



Vertical distribution of epibenthic megafauna of a large seamount west of Cape Verde islands (tropical North Atlantic)

Dominik Scepanski¹ · Nico Augustin² · Manon Dünn¹ · Anja Scherwaß¹ · Joana R. Xavier^{3,4} · Johannes Werner¹ · Ann-Marie Waldvogel⁵ · Hartmut Arndt¹

Received: 7 August 2023 / Revised: 4 December 2023 / Accepted: 6 December 2023
© The Author(s) 2024

Abstract

Seamounts are thought to function as hotspots of megafauna diversity due to their topology and environmental characteristics. However, assessments of megafauna communities inhabiting seamounts, including diversity and density, are scarce. In this study, we provide megafauna diversity and density estimates for a recently discovered, not yet characterized seamount region (Boetius seamounts) west of Cape Verde (N17° 16', W29° 26'). We investigated the distribution of epibenthic megafauna over a large depth gradient from the seamount's summit at 1400 m down to 3200 m water depth and provided qualitative and quantitative analyses based on quantified video data. In utilizing an ocean floor observation system (OFOS), calibrated videos were taken as a horizontal transect from the north-eastern flank of the seamount, differentiating between an upper, coral-rich region (−1354/−2358 m) and a deeper, sponge-rich region (−2358/−3218 m). Taxa were morphologically distinguished, and their diversity and densities were estimated and related to substrate types. Both the upper and deeper seamount region hosted unique communities with significantly higher megafauna richness at the seamount's summit. Megafauna densities differed significantly between the upper (0.297 ± 0.167 Ind./m²) and deeper community (0.112 ± 0.114 Ind./m). The seamount showed a vertical zonation with dense aggregations of deep-sea corals dominating the seamount's upper region and colonies of the glass sponges *Poliopogon amadou* dominating the deeper region. The results are discussed in light of detected substrate preferences and co-occurrence of species and are compared with findings from other Atlantic seamounts.

Keywords Biodiversity · Habitat preferences · Video recording · Deep-sea ecology · Deep-sea corals · Glass sponges

Communicated by K.H. George

This article is a contribution to the Topical Collection *Seamounts and oceanic archipelagos and their role for the biodiversity, biogeography, and dispersal of marine organisms*

✉ Hartmut Arndt
Hartmut.Arndt@uni-koeln.de

¹ Institute of Zoology, General Ecology, University of Cologne, Zulpicher Str. 47b, 50674 Cologne, Germany

² Helmholtz Zentrum für Ozeanforschung GEOMAR, Wischhofstrasse 1-3, 24148 Kiel, Germany

³ CIIMAR—Interdisciplinary Centre of Marine and Environmental Research of the University of Porto, 4450-208 Matosinhos, Portugal

⁴ Department of Biological Sciences, University of Bergen, Thormøhlensgate 53A, 5006 Bergen, Norway

⁵ Institute of Zoology, Ecological Genomics, University of Cologne, Zulpicher Str. 47b, 50674 Cologne, Germany

Introduction

By covering more than 50% of the Earth's surface, the deep-sea is known as the planet's largest habitat, containing a variety of unique geomorphological structures (Watling et al. 2013; Kennedy et al. 2020). With estimates of at least 14,000 (Yesson et al. 2011; Lapointe et al. 2020a, b) and up to three million (Consalvey et al. 2010) globally distributed submerged mountains, so-called seamounts constitute one of the most common geomorphological features of this habitat (Clark et al. 2011). Traditionally defined as structures of volcanic origin rising a minimum of 1000 m above the seabed (Consalvey et al. 2010; Du Preez et al. 2016), modern definitions include all topographically distinct and fully submerged elements having an elevation greater than 100 m (Consalvey et al. 2010; Kvile et al. 2014; Victorero et al. 2018). Consequently, seamounts typically differ in depth, morphology and their local environments, further resulting in different faunal communities across and within structures (e.g. Victorero et al. 2018; Lapointe et al. 2020a, b).

Overall, deep-sea taxa often accumulate at seamounts, as topography-induced upwellings provide access to higher amounts of food particles (Genin 2004; Rowden et al. 2010; Clark et al. 2010) in the otherwise nutrient-poor deep-sea (e.g. Smith and Demopoulos 2003; Johnson et al. 2007; Smith et al. 2008). The topology of seamounts may alter currents of deep water and create sites with varying hydrographic conditions, resulting in local removal and deposition of soft sediments (e.g. Consalvey et al. 2010; Clark et al. 2010; Davies et al. 2015). Combined with their great physical complexity including craters, canyons and terraces, a variety of unique microhabitats, scattered all over a seamount, provides favourable conditions for numerous deep-sea taxa (e.g. Roberts et al. 2006; Buhl-Mortensen et al. 2010; Ramiro-Sánchez et al. 2019). Considered as biodiversity hot spots hotspots (Morato et al. 2010; Davies et al. 2015) not only include aggregations of suspension-feeding deep-sea corals or sponges (e.g. Xavier et al. 2015; Perez et al. 2020, Meyer et al. 2022) but also attract large marine predators like sharks and others (Morato et al. 2008). Both deep-sea corals (Roberts et al. 2006; Baillon et al. 2012; Braga-Henriques et al. 2013) and Porifera (e.g. Beaulieu 2001; Beazley et al. 2013; Ramiro-Sánchez et al. 2019) are in addition known to form structural habitats which further supports the coexistence of a variety of deep-sea fauna.

Due to the unique topological characteristics of most seamounts, each structure possesses distinctive environmental characteristics (Victorero et al. 2018). Combined with benthic seamount communities being highly affected by depth-related variables, faunal communities typically differ across systems, forming unique zonings (e.g. Kovalenko et al. 2012; Victorero et al. 2018; Lapointe et al. 2020a, b; Lapointe 2021). For this reason, a general ecological and environmental characterization is challenging, if at all possible without a broad assessment and comparison across seamount habitats. However, even today, the number of studies comprehensively investigating and comparing seamount megafauna communities is still low (Kvile et al. 2014; Victorero et al. 2018). In a decade marked by growing concerns about destructive activities like seafloor mining or oil drilling (Clark et al. 2010; Watling et al. 2013), the lack of studies is significant, given the importance of obtaining data for implementing effective conservation measures in seamount ecosystems. With our study, we extend available resources by providing novel and unique data on epi-megafauna from a deep, not yet characterized seamount west of Cape Verde Islands (Augustin in Arndt et al. 2017). We named this group of seamounts “Boetius Seamounts” to honour Antje Boetius for her commitment to protecting the oceans. The community composition, structure and density of epi-megafauna were studied using video-recordings taken during the deep-sea expedition of R/V Meteor (M139). Besides estimating the impact of substrate type, water depth, as well as species coexistence, we

investigated the following hypotheses: (i) megafauna communities inhabiting the seamount’s upper region will show greater diversity and quantity than those residing in deeper regions, (ii) megafauna communities will accumulate in a characteristic zonation with changes in depths and (iii) megafauna taxa will show a preference for specific substrates.

Material and methods

Study area and habitat description

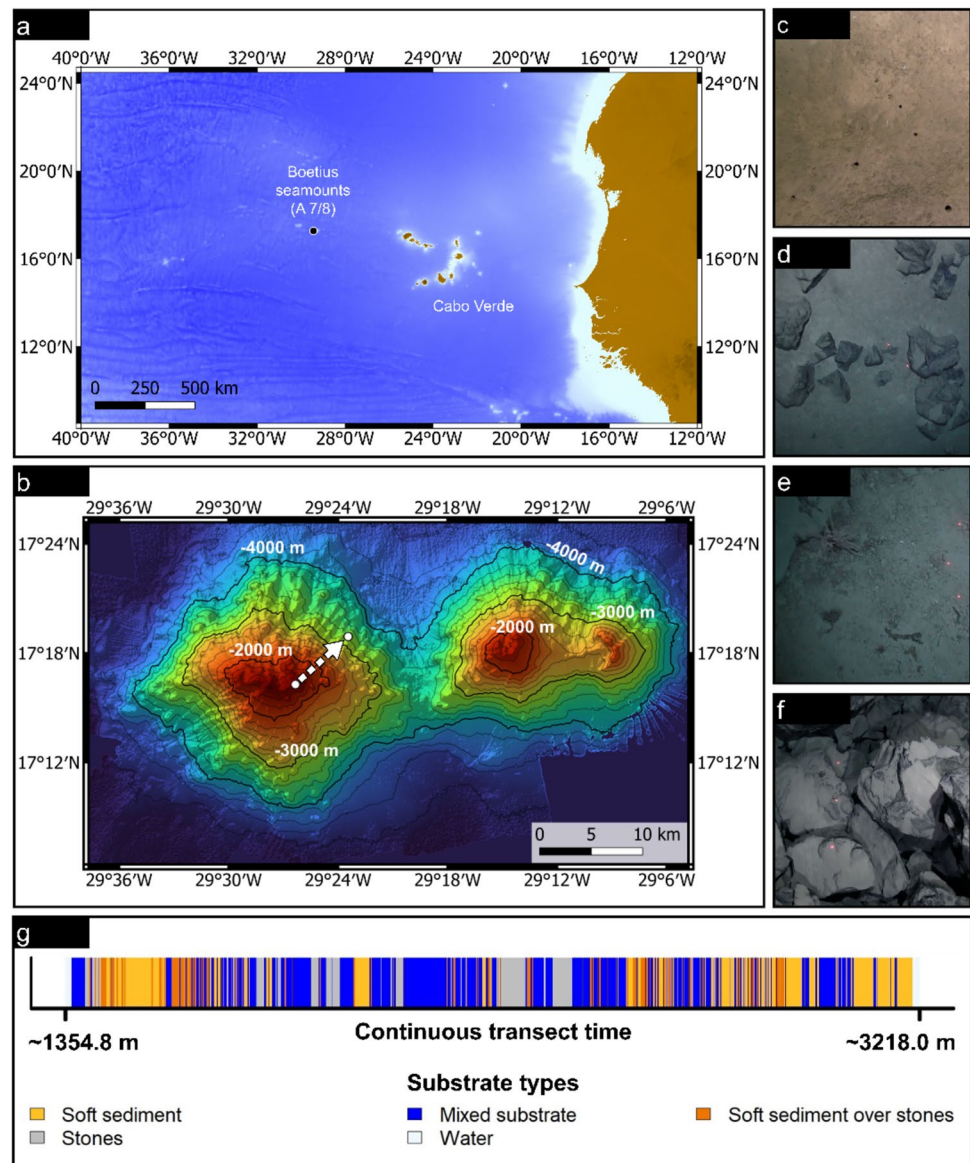
Following the R/V Meteor expedition M139, a previously unexplored, tropical North Atlantic seamount (Boetius Seamounts) was chosen as the study area and investigated using the ocean floor observation system (OFOS) camera dive at the 6th of August 2017 (Fig. 1; Arndt et al. 2017). Despite being recorded with a single OFOS dive, the seamount’s upper and deeper regions were handled as separate sampling stations. As a result, there were two sampling stations: an upper (station A7/8 [1]) and a deeper (station A7/8 [2]) seamount region (see Online Supplement Tab. S5).

The investigated seamount was located in an area of a group of three solitary, conical-shaped seamounts (Boetius Seamounts) west of Cape Verde, being the largest and most western located (Fig. 1a, e). OFOS videos were taken downslope as a single transect between N 17° 16.28', W 29° 26.32', at 1355 m and N 17° 18.91', W 29° 23.45', at 3218 m depth, covering a total surface area of approximately 28070 m². In its entirety, the seamount’s topology was dominated by a rough and heterogeneous, rock-dominated surface with several observable talus flows and smaller cones (Fig. 1k). Furthermore, the upper region of the seamount (station A 7/8 [1]) showed relatively low rates of sediment deposition, while the amount of soft substrate covering the seamount’s surface noticeably increased towards the deeper part (station A 7/8 [2]; Fig. 1k).

Video sampling and surveyed parameters

High-resolution video documentation was conducted using an ocean floor observation system (OFOS), providing a continuous documentation through several, automatically generated video files without time gaps in between. Given by the Helmholtz Centre for Ocean Research GEOMAR, the OFOS consisted of a Launcher, a HD-CS-camera system from Sea & Sun Technology GmbH (Trappenkamp, Germany) with a HD camcorder (CANON Legria, Tokio, Japan, 1920 × 1080 pixels resolution) integrated in a titanium housing with borosilicate dome port, LED floodlights from Bowtech (Bowtech Products Ltd., Aberdeen, UK), as well as three laser pointers. Towed behind the research vessel and moving at an approximate speed of 0.4 kn (0.206 m s⁻¹), the OFOS was mounted in a downward position with a

Fig. 1 Collective image of the Boetius Seamount's location and topology (**a, b**; modified from Arndt et al. (2017) and created with the GEBCO Grid tool (© GEBCO 2020)); distinguished substrate types (**c–f**); and the changes in substrate composition along the seamount transect (**g**). **a, b** Represent the overall location and topology of the western seamount station A 7/8 investigated by the M139 expedition, with a white arrow showing the direction of the dive track. **c–f** Display the different substrate types soft sediment (**c**); mixture of hard and soft sediment (**d**); soft sediment covering stones (**e**); and stones (**f**). **g** Displays the substrate composition along the seamount transect, differentiating between water (camera in water column without visible seafloor) and in displayed substrate types



camera system and its surrounding laser pointers all facing the ocean floor. While the upper and lower lasers are fixed in a straight, downward-facing position to throw two stationary laser points on the ocean floor, the third one is tilted down sideways, producing a red spot moving, depending on the distance between ground and OFOS on a horizontal line between the other dots. Because of their constant distance of 50 cm, the location of the produced upper and lower laser points enabled size measurements of documented fauna as well as the observed ground area. When all three laser points appeared in one line on the ground, the distance between OFOS and the seafloor is exactly 1.5 m, with the assumed average distance between OFOS and the ocean floor being slightly greater than this (assumingly 2 to 3 m).

Video data were live transmitted to the research vessel. Assessment and processing, including the comprehensive

manual inspection of the videos, were carried out after the expedition. Surveyed parameters included quantification and classification of deep-sea fauna along the transect. Additional parameters registered were associations of morphotaxa to each other and to the substrate. Megafauna (epifauna) visible on/above the deep-sea floor were considered here to be exclusively epi-megafauna, i.e. exclusively taxa larger than 2 cm, while buried organisms, such as polychaetes, were excluded from quantification here. Furthermore, sediment composition was continuously recorded throughout the OFOS dive. Four substrate categories were considered, partially adapted from Wentworth (1922): (1) soft sediment (more than 80% soft sediment), (2) mixed substrate, (3) soft sediment over rocks and (4) rocks (more than 80% rubble/bedrock; Fig. 1c–f).

To enable further quantitative calculations, the areas of the observed deep-sea floor were measured for every video

file and the complete dive. Travel distance was estimated based on traveling speed and the time between critical situations (e.g. ground visibility, change in speed, start hoisting). Three randomly selected moments of each replicate (video file) were used for width calculation (mean width 4.28 m). We estimated the density of organisms for each video file by combining the length and width of observation of the complete dive together with the duration of each video file that showed the ocean floor. This was then summed up for the whole dive.

Morphotaxa annotations and diversity assessment

To quantify and classify the seamount's epibenthic megafauna community, we identified observed animals to the lowest possible taxonomic rank by examining their morphological characteristics. Besides online research, we utilized the photographic identification catalogue from Vinha et al. (2022), the deep-sea species identification application Deep Sea ID v1.2 (Glover et al. 2015), its underlying database,

the World Register of Deep-Sea Species (WoRDSS) (Glover et al. 2023), as well as the consultation of experts for specific groups. Nevertheless, circumstances emerged where animals, despite distinctive morphological characters, could not be taxonomically distinguished but were dealt as different morphotaxa. Consequently, the number of morphotaxa (morphotaxa richness) was used as the primary metric for diversity (see Table 1). Megafauna morphotaxa were assigned to artificially created higher-taxon groups for comparisons. Those groups comprised Porifera, Actiniaria, deep-sea corals, Crustacea, Crinoidea, Holothuroidea, Asterozoa, Echinoidea and Teleostei. To cover all Cnidaria with the characteristic coral form, we opted for the term "deep-sea corals", although it is not a taxonomic category to separate Actiniaria and highlight coral gardens' role as structural habitats (Roberts et al. 2006). Roberts et al. (2006) grouped soft corals (Octocorallia), stony corals (Scleractinia), black corals (Antipatharia) and hydrocorals (Stylasteridae) under this term, despite their distinct ecological lifestyles. The nomenclature was also chosen to ease comparisons with

Table 1 List of the total number of morphotaxa and mean morphotaxa richness (mean \pm SD) of the upper, deeper and entire seamount transect region

Taxa	Upper region A 7/8 [1] ($n = 7$)		Deeper region A 7/8 [2] ($n = 7$)		Total ($n = 14$)	
	Number of morphotaxa	Mean richness	Number of morphotaxa	Mean richness	Number of morphotaxa	Mean richness
Total	40	22 \pm 2.449	30	12.286 \pm 6.184	44	17.143 \pm 6.769
Porifera	3	2 \pm 1.155	3	2.143 \pm 1.069	3	2.071 \pm 1.072
<i>Poliopogon amadou</i>	1	0.429 \pm 0.535	1	0.857 \pm 0.378	1	0.643 \pm 0.497
Undet. Hexactinellid	2	1.571 \pm 0.787	2	1.286 \pm 0.756	2	1.429 \pm 0.756
Actiniaria	5	2.429 \pm 1.272	2	0.571 \pm 0.535	5	1.5 \pm 1.345
Deep-sea corals	12	9.143 \pm 1.952	7	1.714 \pm 1.976	12	5.429 \pm 4.292
<i>Iridogorgia</i> sp.	1	0.571 \pm 0.535	/	/	1	0.286 \pm 0.469
Undet. Scleralcyonacea	1	0.857 \pm 0.378	1	0.714 \pm 0.488	1	0.786 \pm 0.426
Undet. Octocorallia	2	1.857 \pm 0.378	2	0.286 \pm 0.756	2	1.071 \pm 0.997
Undet. deep-sea corals	8	5.857 \pm 2.116	4	0.714 \pm 1.254	8	3.286 \pm 3.148
Crustacea	3	1.429 \pm 0.787	2	1.429 \pm 0.535	3	1.429 \pm 0.646
<i>Cancer</i> sp.	1	0.429 \pm 0.535	/	/	1	0.214 \pm 0.426
<i>Benthesicymus</i> sp.	1	0.143 \pm 0.378	1	0.571 \pm 0.535	1	0.357 \pm 0.497
Undet. Pandalidae	1	0.857 \pm 0.378	1	0.857 \pm 0.378	1	0.857 \pm 0.363
Crinoidea	2	0.857 \pm 0.69	1	0.286 \pm 0.488	2	0.571 \pm 0.646
Holothuroidea	1	0.286 \pm 0.488	4	1.571 \pm 1.134	4	0.929 \pm 1.072
Asterozoa	7	3.714 \pm 2.69	5	1.857 \pm 1.574	7	2.786 \pm 2.326
Undet. brisingid asteroid	1	0.571 \pm 0.535	1	0.714 \pm 0.488	1	0.643 \pm 0.497
Undet. Asterozoa	6	3.143 \pm 2.193	4	1.143 \pm 1.215	6	2.143 \pm 1.994
Echinoidea	/	/	1	0.571 \pm 0.535	1	0.286 \pm 0.469
Teleostei	7	2.143 \pm 1.069	5	2.143 \pm 1.464	7	2.143 \pm 1.231
Lophiidae	1	0.286 \pm 0.488	/	/	1	0.143 \pm 0.363
Macrouridae	1	0.286 \pm 0.488	1	0.286 \pm 0.488	1	0.286 \pm 0.469
Undet. Teleostei	5	1.571 \pm 0.976	4	1.857 \pm 1.464	5	1.714 \pm 1.204

similar designations in studies of Lapointe et al. (2020a, b), Victorero et al. (2018) or Davies et al. (2015).

Data analysis

Presented graphs and statistical tests were conducted using RStudio version 4.0.2 (RStudio®, Boston, MA, USA; R Core Team 2020). The following R packages were used: “car” (Fox and Weisberg 2019), “colorspace” (Zeileis et al. 2020), “cowplot” (Wilke 2020), “dplyr” (Wickham et al. 2021), “ggplot2” (Wickham 2016), “grid” (R Core Team 2020), “gridExtra” (Auguie 2017), “hrbrthemes” (Rubis 2020), “indicspecies” (de Cáceres and Legendre 2009, “janitor” (Firke 2023), “lawstat” (Gastwirth et al. 2020), “PMCMRplus” (Pohlert 2022), “RColorBrewer” (Neuwirth 2014), “Rcpp” (Eddelbuettel 2013), “reshape2” (Wickham 2007), “scales” (Wickham and Seidel 2020), “svglite” (Wickham et al. 2020), “tidyr” (Wickham 2020) and “tidyverse” (Wickham et al. 2019) as well as “vegan” (Oksanen et al. 2019). Furthermore, most graph arrangements were performed with Inkscape version 1.0.1 (© 2020 Inkscape Community), while maps were created using the GEBCO Grid tool (© GEBCO 2020) together with the open-source software QGIS version 3.28.3.

Despite continuous filming, we used video files automatically generated during video acquisition as replicates in order to obtain comparable replicates for statistical testing. Duration of filming was relatively consistent between files (video recordings with mostly similar lengths and a mean duration of 34 min and 46 s \pm 8 min and 38 s) (see Online Supplement Tab. S5). It must be stated that the OFOS dive, its speed and individual direction above ground could not be manipulated from the board, producing video files of variable areas and duration of random choice independent from the observer. In the end, a total amount of fourteen replicates were obtained from the OFOS dive recording. As mentioned before, the seamount was further split into two separate stations of different depths, the upper seamount region A7/8 [1] (with -1700 to -2100 m depth) and the deeper seamount region A7/8 [2] (with -2100 to -3300 m depth). Each station contained seven video files/replicates. We generated accumulation curves based on morphotaxa richness to clarify if enough area had been sampled to adequately represent the seamount’s megafauna community. This was done for the complete dive, as well as for the upper and deeper seamount region. Therefore, we utilized the vegan package’s `specaccum()` function, using the random method for 100 permutations. Corresponding graphs are provided in the Online Supplement (see Online Supplement Fig. S4).

We tested homoscedasticity of variances between variables and normal distribution within replicates with a Levene test and a Shapiro–Wilk test, respectively, for all parameters. In case of homoscedasticity and normal distribution of the

data, comparisons were performed using a one-way ANOVA followed by a post hoc Tukey test. Otherwise, comparisons were conducted using Kruskal–Wallis one-way analysis of variance and post hoc tests according to Dunn (pairwise comparisons using Dunn’s test for multiple comparisons of independent samples). To avoid unnecessary repetition while describing the results of statistical testing, information concerning the conducted test, sample size, degrees of freedom and p -value were only given at the respective text passage if no figure contained the corresponding data. Only differences with p -values below 0.05 were considered significant.

Concerning quantitative differences in megafauna diversity, the upper and lower seamount’s morphotaxa richness was calculated and compared between the corresponding locations. Using morphotaxa richness as a base, Shannon diversity, as well as evenness were additionally calculated in order to assess differences in megafauna diversity. For the calculation of the Shannon diversity index, means were acquired from the previously mentioned numbers of replicates.

The study investigated potential differences in megafauna community composition between the upper and deeper seamount regions by utilizing a non-metric multidimensional scaling (NMDS) plot. We used densities (counts of individuals per m^2) for each morphotaxon at the upper and lower seamount region together with Bray–Curtis distance measures. Replicates were identical to those used for calculating Shannon diversity (see above). Two additional NMDS plots explored whether higher taxonomic groups and morphotaxa favoured specific substrate types (soft sediment, stones, combinations of both as well as soft sediment covering stones). Here, the density of individuals was calculated for the distinguished substrate types, and Bray–Curtis distance measures were applied. As Bray–Curtis transformation cannot account for empty replicates, those lacking megafauna sightings over the corresponding substrate were excluded, resulting in a variable number of replicates per substrate type (soft sediment = 12 video files; mix = 11 video files; soft sediment over stones = 12 video files; stones 13 video files). For all three NMDS plots, stress values below 0.2 were considered reliable, values equal or higher than 0.3 were considered suspect, and those in between were interpreted cautiously. An analysis of similarity (ANOSIM) was conducted for each NMDS plot to validate if both seamount regions and distinguished substrate types differ in communities based on morphotaxa and/or higher taxonomic groupings. ANOSIM 9999 permutations and Bray–Curtis distances for dissimilarity were applied to the corresponding datasets. The “`r.g`” function (R Core Team 2020) was used to recognize correlations among chosen binary vectors. Additional indicator species analyses were conducted to identify whether, and, if so, which morphotaxa and/or higher taxonomic group were significantly associated with which seamount region and/or substrate type.

Potential differences between the upper and deeper seamount regions' total densities were investigated. Furthermore, densities corresponding to each distinguished higher taxonomic group were compared between the upper and deeper seamount regions. Later, presented region and higher taxonomic group-specific means were therefore obtained from the prior mentioned number of replicates. In addition, potential habitat preferences were investigated by comparing densities calculated for specific sediment types between those substrates (data shown in the Online Supplement).

Literature review process on comparable seamount megafauna communities

We performed a literature search to conduct a qualitative and quantitative comparison between this study's megafauna community and that of similar seamount and seamount-like systems of different regions of the North Atlantic. We analysed publications that investigated complete or subsets of megafaunal communities from comparable depths and provided information on their diversity and/or density. If the exact parameters were not available in the corresponding publications' texts or tables, parameters were estimated from graphs or, in case of some richness parameters summed up from provided taxa-lists. Furthermore, most densities had to be calculated based on the provided numbers of individuals, taxa-lists and/or supplementary material. Density calculations were based on dividing megafauna abundances (number of individuals) by the provided area investigated or by multiplying given total densities with given percentual values to estimate higher taxonomic group-specific densities. Overall, we included eight studies, comprising two from the southern and central North Atlantic (Victorero 2018; Victorero et al. 2018), four from the western North Atlantic (Cho 2008; Lapointe et al. 2020a, b; Lapointe 2021; Moore et al. 2003) and one from the northern North Atlantic (Meyer et al. 2022). These studies covered a total of 22 different seamounts and two seamount chains in the North Atlantic and one seamount-like slope in the arctic parts of the North Atlantic (see Online Supplement Tab. S3 and S4). Corresponding tables summarizing the outcomes of this literature review are attached in the Online Supplement.

Results

Megafaunal community structure and diversity

The analysis of the seamount's faunal diversity revealed a total amount of 6131 distinguished megafauna individuals, comprising 44 distinct morphotaxa (Fig. 2; Table 1). These

were summarized into 18 different megafauna morphotaxa belonging to nine higher taxonomic groups (Fig. 2; Table 1). Those higher taxonomic groups included Porifera, Actiniaria, deep-sea corals, Crustacea, Crinoidea, Holothuroidea, Asterozoa, as well as Echinoidea and Teleostei. Crustacea with *Cancer* and *Benthescymus* showed the greatest number of classified genera (Table 1). Other identified genera and species comprised the glass sponge *Poliopogon amadou* and the octocorallia *Iridogorgia*. Additionally, the decapod family Pandalidae as well as the Teleostei families Lophiidae and Macrouridae were observed (see Table 1 for more information).

Morphotaxa richness varied largely within each higher taxonomic group. We distinguished three Porifera, five Actiniaria and twelve deep-sea corals, three crustaceans, two crinoids, four holothurians, seven Asterozoa, one echinoid and seven Teleostei. Morphotaxa richness was significantly higher at the upper seamount region with 40 different morphotaxa, compared to the deeper region with 30 morphotaxa (Table 1), corresponding to a mean richness of 22.0 ± 2.5 morphotaxa ($n = 7$) and 12.3 ± 6.2 forms ($n = 7$), respectively (Fig. 3a).

Overall, neither Shannon diversity (upper region: 1.76 ± 0.51 ; deeper region: 1.21 ± 0.71) nor evenness (upper region: 0.57 ± 0.17 ; deeper region: 0.61 ± 0.25) showed significant differences between upper and deeper seamount regions (Fig. 3b, c).

Based on the NMDS plot, significant differences between the megafauna communities of the upper and deeper seamount regions were recorded, with a clear separation between the communities (Fig. 4). Overall, most morphotaxa were observed plotting inside or in close proximity to the region's occupied space. Supportive, the indicator species analysis revealed ten morphotaxa significantly associated with a specific region, nine with the upper (one Porifera, one Actiniaria, six deep-sea corals, one Holothuroidea and one Teleostei) and one (a Holothuroidea) with the deeper seamount region (see Online Supplement Tab. S1).

General occurrence of megafauna taxa with regard to the substrate type

Revealed by the NMDS plot, significant differences between megafauna communities inhabiting the different substrates on a higher taxonomic level were recorded, nevertheless, no clear separation between substrate types could be observed (Fig. 5). Excluding Echinoidea and Crustacea, all other higher taxonomic groups clustered inside an area covered by one or more habitat categories. Furthermore, the indicator species analysis showed exposed Echinoidea, Crustacea and Teleostei being significantly associated with soft sediment, while Porifera, Actiniaria, Crinoidea

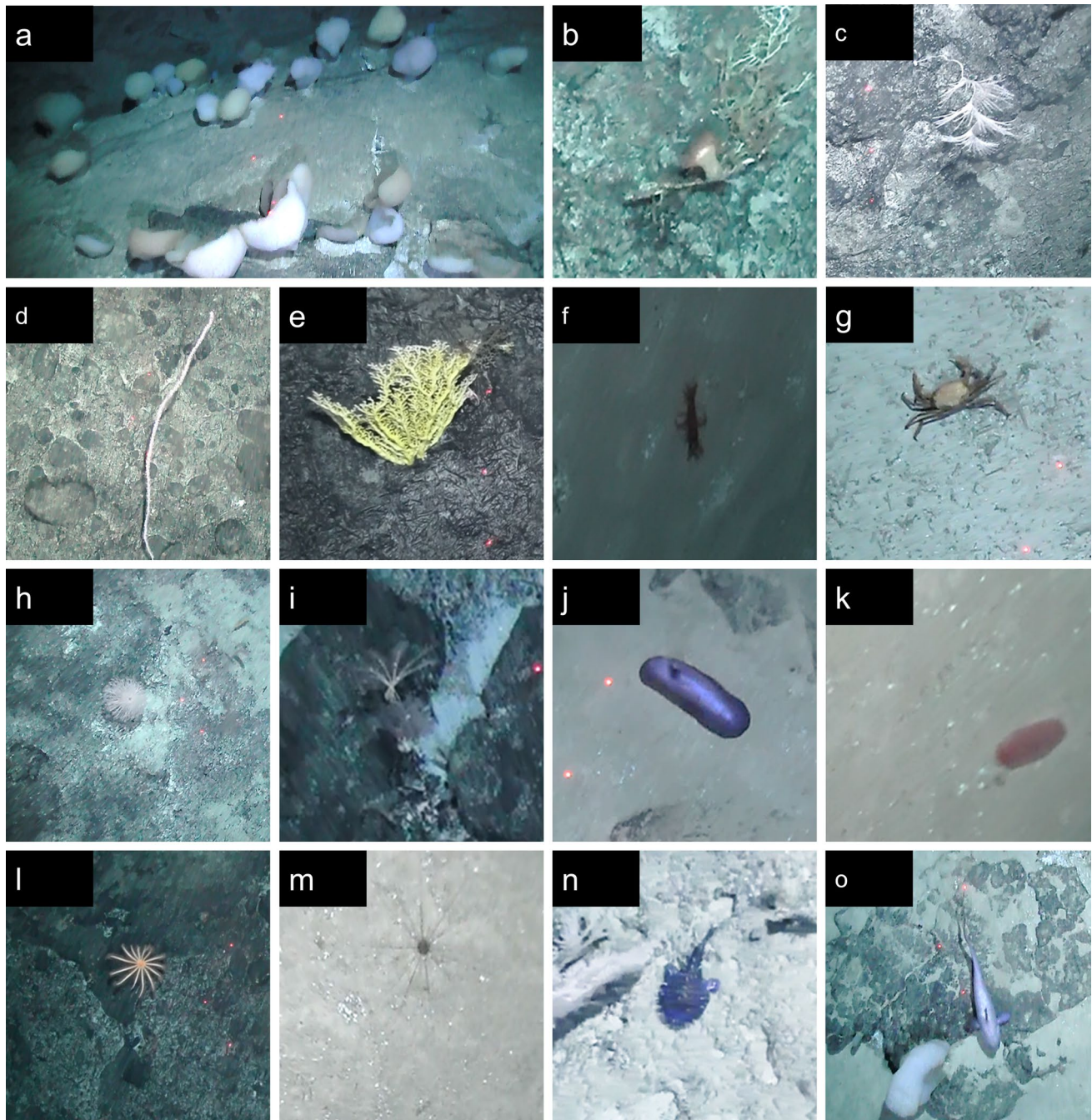


Fig. 2 Exemplary collection of observed (epi-) megafauna covering each distinguished higher taxonomic group. Representatives comprised of the **a** Porifera *Poliopogon amadou*; **b** an undet. Actiniaria; **c** examples of cold-water corals including *Iridogorgia*; **d** an undet. Scleralcyonacea; **e** an undet. deep-sea coral; **f, g** the crustaceans *Ben-*

thesicymus and *Cancer*; **h, i** two undet. Crinoidea; **j, k** two undet. Holothuroidea; **l** an undet. Brisingid asteroid as a representative for observed Asterozoa; **m** an undet. Echinoidea morphotaxon; **n, o** Teleostei of the groups Lophiidae and Macrouridae

and Asterozoa showed significant associations with stony habitats. In addition, all differentiated morphotaxa verified those results, revealing substrates being inhabited by significantly different communities on a morphotaxon level. Fifteen morphotaxa were significantly associated with one specific substrate (see Online Supplement Fig. S2 and Tab.

S2). Regarding distinguished morphotaxa, five were significantly associated with soft sediments (one Holothuroidea, one Echinoidea and three Teleostei) and six to stones (three Porifera, including *Poliopogon amadou*, four deep-sea corals, including *Iridogorgia* sp. and an undet. Scleralcyonacea, one Crinoidea and two Asterozoa).

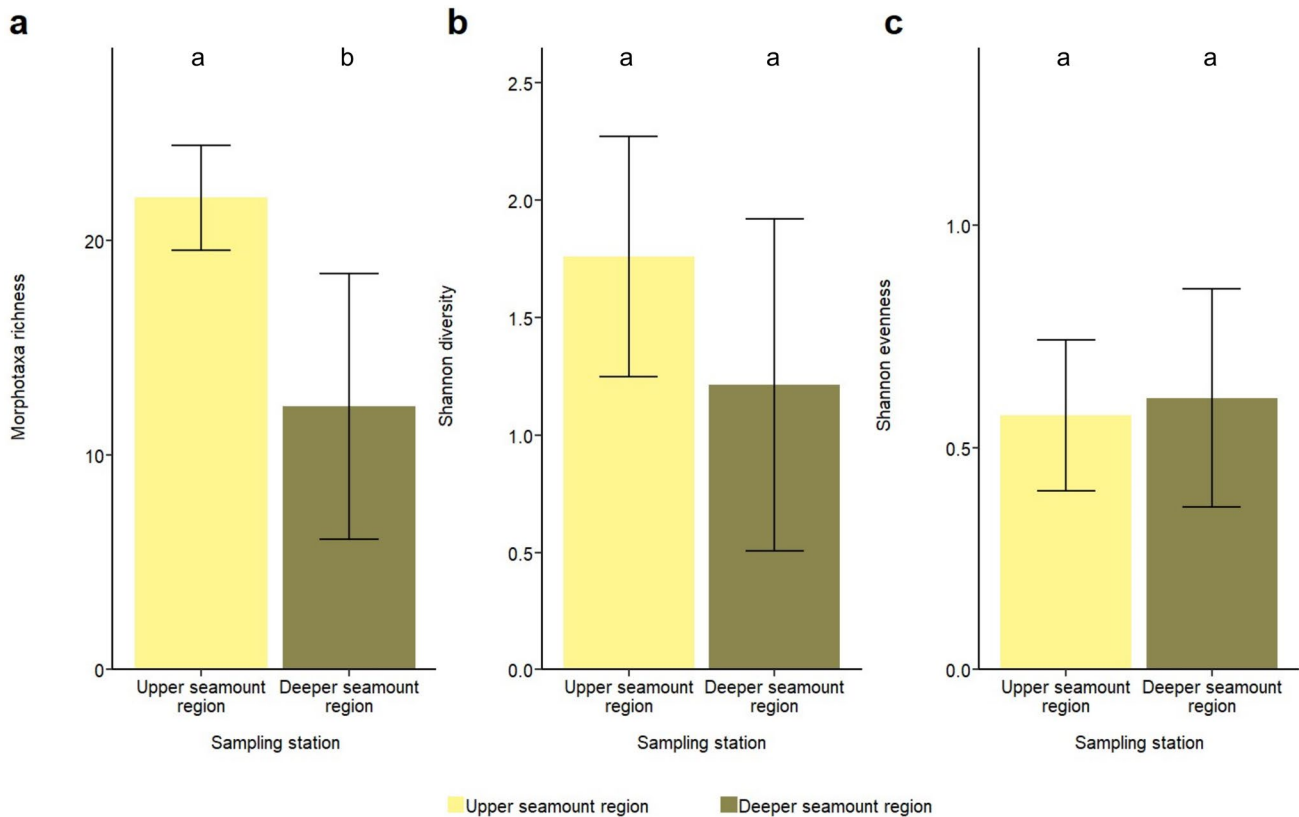


Fig. 3 Megafauna morphotaxa richness; **a** Shannon diversity; **b** and Shannon evenness; **c** based on morphotaxa richness at the different deep-sea regions (mean \pm SD). Area-specific parameters were calculated based on seven replicates each. Bars with different letters mark significant differences between the corresponding seamount regions

(**a** Test = one-way ANOVA with subsequent Tuckey-test, $df = 1$, F -value = 14.93, p -value = 0.00225; **b** Test = one-way ANOVA with subsequent Tuckey test, $df = 1$, F -value = 2.751, p -value = 0.123; **c** Test = one-way ANOVA with subsequent Tuckey-test, $df = 1$, F -value = 0.127, p -value = 0.728)

Investigating the complete seamount transect, Porifera, generally occurred mainly on stony habitats with mean densities of about $5.03 \times 10^{-2} \pm 7.92 \times 10^{-2}$ ind./m² (see Online Supplement Fig. S3). Significantly lower densities were detected when combinations of soft sediment and stones or soft sediment alone prevailed. Several sponge (morpho-) taxa, such as *Poliopogon amadou* (Kruskal–Wallis chi-squared = 19.194, $df = 3$, p -value = 2.49×10^{-4}) shared this preference. Actiniaria were observed on all sediment types, showing a significant preference for stony substrates over mixed ones on an overall level (see Online Supplement Fig. S3). Deep-sea corals mainly occurred on stony habitats with mean densities around $3.49 \times 10^{-2} \pm 5.01 \times 10^{-2}$ ind./m² (see Online Supplement Fig. S3). Four morphotaxa showed significant preferences for this habitat. Those included undetermined Scleractyonacea and *Iridogorgia* sp. preferring stones over soft (Kruskal–Wallis chi-squared = 10.985, $df = 3$, p -value = 1.18×10^{-2}) or all other substrate alternatives (Kruskal–Wallis chi-squared = 12.671, $df = 3$, p -value = 5.41×10^{-3}), respectively. Crustaceans significantly preferred soft sediments over pure stone alternatives

(see Online Supplement Fig. S3). Crinoidea in general (Kruskal–Wallis chi-squared = 11.44, $df = 3$, p -value = 9.57×10^{-3}) as well as one morphotaxon (Kruskal–Wallis chi-squared = 11.44, $df = 3$, p -value = 9.57×10^{-3}) showed significant preferences for rocks compared to both mixed and soft sediments (see Online Supplement Fig. S3). Except for one morphotaxon significantly favouring soft sediment over stony alternatives (Kruskal–Wallis chi-squared = 8.8053, $df = 3$, p -value = 3.20×10^{-2}), Holothurians showed no significant differences between substrates (see Online Supplement Fig. S3). One Asterozoa morphotaxon displayed substrate preferences, showing significantly higher densities on stones compared to mixed and soft sediments (Kruskal–Wallis chi-squared = 10.775, $df = 3$, p -value = 1.30×10^{-2}). Echinoidea occurred exclusively on soft and mixed substrates, lacking any significant preferences. Reaching mean densities of about $1.11 \times 10^{-3} \pm 1.34 \times 10^{-3}$ ind./m², freely swimming fishes were relatively more often observed over soft sediment (see Online Supplement Fig. S3). With the exception of one undetermined fish morphotaxon significantly preferring soft sediment over both mixed and stony habitats (Kruskal–Wallis

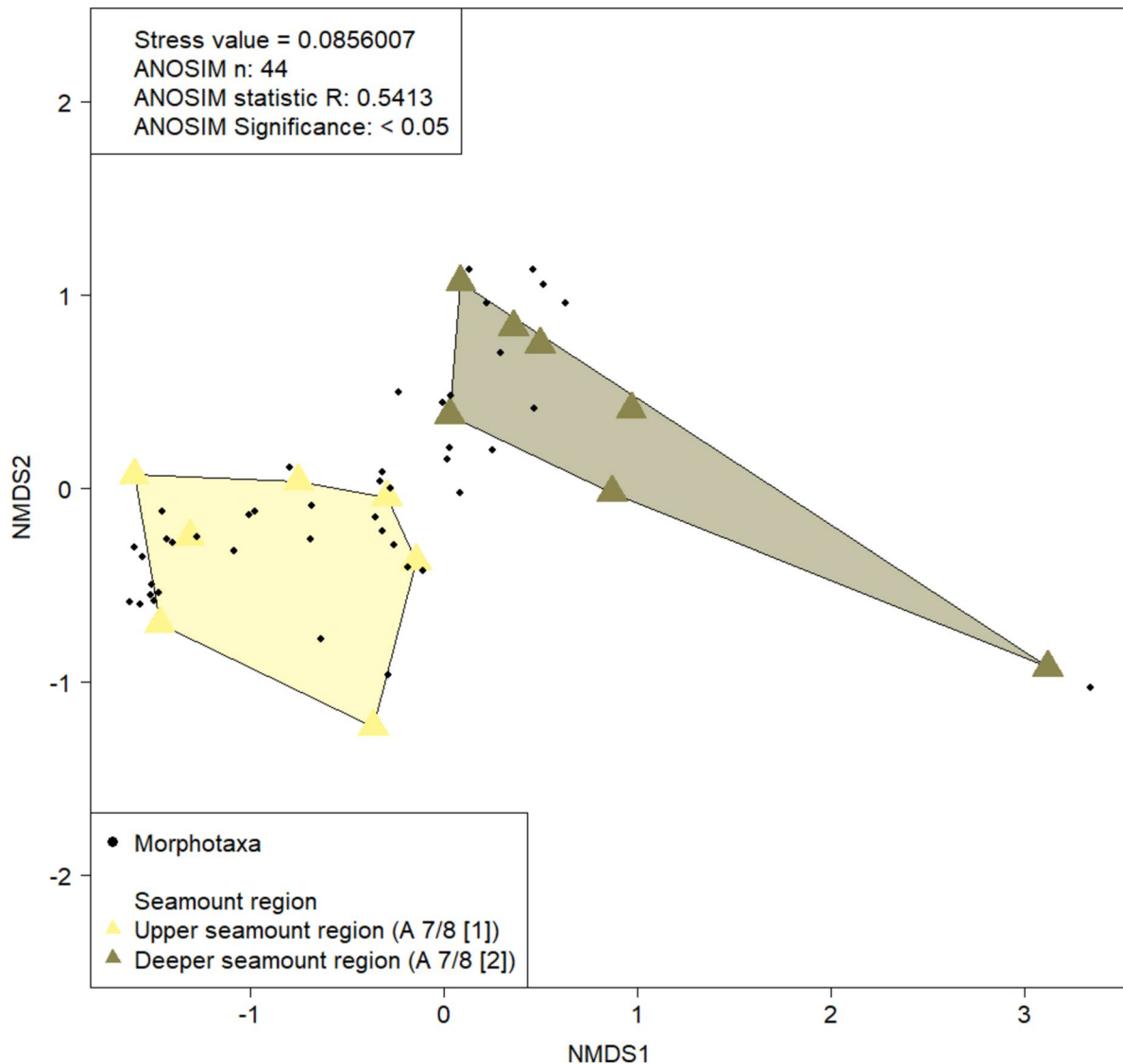


Fig. 4 Non-metric multidimensional scaling plot depicting ordination of all 44 quantifiable morphotaxa from each seamount region based on density data (given as number of individuals per m²), as well as Bray–Curtis distance measures. ANOSIM with 9999 permutations

and based on Bray–Curtis distance (amount of morphotaxa $n = 44$; number of replicates per region $n = 7$; stress-value = 0.0856007; R -value = 0.5413; p -value < 0.05)

chi-squared = 9.4352, $df = 3$, p -value = 2.40×10^{-2}), no significant preferences were detected for Teleostei.

Quantitative comparison of the different seamount regions

Overall megafauna densities were significantly higher at the seamount's upper region compared to the deeper region (Fig. 6, Table 2). There was an influence of depth on the densities of selected higher taxonomic groups as four showed significant differences between the regions (Figs. 7, 8; see Online Supplement Fig. S1). While both Actinaria and deep-sea corals reached significantly greater densities in

upper regions, both Holothuroidea and Echinoidea attained significantly greater densities at the seamount's deeper region. Both Porifera and Asterozoa showed notable—though not significant—changes in overall density with Porifera showing relatively greater values at the seamount's deeper region and Asterozoa reaching relatively greater densities at the upper regions of the seamount (Fig. 7; Table 1).

With increasing water depth, changes in the presence of specific taxa were observed (Figs. 7, 8; see Online Supplement Fig. S1). Deep-sea corals, indicators for the upper region, reached densities of up to 3.62×10^{-1} ind./m² and dominated, together with Asterozoa, the upper seamounts megafauna community by contributing roughly 43% and

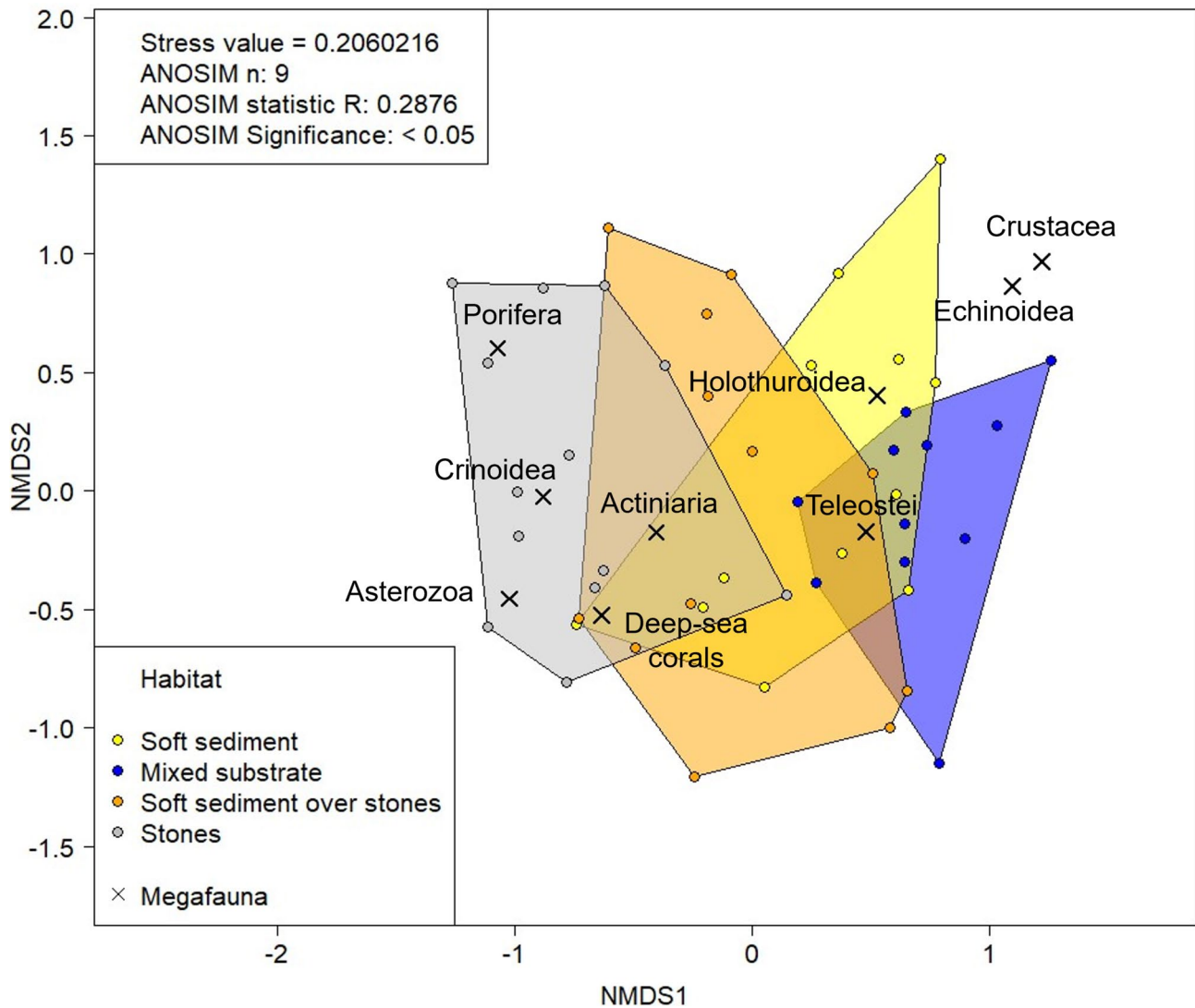


Fig. 5 Non-metric multidimensional scaling plot depicting ordination of all nine higher taxonomic megafauna groups over each substrate type based on density data (given as number of individuals per m^2), as well as Bray–Curtis distance measures. ANOSIM with 9999 per-

mutations and based on Bray–Curtis distance (amount of higher taxonomic groups $n = 9$; number of replicates per substrate: soft sediment = 12, mixed substrate = 11, soft sediment over stones = 12, stones = 13; stress-value = 0.2060216; R -value = 0.2876; p -value < 0.05)

42% to the total megafauna density respectively (Fig. 7 d; see Online Supplement Tab. S1). In the deeper region of the seamount, especially in regions deeper than 2500 m, Porifera dominated in terms of density, contributing about 74% to the deeper region's total megafauna density (Fig. 7e; see Online Supplement Fig. S1) with a local maximum of 3.1×10^{-1} ind./ m^2 (Fig. 8a). Most prominent were colonies of *Poliopogon amadou* (Fig. 8), contributing about 87.1% of the mean Porifera density measured at the lower seamount region (Fig. 7e; see Online Supplement Fig. S1) and a local maximum of 2.74×10^{-1} ind./ m^2 . Other megafauna forms were associated with either or both, deep-sea coral and Porifera aggregations, or the region between their dominance (Figs. 2, 8; see Online Supplement Fig. S1). As an example, teleost fishes reached their

highest relative numbers near deep-sea corals, while Asterozoa, Crinoidea and Actiniaria dominated the region between the aggregations of corals and sponges. Holothurians reached the highest densities in zones with *Poliopogon amadou* colonies (Fig. 8; see Online Supplement Fig. S1).

Discussion

Megafauna communities in comparison to other seamounts

With our investigation of the so far unexplored Boetius Seamounts near Cape Verde, we contribute one of the few

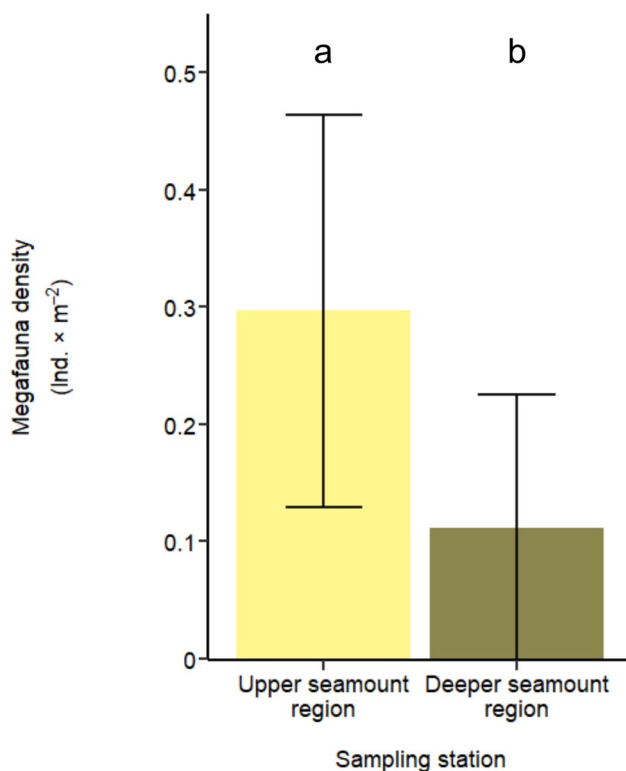


Fig. 6 Megafauna densities at the different seamount regions (mean \pm SD). Area-specific parameters were calculated based on seven replicates each. Different letters above bars mark significant differences between the sampling stations (Test = one-way ANOVA with subsequent Tuckey test, $df = 1$, F -value = 5.839, p -value = 0.0325)

quantitative datasets including both faunal diversity and estimates of densities. To contextualize these findings, we conducted a comparison with literature data from similar systems, including 22 seamounts and two seamount chains in the North Atlantic (Fig. 9). Such a comparison is not trivial, since differences in methodology, parameters and size fractions of the megafauna across studies made the comparison with our data set particularly challenging (see Online Supplement Tab. S3 and S4).

Within a biogeographic context, the North Atlantic Annan, Knipovich and Vayda seamounts, spanning depths from 200 to around 2700 m below the surface (Fig. 9; Victorero 2018; Victorero et al. 2018) were the closest related seamounts to the Boetius Seamounts. A study by Watling et al. (2013) associates these four seamounts with seamounts of the lower bathyal province BY4, the North (-east) Atlantic (Lapointe et al. 2020a, b; Lapointe 2021). The BY4 province is characterized by its specific water mass characteristics and a POC flux to the seafloor of about 5 g/m² per year (Watling et al. 2013). In terms of water mass characteristics, the shallower sections (~200 to 600 m below the surface) are flushed by the South-Atlantic Central Water, the middle sections (~700 to 1400

m below the surface) are flushed by the Antarctic Intermediate Water, and the deepest sections (>1500 m below the surface) are influenced by the North-Atlantic Deep Water (Victorero et al. 2018). Despite these environmental characteristics shared with the Boetius Seamounts, we found lower morphotaxa richness most probably due to the deeper regions included in our study (e.g. Kovalenko et al. 2012; Victorero et al. 2018; Lapointe 2021); however, densities were in a similar range (Fig. 9). In detail, the Annan seamount hosted a higher mean richness and density of about 76 ± 12.7 morphotaxa and 0.63 ± 0.68 ind./m², respectively (Figs. 1, 9; Tables 1, 2; see Online Supplement Tab.S3.1 and S4.1; Victorero 2018; Victorero et al. 2018). However, a subsection with similar depth ranges to our upper seamount region showed comparable densities of 0.245 ind./m² (Victorero 2018) vs. 0.303 ind./m² in our study (Table 2; see Online Supplement Tab. S3.1; Figs. 6, 9). Considering the shallower Knipovich and Vayda seamounts (both 1000 to 2000 m depth below surface), a total richness of 141 and 137 species was recorded (Victorero 2018), surpassing our deeper seamount's 44 morphotaxa. Yet, Knipovich and Vayda's total densities of 0.23 and 0.71 ind./m² are in line with our study.

The Corner Rise and New England seamount chains associated with the Northern Atlantic Boreal Province BY2 (Watling et al. 2013; Lapointe et al. 2020a, b; Lapointe 2021) are influenced by different water masses (Labrador Seawater) and received slightly higher POC sedimentation of about 6.6 g/m² per year (Kovalenko et al. 2012; Watling et al. 2013) compared to the Boetius Seamounts. Nevertheless, megafauna morphotaxa richness with an average of 32.4 (Min.: 22; Max.: 45; Corner Rise) and 38.1 taxa (Min.: 15; Max.: 76; New England chain) were in a similar range as our studies (Lapointe et al. 2020a, b; Lapointe 2021). Another similarity is the occurrence of *Iridogorgia* and *Poliopogon* (Tables 1 and 2; Lapointe 2021).

The third group of seamounts used in the comparisons are the Schulz-Bank seamounts in the Arctic Province BY1 which are under the influence of Arctic Intermediate Water (Watling et al. 2013) being colder but receiving a similar amount of carbon sedimentation. The species richness was comparable to the Boetius Seamounts, but the densities were much higher (Fig. 9).

Overall, the seamounts with similar depths though situated in different provinces showed a relatively similar morphotaxa richness. The few estimates available for a comparison of megafauna densities showed very variable values, while the arctic seamounts showed much higher values (Fig. 9b). In addition to these very general comparisons, local aspects such as upwellings and different flow velocities at investigated transects may play an additional role for the megafauna community. As an example, we observed an obvious downward orientation of glass sponge individuals

Table 2 List of mean megafauna density (Ind./m² ± SD) of the upper and deeper seamount region

Taxa	Upper seamount region A 7/8 [1] (n = 7)	Deeper seamount region A 7/8 [2] (n = 7)
Total	0.297 ± 0.167	0.112 ± 0.114
Porifera	2.39 × 10 ⁻² ± 3.65 × 10 ⁻²	8.28 × 10 ⁻² ± 1.08 × 10 ⁻¹
<i>Poliopogon amadou</i>	1.22 × 10 ⁻² ± 2.06 × 10 ⁻²	7.21 × 10 ⁻² ± 9.44 × 10 ⁻²
Undet. Hexactinellid	1.16 × 10 ⁻² ± 1.59 × 10 ⁻²	1.07 × 10 ⁻² ± 1.49 × 10 ⁻²
Actiniaria	6.64 × 10 ⁻³ ± 3.69 × 10 ⁻³	6.05 × 10 ⁻³ ± 1.40 × 10 ⁻²
Deep-sea corals	1.28 × 10 ⁻¹ ± 1.17 × 10 ⁻¹	2.37 × 10 ⁻³ ± 2.96 × 10 ⁻³
<i>Iridogorgia</i> sp.	3.29 × 10 ⁻⁴ ± 3.51 × 10 ⁻⁴	/
Undet. Scleralcyonacea	4.36 × 10 ⁻³ ± 3.53 × 10 ⁻³	1.58 × 10 ⁻³ ± 1.59 × 10 ⁻³
Undet. Octocorallia	6.53 × 10 ⁻² ± 9.80 × 10 ⁻²	1.31 × 10 ⁻⁴ ± 3.48 × 10 ⁻⁴
Undet. deep-sea corals	5.78 × 10 ⁻² ± 4.68 × 10 ⁻²	6.58 × 10 ⁻⁴ ± 1.38 × 10 ⁻³
Crustacea	1.68 × 10 ⁻³ ± 1.33 × 10 ⁻³	4.43 × 10 ⁻³ ± 7.89 × 10 ⁻³
<i>Cancer</i> sp.	2.04 × 10 ⁻⁴ ± 2.55 × 10 ⁻⁴	/
<i>Benthesicymus</i> sp.	6.67 × 10 ⁻⁵ ± 1.76 × 10 ⁻⁴	3.38 × 10 ⁻³ ± 8.33 × 10 ⁻³
Undet. Pandalidae	1.41 × 10 ⁻³ ± 1.27 × 10 ⁻³	1.05 × 10 ⁻³ ± 7.84 × 10 ⁻⁴
Crinoidea	9.94 × 10 ⁻³ ± 1.74 × 10 ⁻²	1.32 × 10 ⁻³ ± 3.09 × 10 ⁻³
Holothuroidea	2.66 × 10 ⁻⁴ ± 5.27 × 10 ⁻⁴	5.45 × 10 ⁻³ ± 6.64 × 10 ⁻³
Asterozoa	1.23 × 10 ⁻¹ ± 1.87 × 10 ⁻¹	5.85 × 10 ⁻³ ± 1.10 × 10 ⁻²
Undet. brisingid asteroid	7.90 × 10 ⁻⁴ ± 8.64 × 10 ⁻⁴	6.57 × 10 ⁻⁴ ± 5.86 × 10 ⁻⁴
Undet. Asterozoa	1.22 × 10 ⁻¹ ± 1.86 × 10 ⁻¹	5.19 × 10 ⁻³ ± 1.07 × 10 ⁻²
Echinoidea	/	2.04 × 10 ⁻³ ± 2.74 × 10 ⁻³
Teleostei	3.10 × 10 ⁻³ ± 3.58 × 10 ⁻³	1.44 × 10 ⁻³ ± 1.28 × 10 ⁻³
Lophiidae	1.37 × 10 ⁻⁴ ± 2.34 × 10 ⁻⁴	/
Macrouridae	1.39 × 10 ⁻⁴ ± 2.37 × 10 ⁻⁴	1.97 × 10 ⁻⁴ ± 3.61 × 10 ⁻⁴
Undet. Teleostei	2.82 × 10 ⁻³ ± 3.35 × 10 ⁻³	1.25 × 10 ⁻³ ± 1.12 × 10 ⁻³

on the Boetius Seamount transect in depths between 2800 and 3200 m (Fig. 2a). However, these local specificities probably typical for all seamount investigations are difficult to consider.

Deep-sea megafauna shows significant habitat preferences

In line with literature, the most observed sessile taxa, including corals (e.g. Roberts et al. 2010), Actiniaria (e.g. Ammons and Daly 2008), sponges (e.g. Xavier et al. 2015; Ramiro-Sánchez et al. 2019) and Crinoidea (e.g. Eléaume et al. 2012) were shown to prefer hard substrates (Fig. 5; see Online Supplement Fig. S1-S3 and Online Supplement Tab. S2). This pattern is often explained by their need for hard substrates as a fundament to resist strong currents at exposed sites (e.g. Roberts et al. 2010; Ramiro-Sánchez et al. 2019). Despite the preference for hard substrates, observations of sessile taxa on soft substrates (see Online Supplement Fig. S1-S3) might have multiple reasons. Although it is likely that for most specimens, hard substrates were initially exposed during settlement and later became covered by soft substrate (Lapointe et al. 2020b; Lapointe 2021), others, such as burrowing and mud grasping Actiniaria, might

have settled for this substrate to gain advantages over sessile competitors (Ammons and Daly 2008). Able to anchor themselves on both hard and soft substrates, Actiniaria might have a broader range of distribution (Ammons and Daly 2008). This behaviour might be considered a strategy to evade competition with sessile taxa.

Associating vagile megafauna with a specific substrate type gives only tentative information on their preferred habitat as individuals may switch between substrates. Asterozoa were associated with hard surfaces (Fig. 5; see Online Supplement Fig. S3 and Online Supplement Tab. S2) which is in line with a study on habitat associations of shallow, bathyal echinoderms in the Central Mediterranean (Leonard et al. 2020). Holothurians, both on higher taxonomic and on morphotaxon level, were significantly associated with soft sediments (Fig. 5; see Online Supplement Fig. S3 and Online Supplement Tab. S2). This is in accordance with the preference of holothurians for soft sediments in shallow waters (Kerr et al. 1993) and also confirms observations of traces left by deep-sea holothurians on soft sediment (Bell et al. 2013). This preference for soft bottoms can be explained by their prevailing feeding habit of consuming detritus from the sediment surface (Thurston et al. 1994; Bett et al. 2001; Pawson et al. 2010). Sea urchins, which

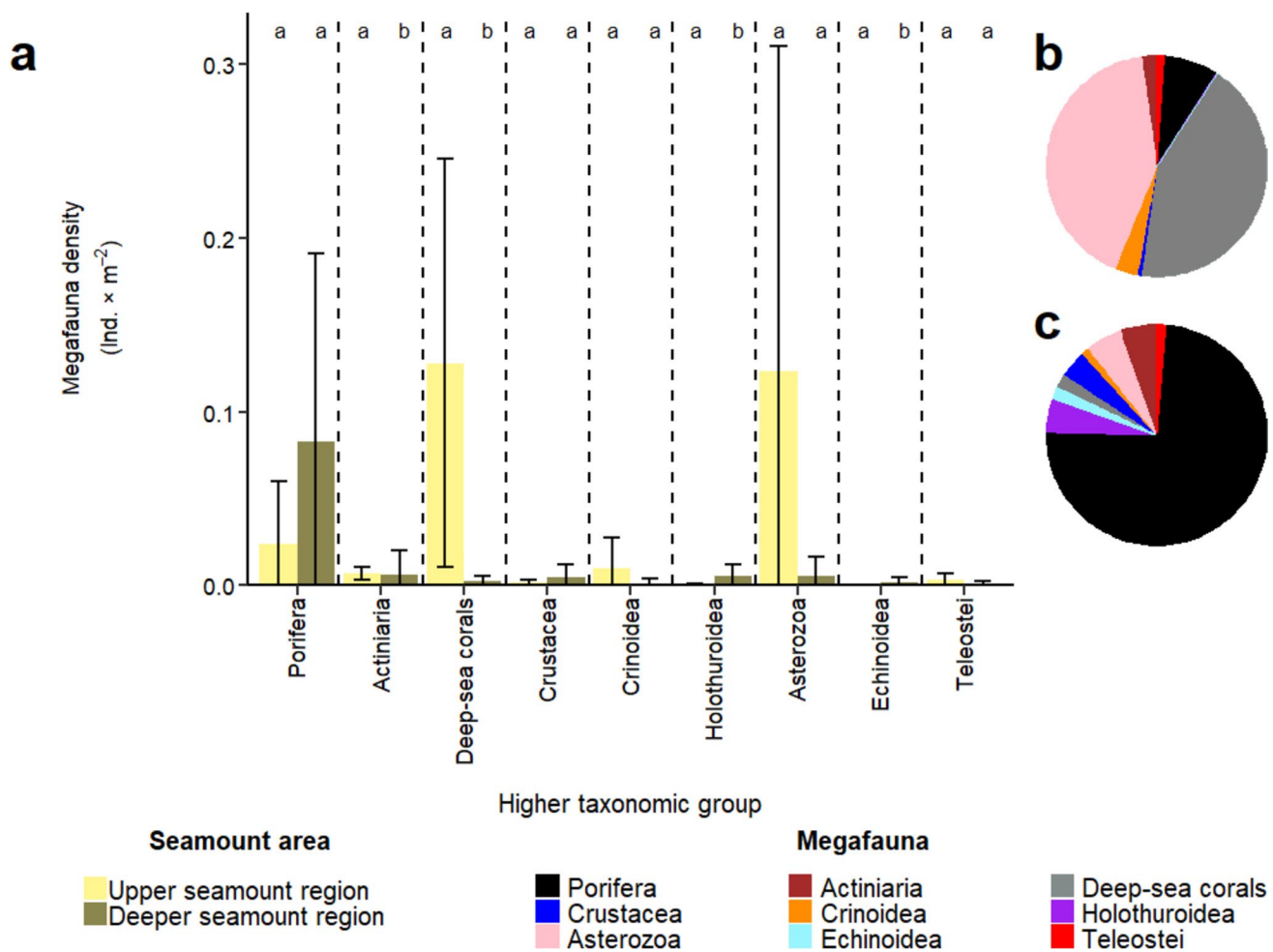


Fig. 7 Seamount region-specific mean (\pm SD) megafauna densities in individuals per m² ($n = 7$) for each higher taxonomic group; **a** and their contribution to the upper; **b** and deeper; **c** region's total density. Different letters above bars mark significant differences between the regions (Porifera: Kruskal–Wallis chi-squared = 2.3562, $df = 1$, p -value = 0.1248; Actiniaria: Kruskal–Wallis chi-squared = 3.966 $df = 1$, p -value = 0.04643; Deep-sea coral: Kruskal–Wallis chi-squared = 9.8216, $df = 1$, p -value = 1.73×10^{-3} ; Crustacea:

Kruskal–Wallis chi-squared = 0.20044, $df = 1$, p -value = 0.6544; Crinoidea: Kruskal–Wallis chi-squared = 2.4622, $df = 1$, p -value = 0.1166; Holothuroida: Kruskal–Wallis chi-squared = 4.473, $df = 1$, p -value = 0.03444; Asterozoa: Kruskal–Wallis chi-squared = 3.0019, $df = 1$, p -value = 0.08317; Echinoidea: Kruskal–Wallis chi-squared = 5.0381, $df = 1$, p -value = 0.0248; Teleostei: Kruskal–Wallis chi-squared = 0.91837, $df = 1$, p -value = 0.3379)

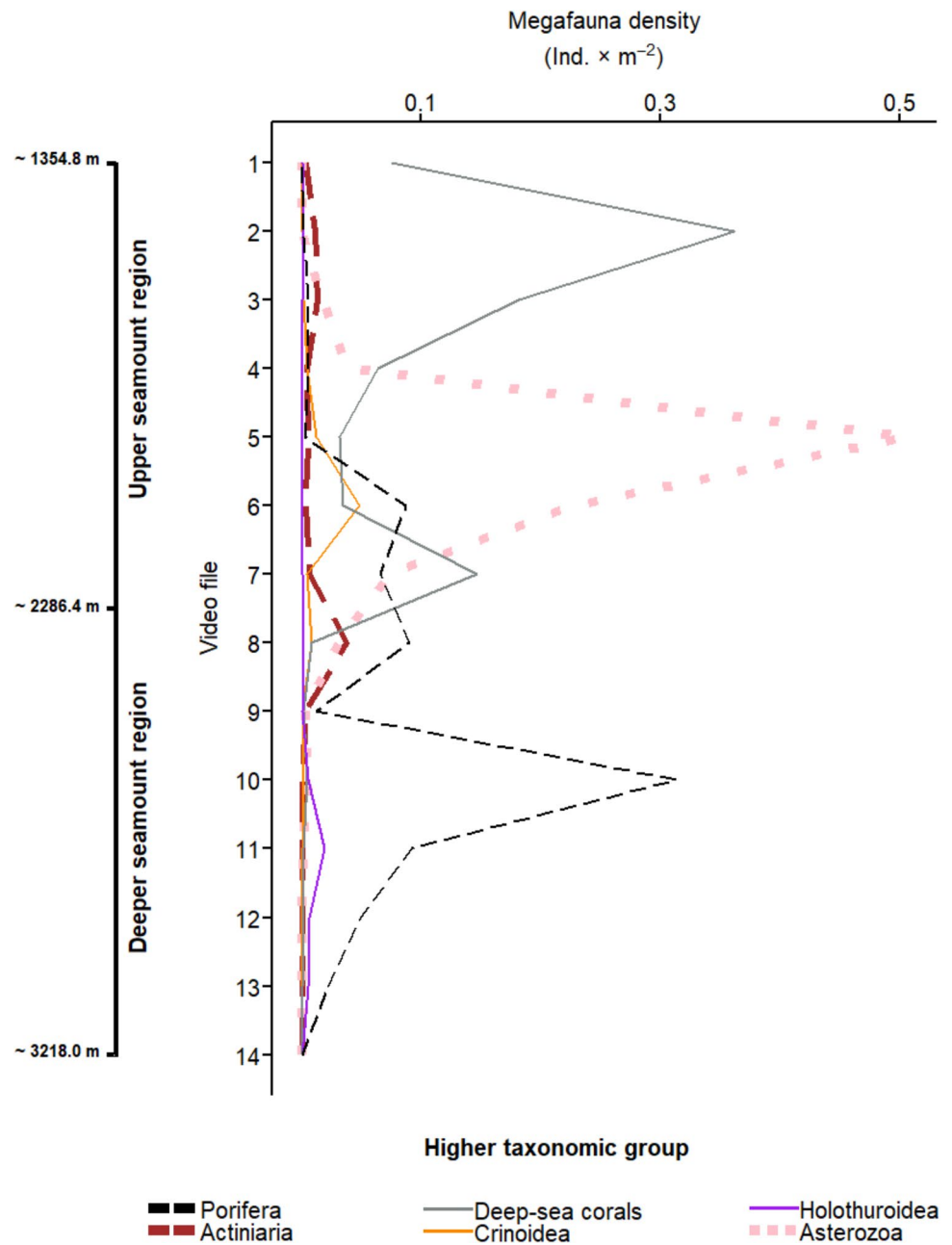
were also significantly associated with soft substrate (Fig. 5; Online Supplement Fig. S3 and Online Supplement Tab. S2), might be in line with the behaviour of bathyal specimens in the Central Mediterranean, consuming both phyto-detritus and holothuroid faecal matter (Stevenson and Kroh 2020; Leonard et al. 2020). Except for Lophiidae, Teleostei were mainly found in association with soft sediments, showing a significant connection at both higher taxonomic and morphotaxa levels (Fig. 5; Online Supplement Fig. S3 and Online Supplement Tab. S2). Even though, rock-associated deep-sea corals provide nurseries for fish larvae (D’Onghia et al. 2010; Roberts et al. 2010; Baillon et al. 2012), Teleostei at the seamount were mainly spotted on soft sediment (Fig. 5; see Online Supplement Fig. S1-S3). Aggregations

of potential prey taxa on soft sediments such as polychaetes, crustaceans and holothurians, which also favour this habitat (e.g. Fig. 5; see Online Supplement Fig. S1-S3 and Online Supplement Tab. S2), might have attracted fishes to soft habitats (Drazen et al. 2008).

Seamount zonation as a result of abiotic and biotic factors

Our investigations revealed significant differences in the diversity and quantity of epi-megafauna communities in the upper and deeper regions of the seamount (Figs. 3, 4, 6 and 7; see Online Supplement Fig. S1 and Online Supplement Tab. S1). The asymptotic shape of all morphotaxa

Fig. 8 Vertical distribution of selected deep-sea (epi-) megafauna density at the seamount in individuals per m^2 . On the left side, the separation of the upper (A7/8 [1]) and deeper seamount regions (A7/8 [2]) is indicated. The legend gives the colour and line-type code for the different megafauna groups

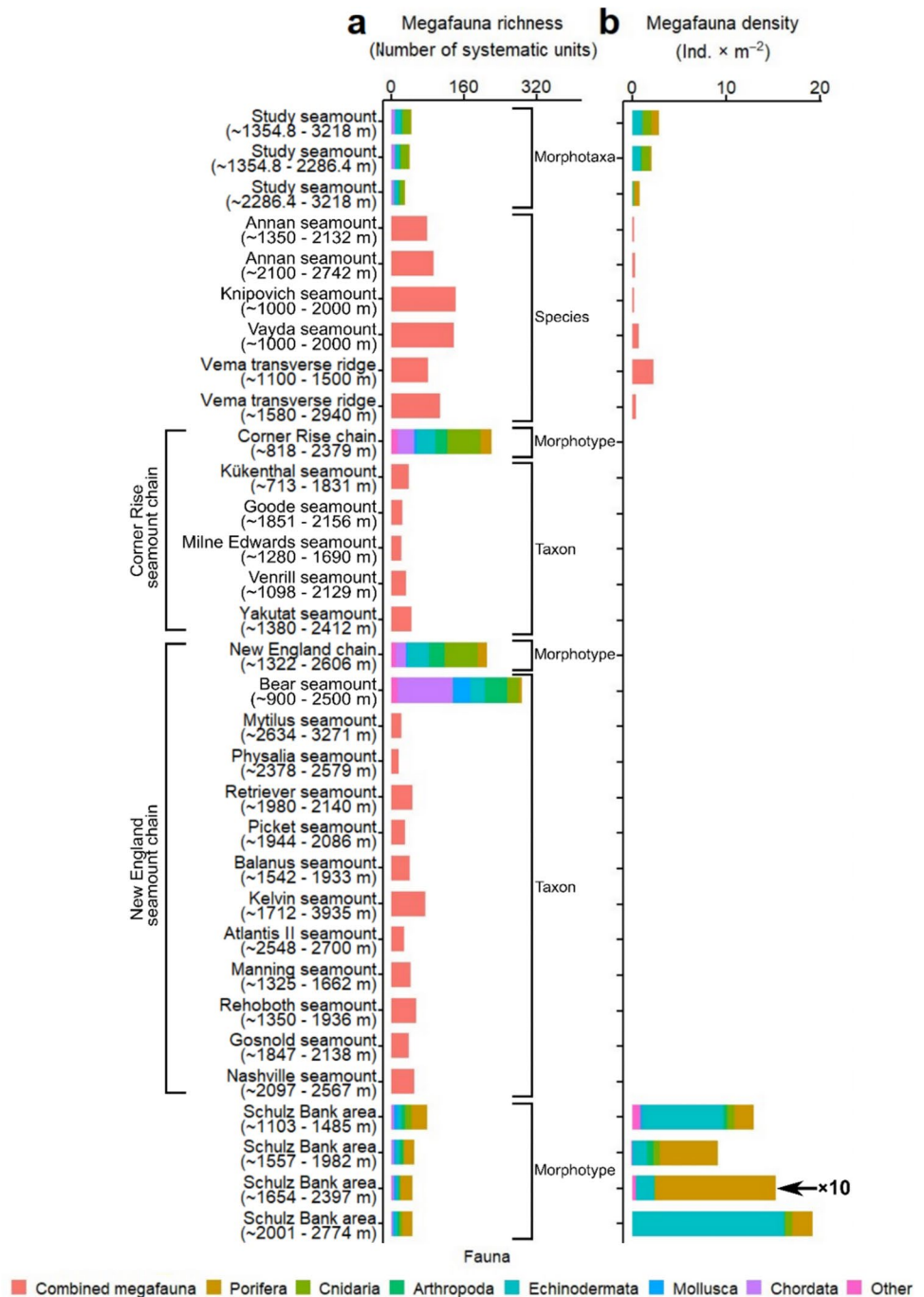


accumulation curves implies a data set that is close to the saturation point and that our OFOS transects should have covered a sufficiently vast area to adequately assess this seamount side's megafaunal community (see Online Supplement Fig. S4).

As shown in literature, community compositions of seamount megafauna are not only affected by the provided substrate arrangement, but especially by depth-related variables, including temperature, specificity of the passing water masses and in particular the food availability (e.g. Kovalenko et al. 2012; Victorero et al. 2018; Lapointe et al. 2020a, b; Lapointe

2021). The reliance on sedimented organic matter (e.g. Smith and Demopoulos 2003; Johnson et al. 2007; Smith et al. 2008) may explain quantitative differences and faunal zonation of the studied system (Figs. 3, 4, 6 and 7; see Online Supplement Fig. S1). Interactions between upwellings (e.g. Genin 2004; Rowden et al. 2010; Clark et al. 2010) and surface water circulations can disperse food particles across the seamount's upper section (e.g. Lutz et al. 2002; Davies et al. 2009; Consalvey et al. 2010). As indicated by Victorero (2018), the amount of POC decreases with seamount depth. Consequently, food limitation on the seamount may increase with depth leading

Fig. 9 Visualization of the conducted literature research on 22 selected seamounts of the North Atlantic. **a** Megafauna richness based on number of species, taxa, morphotaxa or morphotypes. **b** Total densities as individuals per m². Values are based on investigations by Moore et al. (2003, Bear Seamount); Cho (2008, Corner Rise and England seamount chains); Victorero et al. (2018) and Victorero (2018, Annan, Knipovich, Vema seamounts); Lapointe et al. (2020a, b) and Lapointe (2021, Corner Rise and England seamount chains); and Meyer et al. (2022; Schulz Bank). The corresponding depth spectrum is given. Densities of Schulz-Bank between 1654 and 2397 m were divided by 10 for better visualization



to the detected quantitative differences in megafauna density (Figs. 3, 4). In addition, the diverse and changing community structure observed during our investigation may be attributed to the high structural complexity of the seamount and differences in abiotic parameters along the vertical transect. Indeed, similar to other seamounts (Consalvey et al. 2010; Clark et al. 2010), our study area provided a complex volcanism-formed shape with numerous craters, canyons and terraces, and the base lies at the same level as the surrounding abyssal plain

(Fig. 1). With a large habitat complexity, several distinct microhabitats and habitat niches should be available across the seamount, providing a variability of suitable conditions for a wide range of organisms (Jennings et al. 1999; Kovalenko et al. 2012; Reid and Church 2015). For instance, while more current resistant taxa, such as deep-sea corals, may settle at current-exposed locations (e.g. Consalvey et al. 2010; Rowden et al. 2010; Clark et al. 2010) as we have observed at the structure's top, less resistant taxa could populate protected regions

(White 2003; Xavier et al. 2015; Ramiro-Sánchez et al. 2019). This is in accordance with our observations of high concentrations of the glass sponge *Poliopogon amadou* at the seamount's bottom (Fig. 8; see Online Supplement Fig. S1). In addition, soft substrate-preferring megafauna like Echinoidea could have accumulated in areas protected from strong currents (Fig. 7; see Online Supplement Fig. S1).

The specific vertical zonation of deep-sea corals and sponges went along with a change in distribution patterns of associated fauna (Fig. 8; see Online Supplement Tab. S1), which was also recorded for other seamounts (e.g. Du Preez et al. 2016; Serrano et al. 2017; Ramiro-Sánchez et al. 2019). Actiniaria reached their local maxima in an area between the upper parts of the seamount populated by deep-sea corals and the deeper part of the seamount dominated by sponges (Fig. 8; see Online Supplement Fig. S1). Individuals were often closely associated with living and dead corals. Despite being continuously observed during the dives, both Crustacea and Teleostei, were shown to accumulate in deep-sea coral gardens at the seamount's top (Fig. 8; see Online Supplement Fig. S1). We observed individuals resting close by, or, in case of *Cancer*, on cnidarians. This further supports the importance of biotic interactions (e.g. O'Hara et al. 2008; Baillon et al. 2012; Castello-Branco et al. 2020). Crustaceans and fishes might benefit from the various provision of direct and indirect food sources through the cnidarians, including the produced mucus (Cordes et al. 2008; Buhl-Mortensen et al. 2010; le Guilloux et al. 2010) or associated fauna (Buhl-Mortensen and Mortensen 2004; Genin 2004). Several studies have already shown that deep-sea coral gardens serve as hiding places for various taxa (Buhl-Mortensen and Mortensen 2004), but also as nurseries for juvenile fish (D'Onghia et al. 2010; Baillon et al. 2012). The presence of larger Lophiidae and predatory Macrouridae might also be related to the mega-fauna concentration in the coral gardens.

Below a water depth of about 2000 m, the frequency of deep-sea corals was drastically reduced. Restricted to temperatures between 4 and 12 °C, warmer waters at the seamount's top may provide an explanation besides the previously discussed aspects (Roberts et al. 2006). As shown by CTD records from close by and comparable seamounts, the temperature of the studied seamount's upper section might have been in a well-tolerated range of roughly 4.2 to 3.2 °C compared to 3.2 to 2.5 °C in the deeper section (Victorero et al. 2018; Victorero 2018). In addition, pressure related saturation state of calcium carbonate could have limited the vertical distribution of corals (Guinotte et al. 2006; Maier et al. 2009), as the aragonite saturation horizon for the area (approximately 2300 and 2500 m depth; Jiang et al. 2015) fits to the disappearance of corals at the investigated seamount. Deep-sea corals provided more than 27% of all detected morphotaxa and with the decline of deep-sea corals towards greater

depths, densities of both crinoids and Asterozoa increased notably (Fig. 8; see Online Supplement Fig. S1). As passive suspension feeders, crinoids rely on similar food sources as their possible competitors on the seamount (Roberts et al. 2006; Xavier et al. 2015), but prefer moderate bottom currents over the high flow velocities at the upper parts of the seamount (Macurda and Meyer 1974). Recording the majority of crinoids at these depths, all individuals categorized within this group displayed characteristic features like stalks, tendrils and mouths. However, in rare cases, some individuals appeared blurred on video frames and shared similarities with specific deep-sea corals, potentially influencing the observed densities.

Below 2500 m depth, another major shift in the seamount's faunal zonation appeared as large aggregations of the hexactinellid *Poliopogon amadou* became dominant (Figs. 2a, 8; see Online Supplement Fig. S1). While their numbers were notably higher at depths where deep-sea corals were not dominant, colonies of the sponges further expanded to vast gardens down to the seamount's bottom. Only very few studies have observed similar aggregations of *Poliopogon amadou* (e.g. Xavier et al. 2015; Ramiro-Sánchez et al. 2019; Perez et al. 2020). Two of those studies were located on comparable seamounts in the Atlantic Ocean, including the Great Meteor Seamount (Xavier et al. 2015) and the Tropic Seamount (Ramiro-Sánchez et al. 2019). *Poliopogon amadou* aggregations are known to depend primarily on high water depths and strong flow velocities at the seamount flanks (White 2003; Xavier et al. 2015; Ramiro-Sánchez et al. 2019). The colonization of depths below deep-sea coral regions might be a strategy to avoid competition with corals (Tabachnick and Menshenina 2002).

Like deep-sea corals, zones dominated by *Poliopogon amadou* showed a specific associated megafauna community (Fig. 8; see Online Supplement Fig. S1). With one morphotaxon significantly associated with the corresponding region, Holothuroidea were one of those taxa (Fig. 8; see Online Supplement Tab. S1 and Online Supplement Fig. S1). Similar observations were made for the Anton Dohrn Seamount in the northeastern Atlantic (Davies et al. 2015). Like *Poliopogon amadou* (Xavier et al. 2015), some Holothuroidea are known to accumulate in areas with increased food supply while avoiding strong water turbulences (Kerr et al. 1993). Similar to deep-sea corals, we observed Porifera gardens to be also associated with a relatively high number of fishes and crustaceans (Fig. 8; see Online Supplement Fig. S1). Teleostei could have additionally been attracted by the higher densities of Holothuroidea (Bailey et al. 2006). In addition, Bailey et al. (2006) and others reported significant correlations between the occurrence of Macrouridae and the total density of echinoderms, including holothurians (Pearcy and Ambler 1974; Pawson et al. 2010).

Conclusion

Although several studies investigated seamount epi-mega-fauna in a qualitative and/or quantitative manner, there are only very few studies providing an assessment of the community's diversity and density altogether. Here, we present qualitative and quantitative insights into the epibenthic megafauna communities inhabiting a so far unexplored seamount of the southern North Atlantic. By analysing vertical distribution patterns together with fauna richness and density, this study's dataset provides a further mosaic piece to enlarge the baseline knowledge on this kind of habitats which can be utilized for the development of conservation and management strategies of seamount habitats in the future (Clark et al. 2010; Watling et al. 2013).

Morphotaxa richness and density were significantly higher at the seamounts top, while Shannon diversity lacked significant differences. These findings supported our hypothesis that larger megafauna diversity and quantity would be found on the seamount's summit. Both community composition and densities differed significantly between seamount sections, showing a vertical zonation where deep-sea corals and glass sponges (*Poliopogon amadou*) dominated the upper and deeper regions, respectively. Consequently, our hypothesis that megafauna communities will accumulate in a characteristic zonation with changes in depths was supported. Further, several morphotaxa and higher taxonomic groups were found to have specific substrate preferences, confirming the hypothesis of substrate preferences among different megafauna taxa.

In conclusion, we hope that this study offers new insights into the diversity and density of epi-megafauna from a deep seamount in the southern North Atlantic while expanding our knowledge on interactions between fauna and their habitats. Furthermore, the gained insights on seamount megafauna communities might be integrated into management approaches, guiding the planning of protected areas on this or similar seamount systems.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s12526-023-01400-w>.

Acknowledgements We are grateful to the technical crew and the captain of R/V Meteor, Rainer Hammacher, and to the scientific crew for valuable help and support during the cruise M139. We thank Rosita Bieg, Brigitte Gräfe and Bärbel Jendral for their extensive technical support. We also thank the collective team around the GEOMAR OFOS. Special thanks go to the two reviewers for their constructive criticism of an earlier version of the manuscript.

Funding Open Access funding enabled and organized by Projekt DEAL. This work was supported by the German Research Foundation grant MerMet 16-97 and AR288/23, 24 (445025756 & 513269546) to H.A. and MerMet 17-82 to N.A. & C. Devey. J.R.X. research was supported by annual funding attributed by the Portuguese Science and Technology Foundation to CIIMAR - Interdisciplinary Centre of Marine and Environmental Research, University of Porto,

within the scope of UIDB/04423/2020, UIDP/04423/2020 and CEECIND/00577/2018.

Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval No approval of research ethics committees was required to accomplish the goals of this study as fauna exploration was restricted to visual investigation through video recordings.

Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on request.

Author contribution Conceptualization: HA and DS; methodology: DS, HA, NA; fieldwork: NA, HA, MD, AS, JW; sponge species determination: JRX; video analysis: DS; statistics: AW, DS; funding acquisition: HA and NA; supervision: HA and AW; writing of the first draft of the manuscript: DS and HA; all authors contributed to the revision of the draft. All authors read and approved the final manuscript.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Ammons AW, Daly M (2008) Distribution, habitat use and ecology of deepwater anemones (Actiniaria) in the Gulf of Mexico. *Deep-Sea Res 2 Top Stud Oceanogr* 55:2657–2666. <https://doi.org/10.1016/j.dsr2.2008.07.015>
- Arndt H, Ahlers J, Amano C, Augustin N, Dangel G, Feuling Y, Herrero T, Hohlfeld M, Jeuck A, Marx M, Mähner B, Meißner R, Meyer C, Podobnik M, Palgan D, Paulmann C, Prausse D, Romankiewicz T, Schade M, Scherwaß A, Schiwitz S, Schoenle A, Schuffenhauer I, Sintes E, Stefanschitz J, Werner J, Wildermuth B, Živaljić S (2017) Cruise report METEOR 139. https://oceanrep.geomar.de/id/eprint/50010/1/tagungsband_forschungsschiffe_2020_web.pdf
- Auguie B (2017) gridExtra: Miscellaneous functions for “grid” graphics. R package version 2.3. <https://cran.r-project.org/web/packages/gridExtra>
- Bailey DM, Ruhl HA, Smith KL (2006) Long-term change in benthopelagic fish abundance in the abyssal northeast Pacific Ocean. *Ecology* 87:549–555. <https://doi.org/10.1890/04-1832>
- Baillon S, Hamel J-F, Wareham VE, Mercier A (2012) Deep cold-water corals as nurseries for fish larvae. *Front Ecol Environ* 10:351–356. <https://doi.org/10.1890/120022>
- Beaulieu SE (2001) Life on glass houses: sponge stalk communities in the deep sea. *Mar Biol* 138:803–817. <https://doi.org/10.1007/s002270000500>
- Beazley LI, Kenchington EL, Murillo FJ, del Sacau M, M, (2013) Deep-sea sponge grounds enhance diversity and abundance of epibenthic megafauna in the Northwest Atlantic. *ICES J Mar Sci* 70(1471):1490. <https://doi.org/10.1093/icesjms/fst124>

- Bell JB, Jones DOB, Alt CHS (2013) Lebensspuren of the Bathyal Mid-Atlantic Ridge. *Deep-Sea Res 2 Top Stud Oceanogr* 98:341–351. <https://doi.org/10.1016/j.dsr.2012.09.004>
- Bett BJ, Malzone MG, Narayanaswamy BE, Wigham BD (2001) Temporal variability in phytodetritus and megabenthic activity at the seabed in the deep Northeast Atlantic. *Prog Oceanogr* 50:349–368. [https://doi.org/10.1016/S0079-6611\(01\)00066-0](https://doi.org/10.1016/S0079-6611(01)00066-0)
- Braga-Henriques A, Porteiro FM, Ribeiro PA, de Matos V, Sampaio Í, Ocaña O, Santos RS (2013) Diversity, distribution and spatial structure of the cold-water coral fauna of the Azores (NE Atlantic). *Bio-geosciences* 10:4009–4036. <https://doi.org/10.5194/bg-10-4009-2013>
- Buhl-Mortensen L, Mortensen PB (2004) Crustaceans associated with the deep-water gorgonian corals *Paragorgia arborea* (L., 1758) and *Primnoa resedaeformis* (Gunn., 1763). *J Nat Hist* 38:1233–1247. <https://doi.org/10.1080/0022293031000155205>
- Buhl-Mortensen L, Vanreusel A, Gooday AJ, Levin LA, Priede IG, Buhl-Mortensen P, Gheerardyn H, King NJ, Raes M (2010) Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. *Mar Ecol* 31:21–50. <https://doi.org/10.1111/j.1439-0485.2010.00359.x>
- Castello-Branco C, Collins AG, Hajdu E (2020) A collection of hexactinellids (Porifera) from the deep South Atlantic and North Pacific: new genus, new species and new records. *PeerJ* 8:e9431. <https://doi.org/10.7717/peerj.9431>
- Cho W (2008) Faunal biogeography, community structure, and genetic connectivity of North Atlantic Seamounts. PhD thesis, MIT, Woods Hole Oceanographic Institution, USA
- Clark MR, Rowden AA, Schlacher T, Williams A, Consalvey M, Stocks KI, Rogers AD, O'Hara TD, White M, Shank TM, Hall-Spencer JM (2010) The ecology of seamounts: structure, function, and human impacts. *Annu Rev Mar Sci* 2:253–278. <https://doi.org/10.1146/annurev-marine-120308-081109>
- Clark MR, Watling L, Rowden AA, Guinotte JM, Smith CR (2011) A global seamount classification to aid the scientific design of marine protected area networks. *Ocean Coast Manag* 54:19–36. <https://doi.org/10.1016/j.ocecoaman.2010.10.006>
- Consalvey M, Clark MR, Rowden AA, Stocks KI (2010) Life on seamounts. In: McIntyre A (ed) *Life in the world's oceans: diversity, distribution, and abundance*. John Wiley & Sons, Hoboken, pp 123–138
- Cordes EE, McGinley MP, Podowski EL, Becker EL, Lessard-Pilon S, Viada ST, Fisher CR (2008) Coral communities of the deep Gulf of Mexico. *Deep-Sea Res 1 Oceanogr Res Pap* 55:777–787. <https://doi.org/10.1016/j.dsr.2008.03.005>
- Davies AJ, Duineveld GCA, Lavaleye MSS, Bergman MJN, van Haren H (2009) Downwelling and deep-water bottom currents as food supply mechanisms to the cold-water coral *Lophelia pertusa* (Scleractinia) at the Mingulay Reef complex. *Limnol Oceanogr* 54:620–629. <https://doi.org/10.4319/lo.2009.54.2.0620>
- Davies JS, Stewart HA, Narayanaswamy BE, Jacobs C, Spicer J, Golding N, Howell KL (2015) Benthic assemblages of the Anton Dohrn Seamount (NE Atlantic): defining deep-sea biotopes to support habitat mapping and management efforts with a focus on vulnerable marine ecosystems. *PLoS One* 10:e0124815. <https://doi.org/10.1371/journal.pone.0124815>
- de Cáceres M, Legendre P (2009) Associations between species and groups of sites: indices and statistical inference. *Ecology* 90:3566–3574. <https://doi.org/10.1890/08-1823.1>
- D'Onghia G, Maiorano P, Sion L, Giove A, Capezzuto F, Carlucci R, Tursi A (2010) Effects of deep-water coral banks on the abundance and size structure of the megafauna in the Mediterranean Sea. *Deep-Sea Res 2 Top Stud Oceanogr* 57:397–411. <https://doi.org/10.1016/j.dsr.2009.08.022>
- Drazek JC, Popp BN, Choy CA, Clemente T, de Forest L, Smith KL (2008) Bypassing the abyssal benthic food web: macrourid diet in the eastern North Pacific inferred from stomach content and stable isotopes analyses. *Limnol Oceanogr* 53:2644–2654. <https://doi.org/10.4319/lo.2008.53.6.2644>
- Du Preez C, Curtis JMR, Clarke ME (2016) The structure and distribution of benthic communities on a shallow seamount (Cobb Seamount, Northeast Pacific Ocean). *PLoS One* 11:e0165513. <https://doi.org/10.1371/journal.pone.0165513>
- Eddelbuettel D (2013) Seamless R and C++ integration with Rcpp. *Seamless R and C++ Integration with Rcpp* 40:1–220. <https://doi.org/10.1007/978-1-4614-6868-4>
- Eléaume M, Bohn JM, Roux M, Améziane N (2012) Stalked crinoids (Echinodermata) collected by the R/V Polarstern and Meteor in the south Atlantic and in Antarctica. *Zootaxa* 3425:1. <https://doi.org/10.11646/zootaxa.3425.1.1>
- Firke S (2023) janitor: simple tools for examining and cleaning dirty data. R package version 2.2.0. <https://CRAN.R-project.org/package=janitor>
- Fox J, Weisberg S (2019) *An {R} Companion to applied regression*, Third Edition. Thousand Oaks CA: Sage. URL: <https://socialscisearch.com/mcmaster.ca/jfox/Books/Companion/>
- Gastwirth JL, Gel YR, Hui WLW, Lyubchich V, Miao W, Noguchi K (2020) lawstat: tools for biostatistics, public policy, and law. R package version 3.4. <https://CRAN.R-project.org/package=lawstat>
- Genin A (2004) Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. *J Mar Systems* 50:3–20. <https://doi.org/10.1016/j.jmarsys.2003.10.008>
- Glover AG, Higgs ND, Horton T, Porrer A (2015) Deep Sea ID v.1.2 A field guide to the marine life of the deep sea <http://www.marinespecies.org/deepsea>
- Glover AG, Higgs ND, Horton T (2023) World Register of Deep-Sea species (WoRDSS). Accessed at <https://www.marinespecies.org/deepsea> on 2023-07-19. <https://doi.org/10.14284/352>
- Guinotte JM, Orr J, Cairns S, Freiwald A, Morgan L, George R (2006) Will human-induced changes in seawater chemistry alter the distribution of deep-sea scleractinian corals? *Front Ecol Environ* 4:141–146. [https://doi.org/10.1890/1540-9295\(2006\)004\[0141:WHCISC\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2006)004[0141:WHCISC]2.0.CO;2)
- Jennings MJ, Bozek MA, Hatzenbeler GR, Emmons EE, Staggs MD (1999) Cumulative effects of incremental shoreline habitat modification on fish assemblages in north temperate lakes. *N Am J Fish Manag* 19:18–27. [https://doi.org/10.1577/1548-8675\(1999\)019%3c0018:CEOISH%3e2.0.CO;2](https://doi.org/10.1577/1548-8675(1999)019%3c0018:CEOISH%3e2.0.CO;2)
- Jiang L-Q, Feely RA, Carter BR, Greeley DJ, Gledhill DK, Arzayus KM (2015) Climatological distribution of aragonite saturation state in the global oceans. *Global Biogeochem Cycles* 29:1656–1673. <https://doi.org/10.1002/2015GB005198>
- Johnson NA, Campbell JW, Moore TS, Rex MA, Etter RJ, McClain CR, Dowell MD (2007) The relationship between the standing stock of deep-sea macrobenthos and surface production in the western North Atlantic. *Deep-Sea Res 1 Oceanogr Res Pap* 54:1350–1360. <https://doi.org/10.1016/j.dsr.2007.04.011>
- Kennedy BRC, Cantwell K, Malik M, Kelley C, Potter J, Elliott K, Lobecker E, Gray LM, Sowers D, White MP, France SC, Auscavitch S, Mah C, Moriwake V, Bingo SRD, Putts M, Rotjan RD (2020) Corrigendum: the unknown and the unexplored: Insights into the Pacific Deep-Sea following NOAA CAPSTONE Expeditions. *Front Mar Sci* 6:2019–2020. <https://doi.org/10.3389/fmars.2019.00827>
- Kerr AM, Stoffel EM, Yoon RL (1993) Abundance distribution of holothuroids (Echinodermata:Holothuroidea) on a windward and leeward fringing coral reef, Guam, Mariana Islands. *Bull Mar Sci* 52:780–791
- Kovalenko KE, Thomaz SM, Warfe DM (2012) Habitat complexity: approaches and future directions. *Hydrobiologia* 685:1–17. <https://doi.org/10.1007/s10750-011-0974-z>
- Kvile KØ, Taranto GH, Pitcher TJ, Morato T (2014) A global assessment of seamount ecosystems knowledge using an ecosystem evaluation

- framework. *Biol Conserv* 173:108–120. <https://doi.org/10.1016/j.biocon.2013.10.002>
- Lapointe AE (2021) Investigation into the biogeography of the bathyal deep-sea. PhD thesis, University of Hawaii, USA
- Lapointe AE, Watling L, Gontz AM (2020a) Deep-sea benthic megafaunal communities on the New England and Corner Rise Seamounts, Northwest Atlantic Ocean. In: *Seafloor Geomorphology as Benthic Habitat*. Elsevier, pp 917–932
- Lapointe AE, Watling L, France SC, Auster PJ (2020b) Megabenthic assemblages in the lower bathyal (700–3000 m) on the New England and Corner Rise Seamounts, Northwest Atlantic. *Deep-Sea Res 1 Oceanogr Res Pap* 165:103366. <https://doi.org/10.1016/j.dsr.2020.103366>
- Le Guilloux E, Hall-Spencer JM, Söffker MK, Olu K (2010) Association between the squat lobster *Gastroptychus formosus* and cold-water corals in the North Atlantic. *J Mar Biol Assoc UK* 90:1363–1369. <https://doi.org/10.1017/S0025315410000524>
- Leonard C, Evans E, Knittweis L, Aguilar R, Alvarez H, Borg JA, Gracia S, Schembri PJ (2020) Diversity, distribution, and habitat associations of deep-water echinoderms in the Central Mediterranean. *Mar Biodivers* 50:69. <https://doi.org/10.1007/s12526-020-01095-3>
- Lutz M, Dunbar R, Caldeira K (2002) Regional variability in the vertical flux of particulate organic carbon in the ocean interior. *Global Biogeochem Cycles*. <https://doi.org/10.1029/2000GB001383>
- Macurda DB, Meyer DL (1974) Feeding posture of modern stalked crinoids. *Nature* 247:394–396. <https://doi.org/10.1038/247394a0>
- Maier C, Hegeman J, Weinbauer MG, Gattuso J-P (2009) Calcification of the cold-water coral *Lophelia pertusa* under ambient and reduced pH. *Biogeosciences* 6:1671–1680. <https://doi.org/10.5194/bg-6-1671-2009>
- Meyer HK, Davies AJ, Roberts EM, Xavier JR, Ribeiro PA, Glenner H, Birkely S-R, Rapp HT (2022) Beyond the tip of the seamount: distinct megabenthic communities found beyond the charismatic summit sponge ground on an arctic seamount (Schulz Bank, Arctic Mid-Ocean Ridge). *Deep-Sea Res Oceanogr Res Pap* 191:103920. <https://doi.org/10.1016/j.dsr.2022.103920>
- Moore JA, Vecchione M, Collette BB, Gibbons R, Hartel KE, Galbraith JK, Turnipseed M, Southworth M, Watkins E (2003) Biodiversity of Bear Seamount, New England Seamount chain: results of exploratory trawling. *J Northw Atl Fish Sci* 31:363–372. <https://doi.org/10.2960/J.v31.a28>
- Morato T, Varkey D, Damaso C, Machete M, Santos M, Prieto R, Pitcher T, Santos R (2008) Evidence of a seamount effect on aggregating visitors. *Mar Ecol Prog Ser* 357:23–32. <https://doi.org/10.3354/meps07269>
- Morato T, Hoyle SD, Allain V, Nicol SJ (2010) Seamounts are hotspots of pelagic biodiversity in the open ocean. *Proc Natl Acad Sci, USA* 107:9707–9711. <https://doi.org/10.1073/pnas.0910290107>
- Neuwirth E (2014) RColorBrewer: ColorBrewer Palettes. R package version 1.1-2. <https://CRAN.R-project.org/package=RColorBrewer>
- O'Hara TD, Rowden AA, Williams A (2008) Cold-water coral habitats on seamounts: do they have a specialist fauna? *Divers Distrib* 14:925–934. <https://doi.org/10.1111/j.1472-4642.2008.00495.x>
- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, Mcglinn D, Minchin PR, Hara RBO, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2019) *Vegan: Community Ecology Package*. R package version 2.5-6. <https://CRAN.R-project.org/package=vegan>
- Pawson DL, Pawson DJ, King RA (2010) A taxonomic guide to the Echinodermata of the South Atlantic Bight, USA: 1. Sea cucumbers (Echinodermata: Holothuroidea). *Zootaxa* 2449:1. <https://doi.org/10.11646/zootaxa.2449.1.1>
- Pearcy WG, Ambler JW (1974) Food habits of deep-sea macrourid fishes off the Oregon coast. *Deep-Sea Res Oceanogr Abstr* 21:745–759. [https://doi.org/10.1016/0011-7471\(74\)90081-3](https://doi.org/10.1016/0011-7471(74)90081-3)
- Perez JAA, Gavazzoni L, de Souza LHP, Sumida PYG, Kitazato H (2020) Deep-sea habitats and megafauna on the slopes of the São Paulo Ridge, SW Atlantic. *Front Mar Sci* 7:1–17. <https://doi.org/10.3389/fmars.2020.572166>
- Pohlert T (2022) PMCMRplus: calculate pairwise multiple comparisons of mean rank sums extended. R package version 1.9.0. <https://CRAN.R-project.org/package=PMCMRplus>. 2022
- R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>
- Ramiro-Sánchez B, González-Irusta JM, Henry L, Cleland J, Yeo I, Xavier JR, Carreiro-Silva M, Sampaio Í, Spearman J, Victorero L, Messing CG, Kazanidis G, Roberts JM, Murton B (2019) Characterization and mapping of a deep-sea sponge ground on the Tropic Seamount (Northeast Tropical Atlantic): implications for spatial management in the high seas. *Front Mar Sci* 6:1–19. <https://doi.org/10.3389/fmars.2019.00278>
- Reid D, Church M (2015) Geomorphic and ecological consequences of riprap placement in river systems. *J Am Water Resour Assoc* 51:1043–1059. <https://doi.org/10.1111/jawr.12279>
- Roberts JM, Wheeler AJ, Freiwald A (2006) Reefs of the deep: the biology and geology of cold-water coral ecosystems. *Science* 312:543–547. <https://doi.org/10.1126/science.1119861>
- Roberts JM, Wheeler AJ, Freiwald A, Cairns SD (2010) Cold-water corals: the biology and geology of deep sea coral habitats. Cambridge University Press, Cambridge
- Rowden AA, Schlacher TA, Williams A, Clark MR, Stewart R, Althaus F, Bowden DA, Consalvey M, Robinson W, Dowdney J (2010) A test of the seamount oasis hypothesis: seamounts support higher epibenthic megafaunal biomass than adjacent slopes. *Mar Ecol* 31:95–106. <https://doi.org/10.1111/j.1439-0485.2010.00369.x>
- Rubis B (2020) hrbthemes: additional themes, theme components and utilities for “ggplot2”. R package version 0.8.0. <https://CRAN.R-project.org/package=hrbthemes>. URL <http://sites.google.com/site/miqueledcaceres/>
- Serrano A, González-Irusta JM, Punzón A, García-Alegre A, Lourido A, Ríos P, Blanco M, Gómez-Ballesteros M, Druet M, Cristobo J, Cartes JE (2017) Deep-sea benthic habitats modeling and mapping in a NE Atlantic seamount (Galicia Bank). *Deep-Sea Res Oceanogr Res Pap* 126(115):127. <https://doi.org/10.1016/j.dsr.2017.06.003>
- Smith CR, Demopoulos AWJ (2003) The deep Pacific Ocean floor. In: Tyler PA (ed) *Ecosystems of the world*, vol 28. *Ecosystems of the deep oceans*. Elsevier, Amsterdam, pp 179–218
- Smith CR, De Leo FC, Bernardino AF, Sweetman AK, Arbizu PM (2008) Abyssal food limitation, ecosystem structure and climate change. *Trends Ecol Evol* 23:518–528. <https://doi.org/10.1016/j.tree.2008.05.002>
- Stevenson A, Kroh A (2020) Deep-sea sea urchins. In: *Developments in aquaculture and fisheries science*. Elsevier B.V., pp 237–254. <https://doi.org/10.1016/B978-0-12-819570-3.00014-7>
- Tabachnick KR, Menshenina LL (2002) Family Pheronematidae Gray, (1870). In: Hooper JNA, van Soest RWM (eds) *Systema Porifera: A guide to the classification of sponges*. Springer, US, Boston, MA, pp 1267–1280
- Thurston MH, Bett BJ, Rice AL, Jackson PAB (1994) Variations in the invertebrate abyssal megafauna in the North Atlantic Ocean. *Deep-Sea Res 1 Oceanogr Res Pap* 41:1321–1348. [https://doi.org/10.1016/0967-0637\(94\)90100-7](https://doi.org/10.1016/0967-0637(94)90100-7)
- Victorero L (2018) Spatial patterns in benthic seamount habitats: scales, drivers and effects on biodiversity. PhD thesis, University of Southampton, Faculty of Natural and Environmental Sciences, UK
- Victorero L, Robert K, Robinson LF, Taylor ML, Huvenne VAI (2018) Species replacement dominates megabenthos beta diversity in a

- remote seamount setting. *Sci Rep* 8:4152. <https://doi.org/10.1038/s41598-018-22296-8>
- Vinha B, Simon-Lledó E, Arantes R, Aguilar R, Carreiro-Silva M, Colaço A, Piraino S, Gori A, Huvenne V, Orejas C (2022) Deep-sea benthic megafauna of Cabo Verde (Eastern Equatorial Atlantic Ocean) (Version 1). Zenodo. <https://doi.org/10.5281/zenodo.6560869>
- Watling L, Guinotte J, Clark MR, Smith CR (2013) A proposed biogeography of the deep ocean floor. *Prog Oceanogr* 111:91–112. <https://doi.org/10.1016/j.pocean.2012.11.003>
- Wentworth CK (1922) A scale of grade and class terms for clastic sediments. *J Geol* 30:377–392. <https://doi.org/10.1086/622910>
- White M (2003) Comparison of near seabed currents at two locations in the Porcupine Sea Bight—implications for benthic fauna. *J Mar Biol Assoc UK* 83:683–686. <https://doi.org/10.1017/S0025315403007641h>
- Wickham H (2007) Reshaping Data with the reshape Package. *Journal of Statistical Software*, 21(12), 1–20. URL <http://www.jstatsoft.org/v21/i12/>
- Wickham H (2016) *ggplot2: Elegant graphics for data analysis*. Springer International Publishing
- Wickham H (2020) *tidyr: Tidy Messy Data*. R package version 1.1.2. <https://CRAN.R-project.org/package=tidyr>
- Wickham H, Seidel D (2020) *Scales: scale functions for visualization*. R package version 1.1.1. <https://CRAN.R-project.org/package=scales>
- Wickham H, Averick M, Bryan J, Chang W, McGowan L, François R, Grolemund G, Hayes A, Henry L, Hester J, Kuhn M, Pedersen T, Miller E, Bache S, Müller K, Ooms J, Robinson D, Seidel D, Spinu V, Takahashi K, Vaughan D, Wilke C, Woo K, Yutani H (2019) Welcome to the Tidyverse. *J Open Source Softw* 4:1686. <https://doi.org/10.21105/joss.01686>
- Wickham H, Henry L, Pedersen TL, Luciani TJ, Decorde M, Lise V (2020) *svglite: an “SVG” Graphics Device*. R package version 1.2.3.2. <https://CRAN.R-project.org/package=svglite>
- Wickham H, François R, Henry L, Müller K (2021) *dplyr: a grammar of data manipulation*. R package version 1.0.7. <https://CRAN.R-project.org/package=dplyr>
- Wilke CO (2020) *cowplot: streamlined plot theme and plot annotations for “ggplot2”*. R package version 1.1.1. <https://CRAN.R-project.org/package=cowplot>. 2020
- Xavier JR, Tojeira I, van Soest RWM (2015) On a hexactinellid sponge aggregation at the Great Meteor seamount (North-east Atlantic). *J Mar Biol Assoc UK* 95:1389–1394. <https://doi.org/10.1017/S0025315415000685>
- Yesson C, Clark MR, Taylor ML, Rogers AD (2011) The global distribution of seamounts based on 30 arc seconds bathymetry data. *Deep-Sea Res 1 Oceanogr Res Pap* 58:442–453. <https://doi.org/10.1016/j.dsr.2011.02.004>
- Zeileis A, Fisher JC, Hornik K, Ihaka R, McWhite CD, Murrell P, Stauffer R, Wilke CO (2020) *Colorspace: a toolbox for manipulating and assessing colors and palettes*. *J Stat Softw* 96:1–49. <https://doi.org/10.18637/jss.v096.i01>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.