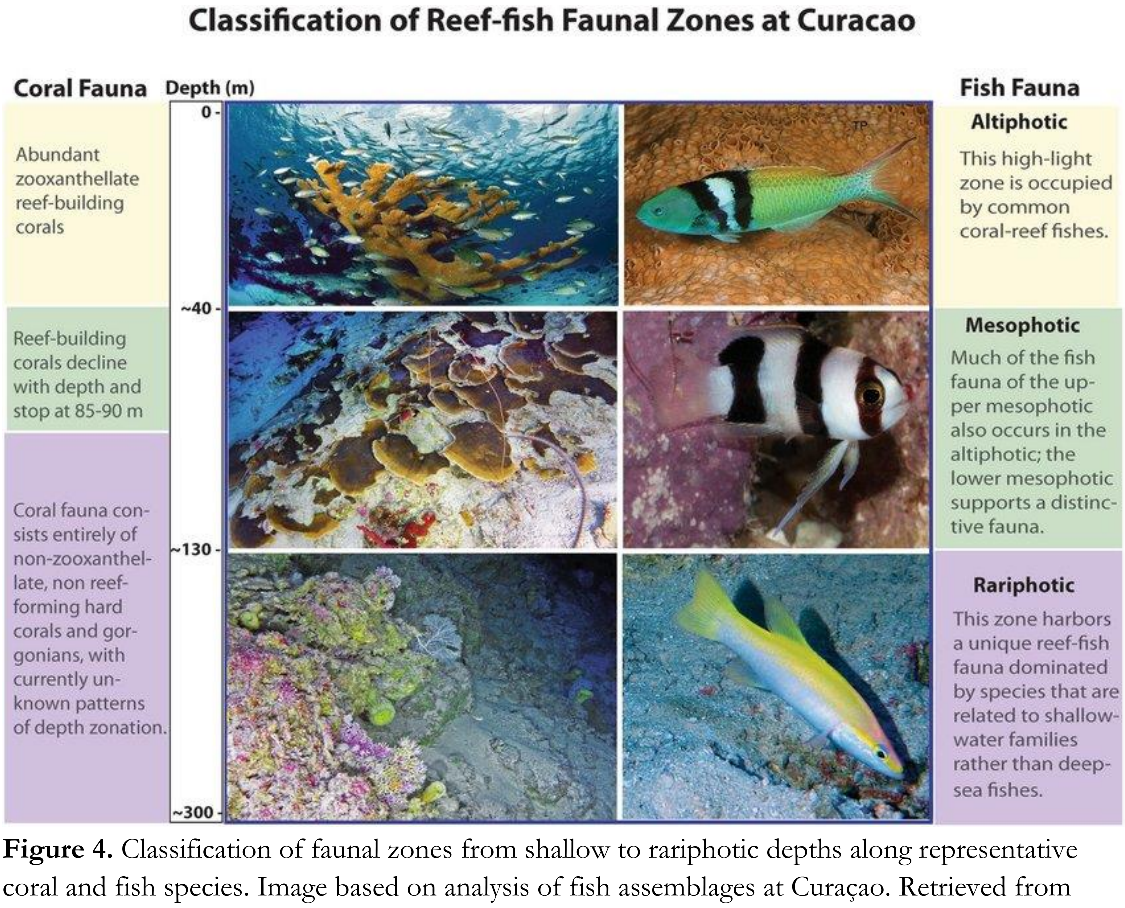


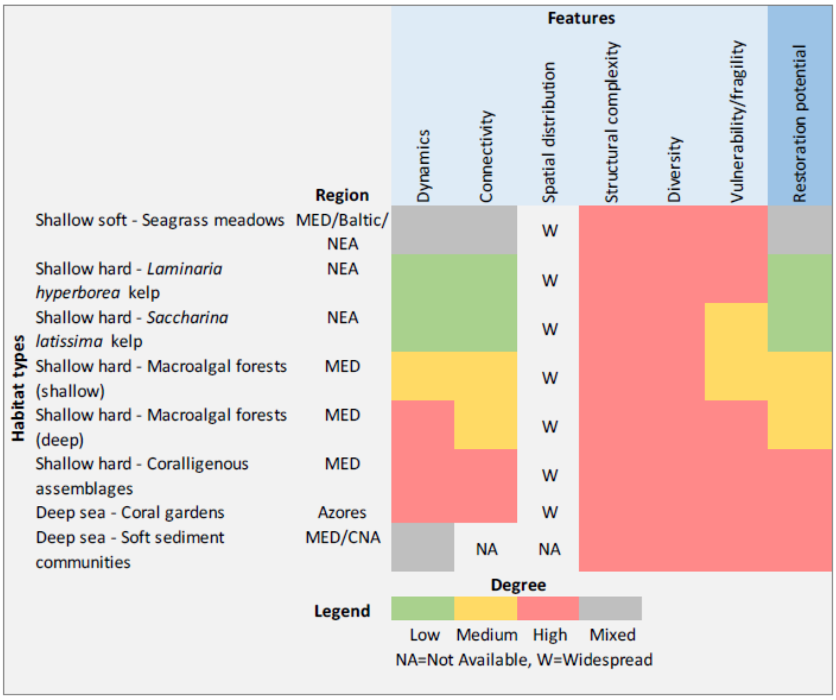
Figure 4. Classification of faunal zones from shallow to rariphotic depths along representative coral and fish species. Image based on analysis of fish assemblages at Curaçao. Retrieved from Baldwin et al., 2018.

VULNERABLE MARINE ECOSYSTEMS (VMEs)

In the past decades, major priority was directed to protecting bottom habitats stemming from an urgent need to halt the already mentioned biodiversity loss mainly due to increasing destructive fishing activities. In this regard, particular emphasis was attributed to identification and further protection of vulnerable marine ecosystems (VMEs). These were defined by the Food and Agriculture Organization of the United Nations (FAO) Deep-sea Fisheries Guidelines as populations, communities or habitats that are susceptible to disturbance from human activities, especially fishing, and that are slow or unable to recover from that impinged disturbance. Such inherent vulnerability arises from characteristics, defined as criteria by FAO, including uniqueness or rarity of an area (e.g., owing to an endangered species or discrete feeding area), functional significance (e.g., important areas for reproduction or recovery), fragility (susceptibility to human disturbance), life-history traits of species (slow growth rate or low recruitment) and structural complexity (complex physical structures) (Buhl-Mortensen et al., 2019; F Enrichetti et al., 2019; Thompson et al., 2016).

Although fishing represents the major threat to VMEs, other relevant human activities are also responsible for their damage as is the case for mining, dredging, anchoring, drilling, producing oil and gas, telecommunications, pollution (from shipping, litter, waste), biological invasions and climate changing (ocean warming and acidification) which can physically impact the seabed as well as enhance sedimentation and change other key ecosystem conditions (Aguilar et al., 2017; Kazanidis et al., 2019; Piazzi et al., 2019; Thompson et al., 2016).

In this regard, algal and animal forests (i.e., animal aggregations and reefs), from shelf to deep-sea habitats, are prone to constitute vulnerable ecosystems owing to their important functionality and complex three-dimensional structure (Bekkby et al., 2017; Francesco Enrichetti et al., 2019). These include seagrass meadows, kelp and macroalgal forests, coralligenous (including maërl) beds, coral gardens, sponge aggregations, areas with gorgonian forests and various deep-sea habitats as seamounts, canyons, coral gardens and hydrothermal vents. Additionally, these ecosystems have an important representation in the North-East Atlantic Ocean and Mediterranean Sea and most of the ones occurring at shelf depths can be found at the circalittoral zone – macroalgal forests, coralligenous beds, coral gardens, sponge aggregations, areas with gorgonian forests (Bekkby et al., 2017; EUSeaMap, n.d.-a, n.d.-b; Evans et al., 2016; Tempera et al., 2013). According to Bekkby et al. (2017), complex three-dimensional animal forests comprise the most challenging ecosystems to successfully protect and restore (also evident on Fig. 5).



Features

Habitat types	Region	Dynamics	Connectivity	Spatial distribution	Structural complexity	Diversity	Vulnerability/fragility	Restoration potential
Shallow soft - Seagrass meadows	MED/Baltic/ NEA	⬜	⬜	W	🟥	🟥	🟥	⬜
Shallow hard - *Laminaria hyperborea* kelp	NEA	🟩	🟩	W	🟥	🟥	🟥	🟩
Shallow hard - *Saccharina latissima* kelp	NEA	🟩	🟩	W	🟥	🟥	🟨	🟩
Shallow hard - Macroalgal forests (shallow)	MED	🟨	🟨	W	🟥	🟥	🟨	🟨
Shallow hard - Macroalgal forests (deep)	MED	🟥	🟨	W	🟥	🟥	🟥	🟨
Shallow hard - Coralligenous assemblages	MED	🟥	🟥	W	🟥	🟥	🟥	🟥
Deep sea - Coral gardens	Azores	🟥	🟥	W	🟥	🟥	🟥	🟥
Deep sea - Soft sediment communities	MED/CNA	⬜	NA	NA	🟥	🟥	🟥	🟥

Legend — **Degree**: 🟩 Low 🟨 Medium 🟥 High ⬜ Mixed

NA=Not Available, W=Widespread

Figure 5. Illustration of the degree each biological trait impacts the achievement of restoration goals of several examples of VMEs. Retrieved from Bekkby et al., 2017.

Tropical and temperate circalittoral biogenic reefs (or coralligenous assemblages) were shown to be highly influenced by light levels, to have slow growth rates and low recruitment rates of structuring species as sponges, cnidarians, bryozoans and tunicates, which have similarly shown slow growth rates and long-life span. Furthermore, the coralligenous communities seem to be greatly affected by global stressors such as climate change (e.g., thermal anomalies) and mechanical damage from fishing, although the presence of invasive species, the increase in sedimentation and nutrient enrichment pose also serious threats. Plus, these pressures usually act simultaneously (Bekkby et al., 2017; Piazzi et al., 2019). Protecting such assemblages also stems from their crucial role on providing important ecological services and goods regarding, for instance, fisheries and the balance of CO_2, as well as on representing key indicators of environmental quality (Francesco Enrichetti et al., 2019; Piazzi et al., 2019).

Cold-water corals, either reefs, composed of scleractinian species, or gardens, built by conspicuous gorgonians, soft corals, seapens, antipatharians and hydrocorals sustain a complex structural habitat which provides both functional significance, as refuge, source of food, spawning areas, nursery areas; and services, such as carbon storage and nutrient remineralization. However, such habitat bioengineers are also slow-growing and long-lived species which normally colonize small and fragmented areas on hard substrate and high current flow habitats. Thus, these biotopes are threatened as well by ocean acidification and warming (climate change) and demersal fishing which can change the community composition since complex black corals and gorgonians' morphotypes are more vulnerable/exposed (Bekkby et al., 2017).

Similarly, sponge aggregations form complex three-dimensional habitats of slow-growth organisms that can display arborescent and fragile forms vulnerable to sedimentation and hydrodynamics (EUNIS, n.d.; Kazanidis et al., 2019; Tempera et al., 2013).

Thus, the urgent need to identify and protect these ecosystems requires detailed documentation of traits regarding the referred FAO criteria together with the bottom fishing footprint on those areas in order to ensure fishing grounds do not match areas where VMEs occur or are likely to occur (F Enrichetti et al., 2019; Thompson et al., 2016). This identification process has been done by directives as the MSFD based on habitat maps using the EUNIS habitat classification common language to ensure a common direction of VMEs protection and/or restoration between member states (Allee et al., 2000; Bekkby et al., 2017; F Enrichetti et al., 2019; Galparsoro et al., 2012).

The Azores archipelago already encompasses VMEs as seamounts and deep-sea fields of hydrothermal vents, cold-water corals and deep-sea sponge aggregations (Abecasis et al., 2015; Bekkby et al., 2017). Nevertheless, knowledge regarding the full spatial distribution of these ecosystems is still lacking in this region, as for many others (Bekkby et al., 2017; Pham et al., 2015).

THE AZORES

The Azores is a mid-north Atlantic archipelago composed of nine islands scattered across an extent of 617 km between the latitudes 39° 44' N – 36° 55' N and longitudes 31° 15' W – 25° 00' W. It is located on the Azorean Microplate in the junction between the Eurasian, North-American and African plates (Fig. 6) as well as at the northern edge of the North Atlantic Subtropical Gyre. The archipelago is divided in three groups of islands: Flores and Corvo in the Western group; Faial, Pico, São Jorge, Graciosa and Terceira in the Central group; São Miguel and Santa Maria in the Eastern group, together with several rocks and reefs known as the Formigas islets (at northeast of Santa Maria). The Azores belong to the Macaronesia biogeographical zone as well as the Madeira archipelago (Portugal), Cape Verde (Cape Verde) and the Canary Islands (Spain) (Amorim et al., 2015; Ojamaa, 2015; Tempera et al., 2013; Wallenstein, Neto, Alvaro, & Santos, 2008; Wallenstein, Neto, Alvaro, & Tittley, 2008).

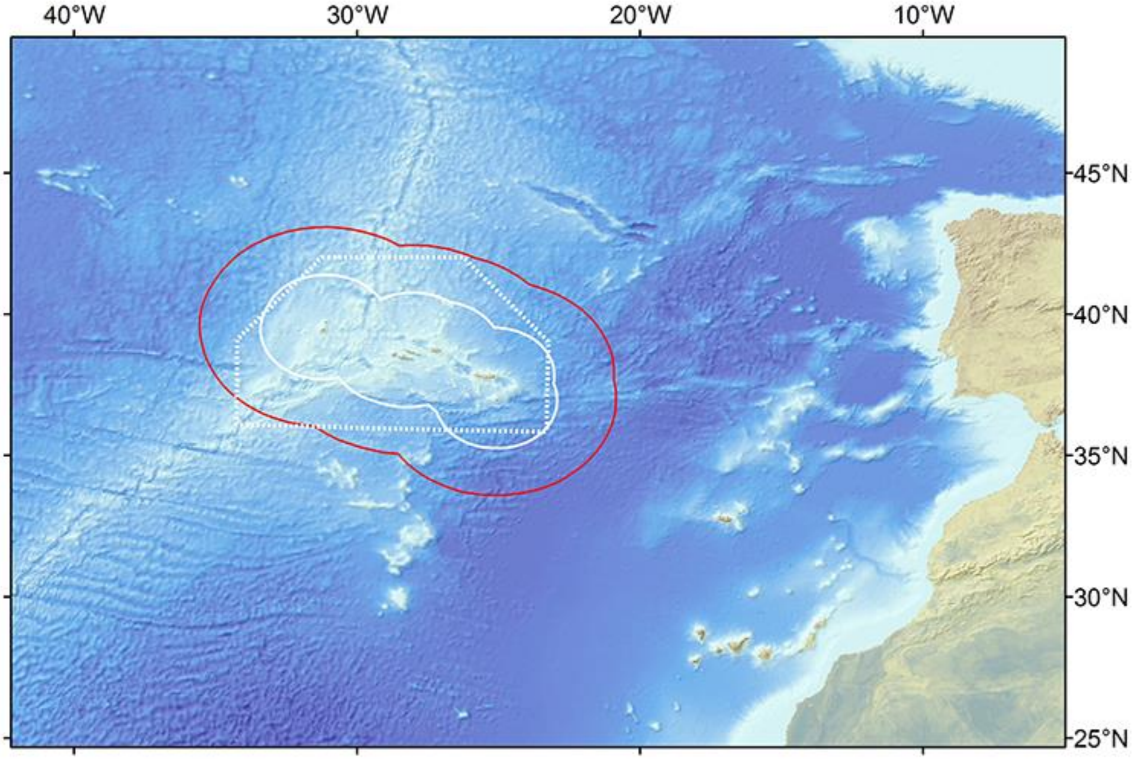


Figure 6. The mid-north Atlantic Ocean showing the Azores archipelago region, its exclusive economic zone (red line), the 100 nm limit (solid white line) and the area in which trawling is banned area (dotted white line). Retrieved from Morato et al. (2016) https://www.frontiersin.org/articles/10.3389/fmars.2016.00245/full

The islands have a volcanic origin which explains their narrow shelves (from a few hundred meters to a few kilometers) and the subsequent flanks reaching 1000 m depth ca. 200 m offshore (Amorim et al., 2015; Ojamaa, 2015; Tempera et al., 2013; Wallenstein, Neto, Alvaro, & Tittley, 2008). The shoreline is predominantly rocky with a geomorphology varying between cliffs and rocky beaches of irregular rock sizes. Only pocket beaches and sheltered areas are composed by sediment. These geomorphological characteristics are the outcome of the shoreline exposure to the Azores Current and the North Atlantic Current's southern branch (both branches of the Gulf Stream), with a small tidal range, as well as to medium/high levels of wave action. Being in a low vortex activity area, the currents represent the main source of water dynamic and temperature variability (Amorim et al., 2015; Bashmachnikov et al., 2004; Ojamaa, 2015; Tempera et al., 2013; Wallenstein, Neto, Alvaro, & Tittley, 2008). These currents also maintain Azorean waters at an average temperature of 17 – 23 ºC. The combination of shore geomorphology, continental shelf and wave dynamics provide an environment for a wide variety of fauna and flora communities to develop very differently when compared to those of the mainland Europe (Wallenstein, Neto, Alvaro, & Tittley, 2008).

Apart from the islands, the Azorean Plateau is marked by its rich topography owing to the 400 seamounts, fracture zones, hydrothermal vents and deep coral reefs (Amorim et al., 2015; Ojamaa, 2015).

The archipelago's almost 1 million km^2 of water column and seafloor surrounding the islands are under Portugal's marine jurisdiction (the Azores Exclusive Economic Zone, EEZ) and, as Portugal is a member of the Marine Strategy Framework Directive, the country is responsible to fulfill the policies stablished by the directive in order to maintain or obtain a good marine environmental state until 2020. Moreover, Portugal recently claimed the extension of the continental shelf that expands Portuguese sovereignty, of the seafloor, to approximately twice the area above mentioned (EMEPC, 2014; Governo dos Açores, 2014; Tempera et al., 2013).

As a result of its conditions, the Azorean rocky intertidal and sublittoral shore is dominated by mats of turf forming algae without abundance of the characteristic canopy-forming brown algae of the North European sheltered and moderately wave-exposed shores of temperate zones (Wallenstein, Neto, Alvaro, & Santos, 2008; Wallenstein, Neto, Alvaro, & Tittley, 2008).

With no clear definition regarding the limits of the circalittoral for Azores, it was suggested to start around 80 m as the last infralittoral macrophyte *Laminaria ochroleuca* disappears and the seabed receives 1% of surface irradiance, concordant with the previously used threshold to mark the transition to the circalittoral (Amorim et al., 2015; UKSeaMap, 2010; Wallenstein, Neto, Alvaro, & Tittley, 2008). *L. ochroleuca* can, although seldomly, occur in some of these biotopes as in rocks covered by "mixed beds of circalittoral oysters (Neopycnodonte cochlear) and sessile clams (Chama circinata)" (Amorim et al., 2015; Tempera et al., 2013; Wallenstein, Neto, Alvaro, & Santos, 2008; Wallenstein, Neto, Alvaro, & Tittley, 2008).

As Azorean circalittoral biotopes were poorly surveyed, efforts were done to assess these biotopes through already published literature (of the supralittoral, eulittoral, infralittoral biotopes found on Azores shelves) and infralittoral and circalittoral surveys performed by IMAR/DOP-UAç such as the sampling of habitats at 80 – 255 m depth from the Faial-Pico channel by a ROV (Remote Operated Vehicle) (Tempera et al., 2013). This habitat inventory highlighted that various biotopes at levels 4 to 6 (of the EUNIS habitat classification) illustrated previously undescribed assemblages, including the circalittoral zone. Among the several biocenosis found, some were particularly 'charismatic' when referring to this biological zone. These include oyster beds, on hard and mixed sediments (Tempera et al., 2013). In hard bottoms, the main habitats were *Polyplumaria flabellata* gardens and sponge aggregations along with habitats characterized by mono-specific aggregations of *Nemertesia ramosa* or *Antipathes subpinnata* as well as by dominance of sponge and hydrarian communities. In contrast to other hardbottom island slopes and seamounts rich in cold-water coral communities, in the Azores, *A. subpinnata* is one of the sole two species of black coral reported to form dense aggregations in the archipelago (alongside *Antipathella wollastoni*) describing patches of colonies on highly hydrodynamic vertical bedrock facies. Plus, it is considered to constitute the deepest black coral garden recorded so far in the Northeastern Atlantic Ocean and the single one to be monotypic (150-196 m). Coral species are mostly represented by the abundant whip-like gorgonian *Viminella flagellum* spread across the circalittoral depth range and *Alcyonium* spp. recorded between 120 – 170 m (de Matos et al., 2014; Gomes-Pereira et al., 2012; Tempera et al., 2013).

Nevertheless, the habitat inventory also highlighted the lack of information regarding the circalittoral faunal communities and the geographical inconsistency of the data available which, together with the differing biotopes proposed, highlight the pressing need to enhance consistent and comprehensive circalittoral data to continue identifying and mapping the Azorean biotopes (Galparsoro et al., 2012; Peran et al., 2016).

Commercial fishing, tourism and marine traffic, followed by sand dredging comprise essential economic activities for the regional economy, which also pose or are likely to pose threats to the Azorean marine environment. The local commercial fishing fleet is 90% represented by small-scale vessels (<15 m) which use less fuel at the practices of, mainly, longline, handline and pole-and-line techniques. Together with the banning of pelagic and bottom trawling, the Azorean fishing sector was proved to result in both low environmental impact and discards, assuring the protection of vulnerable ecosystems. The cautious nature of these fishing practices leads to a more compatible fishing sector to the conservation direction of the changing economy, mostly MPAs, contrasting with the majority of the European maritime territories. However, some important issues still arise as: (i) non-targeted protected species are sporadically captured by the regional fisheries (which should pose no problem to conservation as long as it is carefully monitored); and (ii) foreign pelagic longline vessels (mainland Portugal and EU) fish on the EEZ unsupervised as well as they land directly on the mainland without reporting their catches to the Azorean authorities (Abecasis et al., 2015; Das & Afonso, 2017; Fauconnet et al., 2019).

Other sector relying on fueled vessels is the sustainable tourism which is considered the most important tertiary activity of the archipelago. This developing eco-tourism is regulated by regional policies and legislation which aim to promote environmental conservation and education. Furthermore, there is an essential marine traffic regarding both marine shipping and inter-island passengers transport which occasionally results in incidents, as oil pollution or collision with marine mammals, and should have been responsible for the introduction of invasive species. The seafloor is exploited by sand dredging, inshore, which impacts the seabed and associated ecosystems (Abecasis et al., 2015).

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