REPORT

Hidden structural heterogeneity enhances marine hotspots' biodiversity

Georgios Kazanidis[1] · Lea-Anne Henry[1] · J. Murray Roberts[1]

Abstract Studies in terrestrial and shallow-water ecosystems have unravelled the key role of interspecific interactions in enhancing biodiversity, but important knowledge gaps persist for the deep sea. Cold-water coral reefs are hotspots of biodiversity, but the role of interspecific interactions and "habitat cascades" (i.e. positive effects on focal organisms mediated by biogenic habitat formation) in shaping their biodiversity is unknown. Associations between macrofaunal hosts and epifauna were examined in 47 stations at the Mingulay Reef Complex (northeast Atlantic). In total, 101 (group level) and 340 (species level) unique types of facultative associations formed by 43 hosts and 39 epifaunal species were found. Molluscs and empty polychaete tubes had higher values for the type and number of host-epifaunal associations, the Shannon–Wiener (H) and Margalef (d) indices of the epifauna than the rest of the taxonomic groups ($p < 0.05$). Hosts' body size, orientation, surface smoothness, and growth form explained a significant amount of variability (32.96%) in epifauna community composition. Epifaunal species richness (S), H and d were 27.4 ($\pm$ 2.2%), 56.2 ($\pm$ 2.8%) and 39.9 ($\pm$ 2.3%) of the respective values for the total sessile communities living on coral framework. This is intriguing as coral framework is orders of magnitude larger than the size of macrofaunal hosts. It is suggested that bivalves, tunicates and empty polychaete tubes increase habitat heterogeneity and enhance biodiversity through "habitat cascades", in a similar way that epiphytes do in tropical rainforests. Most macrofaunal habitat suppliers in the studied cold-water coral reef are calcified species and likely susceptible to ocean acidification. This indicates that the impacts of climate change on the total biodiversity, structure and health of cold-water coral reefs may potentially be more severe than previously thought.

Keywords Macrofauna · Symbiosis · Biodiversity hotspots · Deep sea · Cold-water coral reefs

Introduction

Unravelling the mechanisms that drive the formation of hotspots of species biodiversity is a critical component for the understanding of their structure and functioning. Studies in terrestrial, and aquatic ecosystems have shown the importance of stable environmental conditions over geological time scales (e.g. ancient rivers and lakes—Bolotov et al. 2017), energy availability (e.g. tropical forests—Sullivan et al. 2017), multiple macroevolutionary routes (Igea and Tanentzap 2019) and habitat heterogeneity in shaping hot spots of biodiversity (e.g. in springs—Cantonati et al. 2012; rocky seaweed forests; Thomsen et al. 2010; tropical rain forests—Nakamura et al. 2017).

Evidence from relatively well-studied ecosystems such as tropical rain forests, kelp forests and sandy seagrass beds served the unravelling of "habitat cascades" phenomenon and its role in ecosystem biodiversity (Thomsen et al. 2010). Habitat cascades occur when there are indirect positive effects on focal organisms mediated by successive biogenic formation or habitat modification. They are a general phenomenon that enhances species abundance and diversity (Thomsen et al. 2010). For example, the highest

✉ Georgios Kazanidis
gkazanidis@gmail.com

[1] Changing Oceans Group, School of GeoSciences, Grant Institute, University of Edinburgh, Kings Buildings, James Hutton Road, Edinburgh EH9 3FE, UK

biodiversity in rainforests is often found within the canopy, which is formed by overlapping tree branches and leaves; therein, primary epiphytes (e.g. vascular bromeliads) increase habitat heterogeneity and biodiversity of focal organisms (Nakamura et al. 2017).

Being the largest biome on Earth, the deep sea (typically > 200 m water depth) remains still the least explored. Technological progress, however, over the last thirty years has facilitated the discovery of deep-sea biodiversity hotspots such as reefs formed by scleractinian cold-water corals (CWCRs hereafter; Roberts et al. 2006; Cordes et al. 2021), gorgonian coral forests and similar CWC non-reef environments (Angiolillo and Canese 2017; Li and Wang 2019). These are also hotspots of biomass, carbon cycling and ecosystem services (Cathalot et al. 2015; Henry and Roberts 2017). Patterns in CWCRs biodiversity are related to seafloor bathymetry, hydrography, life histories of the fauna themselves (Henry et al. 2013) as well as to substrate availability/type (Bourque and Demopoulos 2018), food supply (Kazanidis and Witte 2016), social interactions (e.g. foraging, mating) and dispersal (Henry et al. 2013).

Important knowledge gaps remain for CWCR biodiversity and particularly interspecific interactions. For example, are habitat cascades present in CWCRs and if yes, what is their role in biodiversity and how does climate change stand to alter this? Are the relationships between hosts and epifauna facultative or obligate? Are there any common features among habitat suppliers, e.g. are they calcified or non-calcified? Studies on megafaunal hosts have shown facultative relationships with their epifauna (Buhl-Mortensen and Mortensen 2004a) and parasitism (Carreiro-Silva et al. 2017), but almost nothing is known for macrofauna (500 μm–5 cm body length; Gage and Tyler 1991). This is an important knowledge gap as macrofauna are key components in ecosystem functioning: they are extremely species rich (Grassle and Maciolek 1992) and shape benthic elemental cycling (Janas et al. 2019). In CWCRs macrofauna are speciose exceeding by far megafauna species richness (Henry and Roberts 2017). Macrofauna species have also several morphotypes (e.g. erect, horizontal), body texture (soft or calcified) and external morphology (smooth or spiny body surfaces). This high morphotype diversity combined with high macrofaunal density and biomass (Kazanidis and Witte 2016) create many microhabitats and possibly enhance biodiversity, similarly to epiphytes in tropical forests (Nakamura et al. 2017).

Advancing knowledge about the role of macrofauna in ecosystem functioning is crucial for one more reason. Models predict large-scale shifts in water-mass characteristics by 2100 (e.g. pH reduction by 0.37 units; Puerta et al. 2020) which in turn will have negative impacts on the distribution (Morato et al. 2020) and skeletal integrity of habitat-forming cold-water corals (Hennige et al. 2020). These are expected to damage the role of these corals in supporting high biodiversity (Henry and Roberts 2017) and their overall health and environmental status (Kazanidis et al. 2020; Morato et al. 2020). Thus, unravelling (1) the role of macrofauna as habitat suppliers and (2) the features of these species are key things for understanding CWCR sensitivity to climate change. This is especially true for calcified macrofauna as they are expected to be more sensitive to ocean acidification than the non-calcified macrofaunal species (Bell et al. 2018; Byrne and Fitzer 2019). In the present study, macrofaunal communities from a well-studied CWCR, the Mingulay Reef Complex (MRC, hereafter) in the northeastern Atlantic were examined with the aim of unravelling their contributions to CWCR heterogeneity and biodiversity.

Materials and methods

Study area

The MRC is located in the Outer Hebrides Sea, western Scotland (Roberts et al. 2005). Since its discovery in 2003 (Roberts et al. 2005) the MRC has been one of the best studied CWCRs in the world in terms of its bathymetry, hydrography, ecosystem functioning and biodiversity (e.g. Roberts et al. 2009; Henry et al., 2013; De Clippele et al. 2021 and references therein).

Habitat mapping has shown that the MRC's mounded bathymetry was formed by reefs of the scleractinian cold-water coral *Lophelia pertusa* (Roberts et al. 2005). Specifically, surveys using multibeam echosounders and seabed video revealed *L. pertusa* mounds in 5 areas: MRC1, Banana Reef, MRC 5 North, MRC 5 South and Four Mounds (Roberts et al. 2009; Duineveld et al. 2012; Fig. 1). The mounds are 13–60 m wide, 16–108 m long and between 2 and 34 m tall (De Clippele et al. 2017). Studies have shown that CWCR habitats are most well developed at MRC1, Banana Reef and MRC5 North (Roberts et al. 2009; Duineveld et al. 2012; Henry et al. 2013). Geochronology of vibrocore samples showed that *Lophelia* reefs have been present for at least 7000 years (Douarin et al. 2014, 2016).

MRC is primarily bathed by North Atlantic Water (10.0–10.5 °C, 35.4 psu) which flows onto the European shelf from the eastern subpolar North Atlantic (Johnson et al. 2013; Porter et al. 2018). Benthic lander and mooring deployments have shown that rapid downwelling transfers fresh microalgae to the MRC CWCR habitats (Davies et al. 2009; Duineveld et al. 2012). Integration of geophysical, hydrological and species life history traits unravelled that bathymetric and hydrographic gradients were important in

shaping macrofaunal biodiversity across reefs, while within reefs, the assemblages were shaped by recruitment, food supply, foraging and mating interactions (Henry et al. 2010, 2013).

The MRC area is part of the East Mingulay Marine Protected Area and is fully closed to mobile bottom-tending fishing gear, to protect coral features and associated biodiversity (Roberts et al. 2009).

Benthos

Benthic samples for the examination of host-epifauna associations were available from 47 stations which were sampled in 2009, 2010 and 2011; 43 of these stations are found at MRC1 and four are found at Banana Reef, two of the most developed reefs at MRC (Fig. 1, Table 1). The stations have not been recurrently investigated in the three sampling periods (Table 1). The samples were collected using a modified Van Veen Grab (sampling 0.1 m^2 per deployment), and most of them come from dead coral framework or a mixture of dead and live framework habitats (Fig. S1 in the Supplementary Material).

Samples were sieved at 1 mm, macrofauna collected and stored in 4% seawater formalin and transferred to 70% industrial methylated spirit. Hosts and epifauna were identified to the lowest possible taxonomic level using best available taxonomic keys for North Atlantic marine invertebrates and guidance from expert taxonomists (Tables S1-S2 in the Supplementary Material).

The faunal groups that were investigated were the following: anthozoans, arthropods, brachiopods, bryozoans, echinoderms, entoprocts, molluscs, nemerteans, oligochaetes, platyhelminthes, polychaetes (including empty serpulid and eunicid tubes), priapulids, sipunculans, tunicates, and shark eggs. Following Henry et al. (2013), sponges were excluded due to a lack of taxonomic resolution. This exclusion should not be regarded as a deficiency as previous studies have shown that small-/medium-sized sponges at MRC host limited epi- and infaunal communities (Kazanidis et al. 2016).

Accounting for the existence of both colonial and solitary taxa, species' presence/absence was recorded. Data from all stations were compiled in a species assembly matrix using Primer v.7 (Clarke and Gorley 2015) to investigate possible differences among the communities colonizing the macrofaunal hosts (see below for details).

Macrofaunal host species' features considered in explaining variability in their epifaunal communities were (1) body size (A: 0–49 mm^2, B: 50–99 mm^2, C: $\geq$ 100 mm^2), (2) body texture (A: calcified, B: non-calcified), (3) body surface roughness (A: smooth, B: non-smooth), (4) body orientation (A: horizontal, B: erect), (5) growth form (A: solitary, B: colonial) and (6) condition when collected (A: alive, B: dead) (Table S3).

Data analysis

Data in the species assembly matrix were used in the calculation of three biodiversity indices, i.e. species richness (S), Shannon–Wiener (H), Margalef (d) and total taxonomic distinctness ($S\Delta^+$). The species assembly matrix was also used to calculate Bray–Curtis similarities and similarity matrices (Clarke and Gorley 2015).

Based on these matrices, dendrograms using group average (Clarke and Gorley 2015) were constructed showing the clustering of the organisms [at the group (e.g. bivalves, bryozoans) and species levels] hosting epifauna. One-way analysis of similarities (ANOSIM) was carried

Fig. 1 **a** Location of the Mingulay Reef Complex (total area $\sim$ 100 km^2) in the Sea of the Outer Hebrides (northeast Atlantic). **b** Locations of sampling stations at Mingulay Reef Complex 1 (MRC1) and Banana Reef (BR) are shown. Colour shading represents bathymetry, see legend. For more details on stations see Table 1
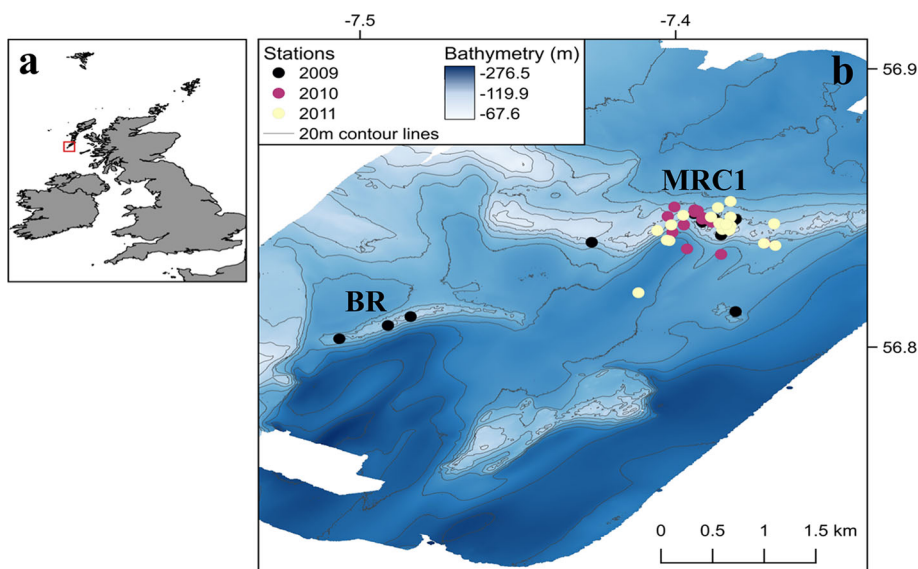
Table 1 Samples analysed for the examination of hosts and their epifauna at Mingulay Reef Complex 1 (MRC1) and Banana Reef (BR)

Station code	Area	Year	Water depth (m)	Latitude	Longitude	Station code	Area	Year	Water depth (m)	Latitude	Longitude
1484	MRC1	2009	133	56.8189	− 7.4133	20100505/002	MRC1	2010	151	56.8252	− 7.4002
1485	MRC1	2009	127	56.823	− 7.3905	20100505/003	MRC1	2010	135	56.8233	− 7.3957
1486	MRC1	2009	133	56.8231	− 7.3939	20100505/004	MRC1	2010	152	56.8243	− 7.39701
1487	BR	2009	138	56.8039	− 7.4456	20100505/005	MRC1	2010	152	56.8245	− 7.3965
1488	BR	2009	118	56.8055	− 7.442	20100505/006	MRC1	2010	138	56.8177	− 7.3982
1489	BR	2009	127	56.8064	− 7.3905	20110608/003	MRC1	2011	131	56.8212	− 7.3926
1490	BR	2009	165	56.8015	− 7.4533	20110608/004	MRC1	2011	167	56.8183	− 7.3842
1491	MRC1	2009	108	56.8202	− 7.3928	20110608/005	MRC1	2011	185	56.8192	− 7.401
1492	MRC1	2009	127	56.8228	− 7.3945	20110608/007	MRC1	2011	124	56.8187	− 7.386
1494	MRC1	2009	127	56.8229	− 7.395	20110608/008	MRC1	2011	164	56.8223	− 7.3931
1495	MRC1	2009	134	56.8232	− 7.3955	20110608/009	MRC1	2011	162	56.8218	− 7.3913
1496	MRC1	2009	125	56.8225	− 7.3958	20110608/010	MRC1	2011	153	56.8211	− 7.3915
1498	MRC1	2009	146	56.824	− 7.3971	20110608/011	MRC1	2011	150	56.8234	− 7.3913
1500	MRC1	2009	131	56.823	− 7.395	20110608/012	MRC1	2011	162	56.8221	− 7.392
20100223/002	MRC1	2010	125	56.823	− 7.3958	20110609/001	MRC1	2011	142	56.8193	− 7.4014
20100223/003	MRC1	2010	130	56.823	− 7.3951	20110609/002	MRC1	2011	162	56.8098	− 7.4059
20100223/004	MRC1	2010	140	56.822	− 7.3928	20110707/003	MRC1	2011	169	56.8262	− 7.3913
20100223/005	MRC1	2010	135	56.822	− 7.3987	20110707/004	MRC1	2011	135	56.822	− 7.4007
20100504/001	MRC1	2010	190	56.8167	− 7.3928	20110707/005	MRC1	2011	121	56.821	− 7.4029
20100504/002	MRC1	2010	156	56.8187	− 7.3859	20110707/006	MRC1	2011	154	56.8222	− 7.3844
20100504/003	MRC1	2010	122	56.8235	− 7.40125	20110707/008	MRC1	2011	134	56.8237	− 7.3988
20100504/004	MRC1	2010	171	56.8207	− 7.4005	20110707/009	MRC1	2011	159	56.8251	− 7.3933
20100504/005	MRC1	2010	123	56.8225	− 7.3943	20110707/010	MRC1	2011	154	56.8234	− 7.3944
20100504/008	MRC1	2010	151	56.8247	− 7.397						

out to check for significant differences in the epifaunal communities hosted by each group (e.g. bivalves vs. bryozoans). Identifying the species that were responsible for the average dissimilarity between the groups was carried out by similarity percentage analysis (SIMPER) (Clarke and Gorley 2015). The identification of obligate and

Fig. 2 Hosts and their epifauna.
a Anthozoan of the family Actiniidae attached on an empty parchment-like eunicid tube; **b** the bryozoans *Disporella hispida* and *Smittoidea reticulata* attached on the brachiopod *Novocrania anomala*; **c** the brachiopod *Eucalathis tuberata* attached on the bivalve *Hiatella arctica*; **d** the bryozoan *Amphiblestrum flemingii* attached on a shark egg; **e** the bryozoan *Terminoflustra barleei* on the erect bryozoan *Omalosecosa ramulosa*; **f** the anthozoan *Parazoanthus anguicomus* on the erect tunicate *Polycarpa pomaria*
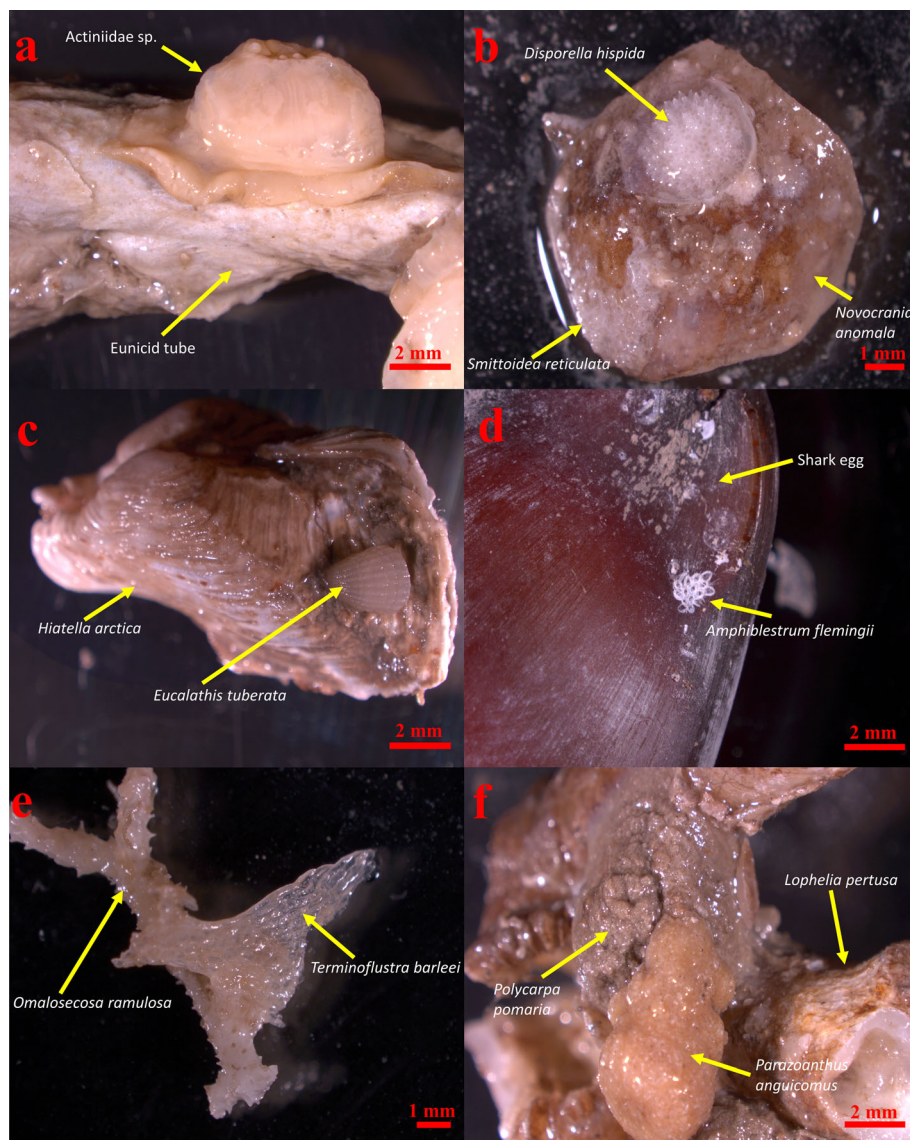
facultative symbionts was carried out following Buhl-Mortensen and Mortensen (2004a) where obligate ones were characterized as the symbionts found in association with only a single taxonomic group.

The presence of statistically significant differences across the groups in terms of (1) types of host-epifaunal associations (T), (2) number of host-epifaunal associations (N), (3) H and (4) d in epifaunal communities, was examined in RStudio (rstatix package). The normality of the distributions was checked with the Shapiro–Wilk test and the equality of variances with the F-test (for two groups) or Bartlett test (for three groups). In the case of normal distribution and equal variances, the hypothesis that the groups have the same mean was tested either through the two-sample t-test (two groups) or one-way ANOVA (three groups). In the case of normal distributions and unequal variances, the hypothesis that the groups have the same mean was tested either through the Welch's two-sample t-test (two groups) or one-way analysis of means (not assuming equal variances) (three groups). Finally, in the case of the normal distribution criterion did not hold, the hypothesis that the groups have the same median was tested either through a Wilcoxon rank sum test (two groups) or a Kruskal–Wallis rank sum test (three groups). These tests were followed by pairwise comparisons to examine for the presence of statistically significant differences in pairs of groups. In the case of one-way ANOVA, multiple comparisons were carried out through the Tukey's test. In the case of one-way analysis of means, the comparisons were carried out through the Games Howell test (Burk 2018). When the Kruskal–Wallis test was used, the pairwise comparisons were carried out through the Dunn
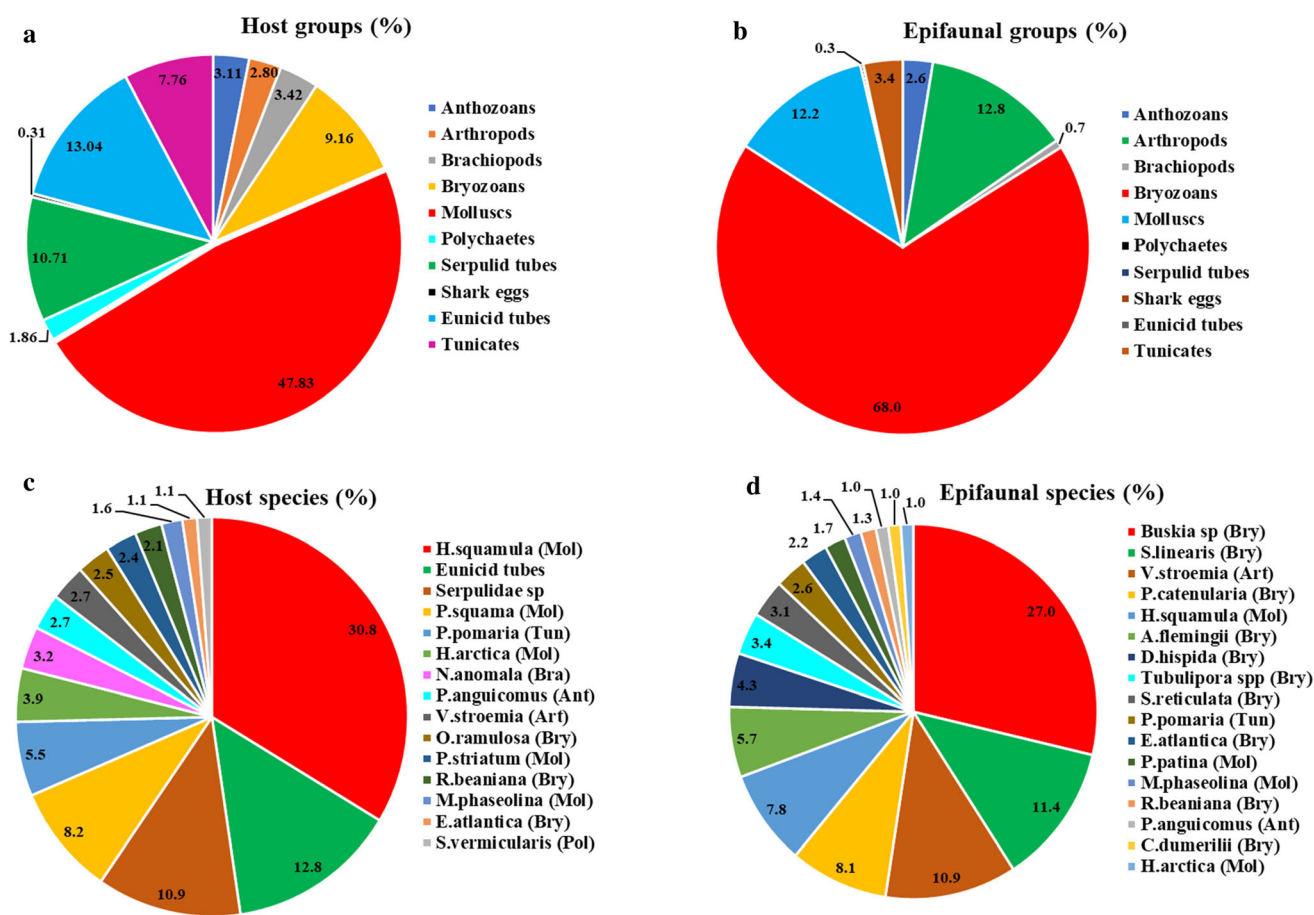
Fig. 3 Relative frequency of hosts and epifauna at the group **a, b** and species **c, d** levels

test (Dinno 2017). Accounting for the multiple comparisons, the *p* values were adjusted using the Bonferroni correction (Armstrong 2014). The role of body size and morphological features in shaping the epifaunal communities was analysed through distance-based linear modelling (Clarke and Gorley 2015). The role of hosts in enhancing local biodiversity was carried out by comparing the biodiversity of hosts' epifauna (S, H and d) with the biodiversity of total sessile macrofaunal communities recorded at MRC previously (Henry et al. 2010, 2013; Kazanidis et al. 2016).

Results

Hosts and epifaunal species

In total, 157 sessile macrofaunal species were identified. Out of them, 43 species were found to host epifauna (Table S1). Most of them (41 out of 43) were "alive" species and the remaining two were empty tubes belonging to families Serpulidae and Eunicidae (calcareous-tube-

building & parchment-like tube-building polychaetes, respectively). Notably, shark eggs (possibly the species *Galeus melastomus*) at station 1485 were hosting epifaunal species, e.g. the encrusting bryozoan *Amphiblestrum flemingii* (Fig. 2). Across these 43 host species, bivalves (mainly *Pododemus squama* and *Heteranomia squamula*) were the most common hosts (∼ 47.83% of total number of associations), followed by the eunicid tubes (13.04%), the serpulid tubes (10.71%), bryozoans (9.16%; mainly the erect species *Omalosecosa ramulosa*) and tunicates (7.76%; mainly the erect species *Polycarpa pomaria*) (Fig. 2; Fig. 3a-–c). Regarding the epifauna, 39 species were identified (Table S2). They were dominated by bryozoans (68%; mainly the species *Schizomavella linearis*, *Buskia* sp., *Pyripora catenularia*, *Amphiblestrum flemingii*, *Disporella hispida*), followed by the barnacle *Verruca stroemia* (12.8%) and molluscs (12.2%; mainly *Heteranomia squamula*) (Fig. 3b–d).

In terms of hosts, molluscs had significantly higher values regarding the types of host-epifauna (e.g. "Bryozoan on Mollusc" or "Mollusc on Tunicate") associations (T) (3.25 ± 0.55), the number of host-epifauna
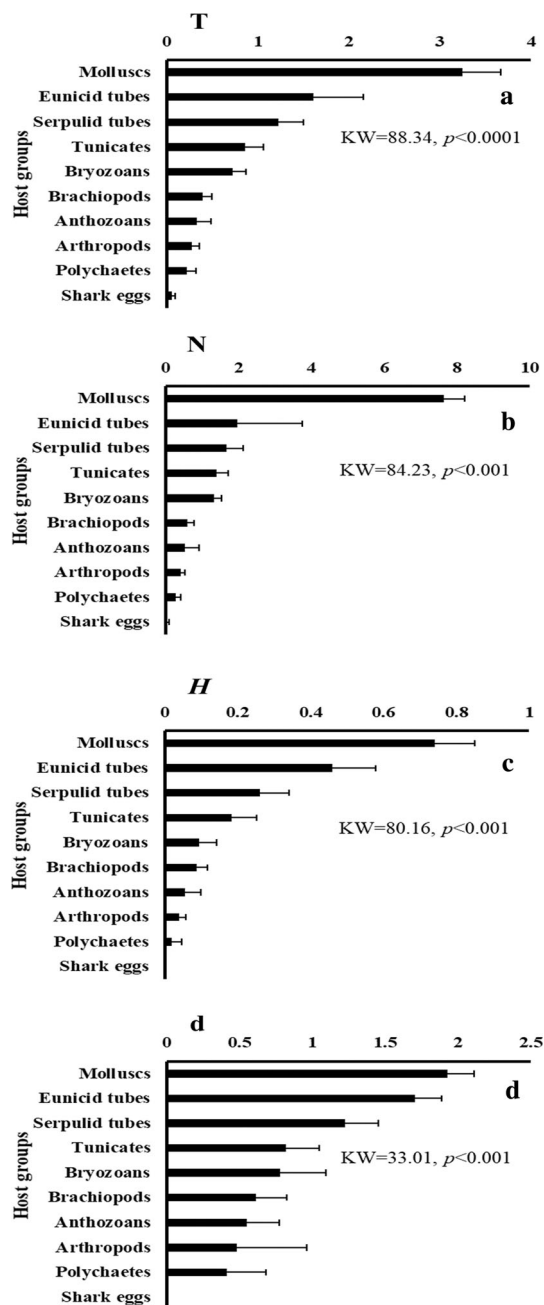
Fig. 4 Analysis of variance for the **a** types of host-epifauna associations (T), **b** number of host-epifauna associations (N), **c** Shannon–Wiener index (H) and **d** Margalef index (d) of epifaunal associations across the host groups. Average values and standard errors are given. "KW": Kruskal–Wallis test. p-values are given

associations (N) (7.63 ± 1.76) and H (0.73 ± 0.12) than all the other groups (Fig. 4; Table 2). Statistically significant differences were also found between other groups. Specifically, regarding the types of host-epifauna associations and H, the eunicid tubes (1.61 ± 0.41 and 0.45 ± 0.11, respectively) and serpulid tubes (1.22 ± 0.27 and 0.26 ± 0.07) had significantly higher values than the anthozoans (0.33 ± 0.10 and 0.05 ± 0.03) and the

arthropods (0.27 ± 0.09 and 0.03 ± 0.02). In terms of d, statistically significant differences were found between molluscs and arthropods (1.70 ± 0.18 vs. 0.41 ± 0.26, respectively), eunicid tubes and arthropods (1.92 ± 0.18 vs. 0.41 ± 0.26), eunicid tubes and bryozoans (1.92 ± 0.18 vs. 0.55 ± 0.22) (Fig. 4; Table 2).

The body size and morphological features of the hosts had a statistically significant contribution ($p < 0.05$) explaining in total 32.96% of the variability in epifaunal communities. Specifically body size (9.88%, $p < 0.01$), body surface's texture (8.51%, $p < 0.01$), body orientation (5.20%, $p < 0.05$), growth form (4.87%, $p < 0.01$), calcification (1.92%, $p > 0.05$) and condition during collection (2.54%, $p > 0.05$) (Table S4). Species with a body size at 50–99 mm^2 had a statistically significant ($p < 0.05$) higher type of associations than smaller ones (0–49 mm^2). Species with a horizontal body orientation had a higher number ($p < 0.05$) of associations than the erect ones and solitary species had statistically higher values ($p < 0.05$) for d than the colonial ones (Fig. 5). It should also be mentioned that in some cases there was a marginal absence of statistically significant differences (e.g. $p = 0.07$), but there was a clear difference in the average values between groups (e.g. for N and H between organisms with smooth and non-smooth surfaces; Fig. 5).

Types of host-epifauna associations

In total, 101 and 339 unique types of host-epifauna associations were recorded at the group (e.g. "Bryozoan on Mollusc") (Fig. 6a; Table S5) and species levels (e.g. "*Buskia* sp. on *Heteranomia squamula*") (Fig. 6b; Table S6), respectively. Almost half of them (51.92%) were composed of a single epifaunal species on a host. This was followed by the type where two species were attached on a host (34.22%), three species (8.55%), four species (1.77%) and five species on a host (0.88%). In a few cases (2.65%), epifaunal species were attached on an organism which was attached on another host (e.g. the bryozoan *Buskia* sp. was attached on the mollusc *Heteranomia squamula* which was attached on an empty serpulid tube).

Fourteen types of associations ("Epifauna_Host") were quite widespread as they composed more than 70% of the number of host-epifauna associations. The most common type of association was bryozoans on molluscs (i.e. "Bryozoan_Mollusc" and Bryozoan-Bryozoan_Mollusc" "30.82%) (Fig. 6a); specifically, "*Buskia_H.squamula*", "*S.linearis_H.squamula*" and "*P.catenularia_H.squamula*" were the most common associations of bryozoans on molluscs (Fig. 6b). "Bryozoan_Mollusc" association was followed by the "Bryozoan_Bryozoan" (6.92%) and "Bryozoan_Serpulid tube" (5.35%) (Fig. 6a).

Analyses using epifauna-host associations did not reveal almost any clustering of groups at a level of similarity

Table 2 Pairwise comparisons for the types of host-epifauna associations (T), number of host-epifauna associations (N), Shannon–Wiener index (*H*) and Margalef index (d) of epifaunal communities across the host groups

Types of associations	ANT	ART	BRA	BRY	MOL	POL	SER	SHA	TUB
ART									
BRA									
BRY									
MOL	− 5.79****	− 6.05****	− 5.88****	− 3.75**					
POL					6.31***				
SER	− 3.31*	− 3.57**	− 3.39*			− 3.82**			
SHA				3.58**	7.33****		4.85****		
TUB					3.36*			− 3.97**	
TUN					3.68**			− 3.65**	
Number of associations	ANT	ART	BRA	BRY	MOL	POL	SER	SHA	TUB
ART									
BRA									
BRY									
MOL	− 5.70****	− 5.86****	− 5.71****	− 3.55**					
POL					6.25****				
SER		− 3.26*				− 3.65**			
SHA				3.74**	7.29****		4.70***		
TUB					3.58**			− 3.71**	
TUN					3.55**			− 3.74**	
H of epifaunal communities	ANT	ART	BRA	BRY	MOL	POL	SER	SHA	TUB
ART									
BRA									
BRY									
MOL	− 5.85****	− 6.07****	− 5.50****	− 5.52****					
POL					6.36****				
SER					3.70**				
SHA					6.64****				
TUB	− 3.57**	− 3.79**				− 4.08**		− 4.36***	
TUN					4.57***				
d of epifaunal communities	ANT	ART	BRA	BRY	MOL	POL	SER	SHA	TUB
ART									
BRA									
BRY									
MOL		− 3.22*							
POL									
SER									
SHA									
TUB		− 3.62**		− 3.55**					
TUN									

The comparisons were done using the Dunn test (DT), following the methodology in Materials and Methods. Only statistically significant results are shown. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; *****$p < 0.0001$. ANT: Anthozoans; ART: Arthropods; BRA: Brachiopods; BRY: Bryozoans; MOL: Molluscs; POL: Polychaetes; SER: Serpulid tubes; SHA: Shark eggs; TUB: eunicid tubes

higher than 50%; the only exception to that was the clustering of most bryozoan species (13 of 15) in a cluster with ~ 60% similarity. Almost all these 13 bryozoans were encrusting forms hosting very little epifauna. The species that were among the most common hosts—i.e. the bivalves *Pododesmus squama* and *Heteranomia squamula*,
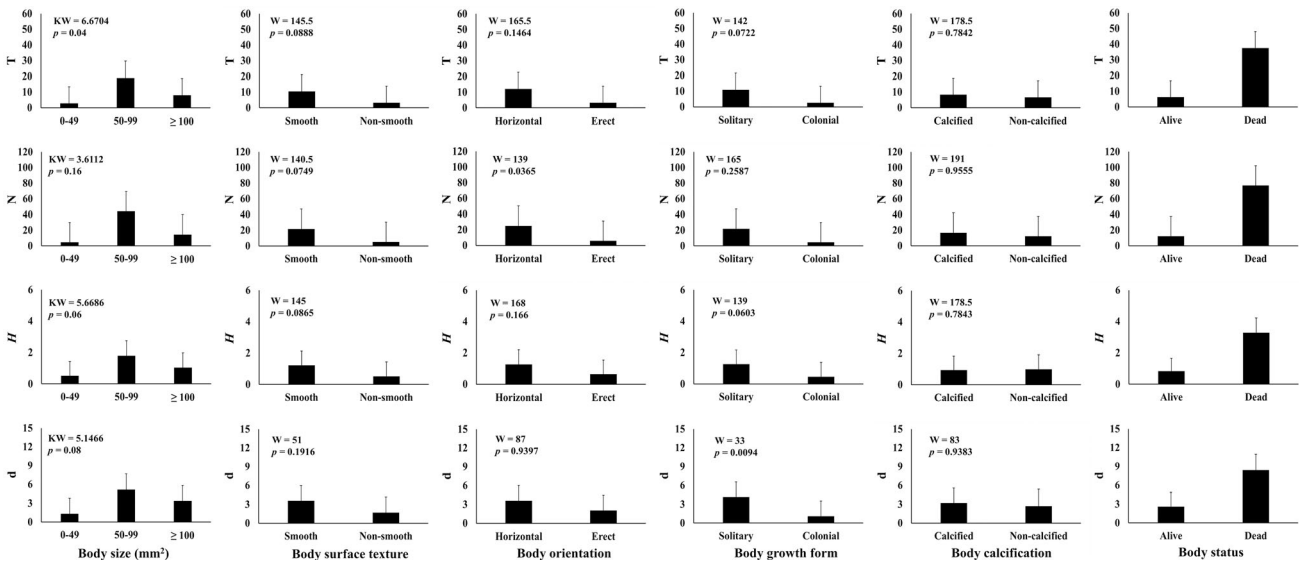
Fig. 5 Comparisons of types of associations (T), number of associations (N), Shannon–Wiener index (H) and Margalef index (d) of epifaunal communities in terms of hosts' body size (0–49, 50–99, ≥ 100 mm²), body surface roughness (smooth, non-smooth), body orientation (horizontal, erect), growth (solitary, colonial), body texture (calcified, non-calcified) and condition (alive, dead). Average values and standard errors are given. "W": Wilcoxon rank sum test; "KW": Kruskal–Wallis test. p-values are given
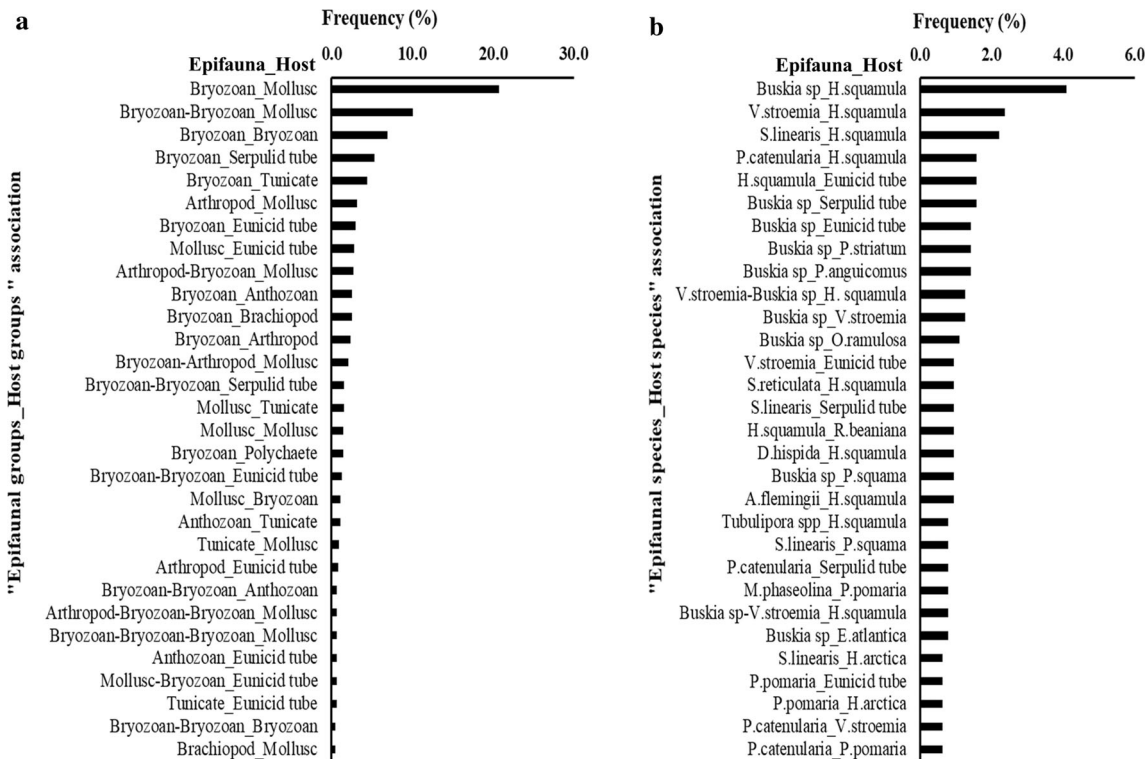
Fig. 6 Frequency of "Epifauna_ Host" associations at the group **a** and species levels **b**. The 30 most frequent associations are shown. For the full list of "Epifauna_Host" associations at the group and species levels please see Tables S5 and S6

the empty eunicid and serpulid tubes and the tunicate *Polycarpa pomaria*—were grouped within the same cluster (Fig. 7). These were the hosts with the most diverse epifaunal communities (e.g. the H index for the bivalves *H.* *squamula* and *P. squama* was 3.605 and 3.537, respectively, for eunicid tubes was 3.337, for serpulid tubes 3.219 and for the ascidian *P. pomaria* was 2.558).
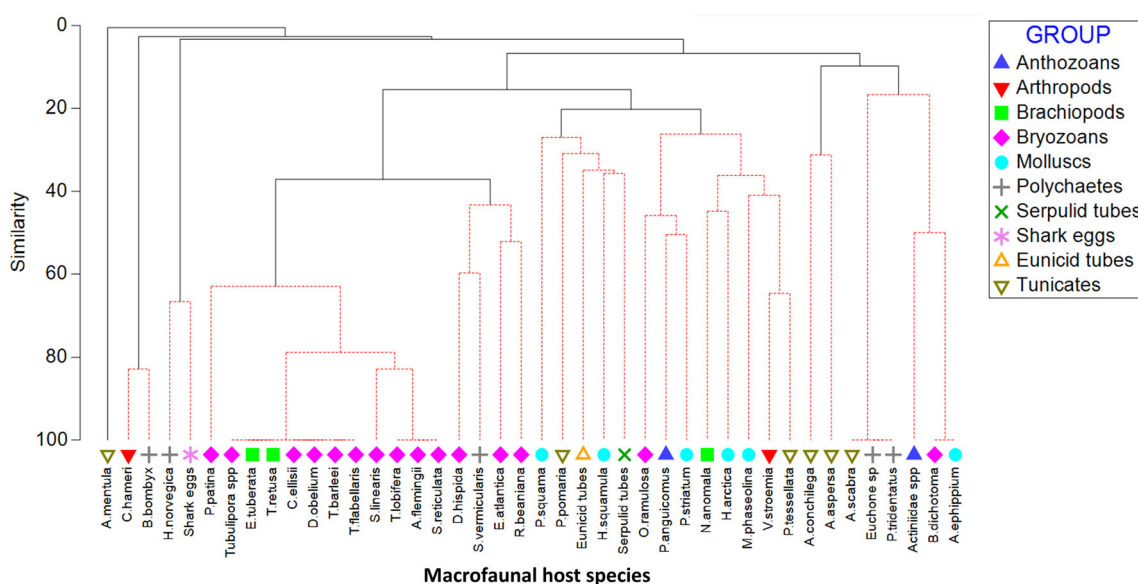
Fig. 7 Dendrogram showing the clustering of macrofaunal host species
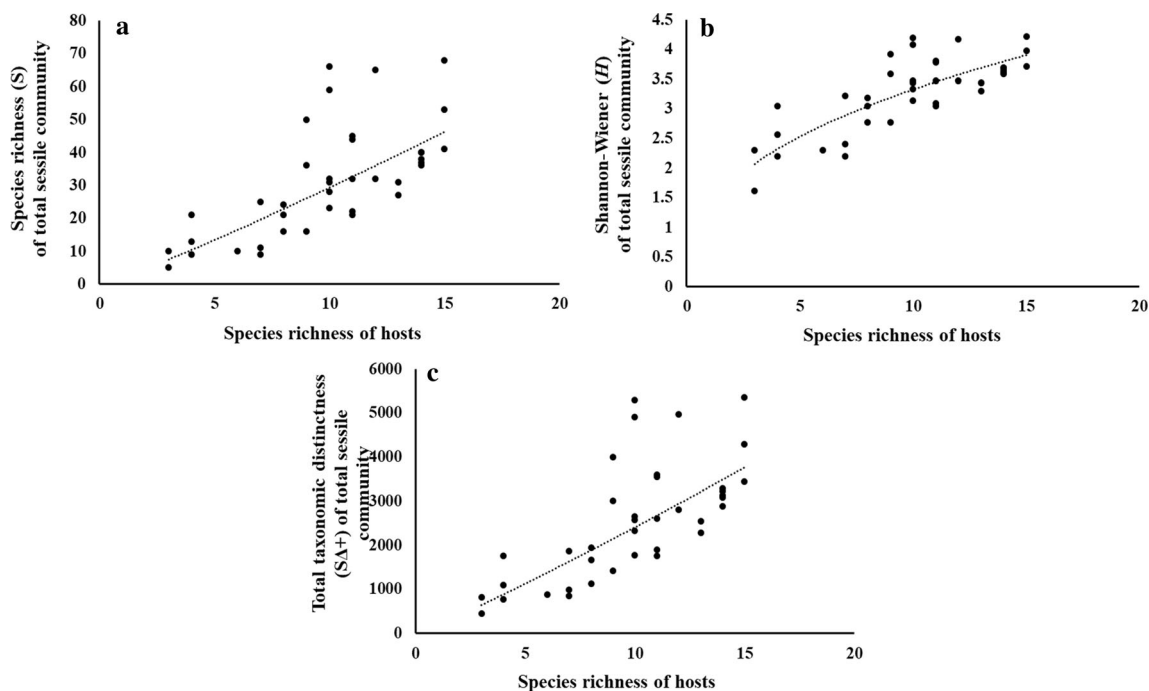
Fig. 8 Scatterplots showing the relationship between the species richness of hosts with **a** species richness (*S*), **b** Shannon–Wiener (*H*) and **c** total taxonomic distinctness (SΔ^+) of the total sessile macrofaunal community

The one-way ANOSIM analysis showed statistically significant differences for six pairs of host groups. These were Anthozoans vs. Bryozoans (R = 0.620, p = 0.02), Arthropods vs. Bryozoans (R = 0.612, p = 0.04), Molluscs vs. Bryozoans (R = 0.586, p = 0.002), Polychaetes vs. Bryozoans (R = 0.631, p = 0.001), Tunicates vs. Bryozoans (R = 0.764, p = 0.001) and Molluscs vs. Tunicates

(R = 0.281, p = 0.015; the full list of pairs, R and p values are shown in Table S7).

For those groups that ANOSIM showed the presence of statistically significant differences, SIMPER analyses were carried out to identify the epifaunal species driving the differences between the host groups. Specifically, SIMPER analysis revealed an average dissimilarity of 82.60 between Anthozoans and Bryozoans. The main species driving this
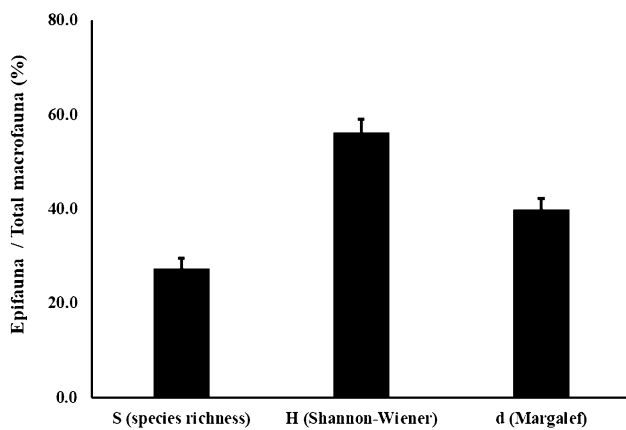
Fig. 9 Comparison (%) of epifaunal communities attached on host species to the species richness (*S*), Shannon–Wiener index (*H*) and Margalef index (*d*) of the total sessile macrofauna

dissimilarity were the bryozoans *Buskia* sp., *Schizomavella linearis* and *Plagioecia patina*, all of which were more abundant in Anthozoans (Table S8). The bryozoans *Buskia* sp., *Pyripora catenularia* and the bivalve *Heteranomia squamula* were the species leading the average dissimilarity of 83.37 recorded between Arthropods and Bryozoans. The average dissimilarity between Bryozoans and Molluscs was 84.60; the bryozoans *Buskia* sp., *Schizomavella linearis*, *Pyripora catenularia*, *Smittoidea reticulata* and the barnacle *Verruca stroemia* had a cumulative contribution of 39.45%. The species list explaining the dissimilarities between Bryozoans and Molluscs was much longer than those recorded in the pairs mentioned above (i.e. Anthozoans vs. Bryozoans, and Arthropods vs. Bryozoans; Table S8). The average dissimilarity between Bryozoans and Polychaetes was 89.36. This dissimilarity was attributed to the bivalve *Heteranomia squamula* and the bryozoans *Buskia* sp., *Pyripora catenularia* and *Schizomavella linearis*. These bryozoans also led the differences between Bryozoans and Tunicates (average dissimilarity 95.02) accompanied by the erect bryozoan *Reteporella beaniana* and Actiniaria spp. Finally, the average dissimilarity between Molluscs and Tunicates was 90.45. Dissimilarities between these two groups were attributed to a relatively long species list (Table S8) including—among other—the bryozoans *Buskia* sp., *Schizomavella linearis*, *Pyripora catenularia*, the erect bryozoan *Reteporella beaniana*, the barnacle *Verruca stroemia*, Actiniaria spp. and the tunicate *Polycarpa pomaria*.

The role of hosts in enhancing local biodiversity

The epifauna on hosts had a substantial contribution in the biodiversity of the total sessile macrofaunal communities. The relationship between the number of hosts with the

richest epifaunal communities (e.g. *P. squama*, *H. squamula*, serpulid and eunicid tubes, *P. pomaria*) and *S*, *H* and $S\Delta^+$ of the total sessile macrofaunal communities can be seen in Fig. 8. The average values of epifaunal sessile biodiversity on macrofaunal hosts compared to total sessile macrofaunal biodiversity recorded in previous studies were 27.4 ($\pm$ 2.2%), 56.2 ($\pm$ 2.8%) and 39.9 ($\pm$ 2.3%) for *S*, *H* and d, respectively (Fig. 9).

Discussion

This study has shown for the first time that sessile macrofauna enhance marine hotspots' biodiversity advancing scientific knowledge about the drivers shaping enigmatic hotspots of biodiversity. It is intriguing that a rather small group of macrofauna can host up to 54.5% of the species found also attached on dead *L. pertusa* framework—a substrate though that has orders of magnitude higher size than sessile macrofauna (Jensen and Frederiksen 1992; Vad et al. 2017). Based on the findings of the present study, it is suggested that sessile macrofauna cause habitat cascades and enhance CWCRs biodiversity in a similar way that epiphytes increase biodiversity of tropical rainforests (Nakamura et al. 2017). The major macrofaunal species that enhance CWCRs biodiversity are either calcified themselves or closely associated with calcified organisms. This suggests that ocean acidification may have negative impacts not only on megafaunal calcified corals (Morato et al. 2020) but also on the macrofauna. The extent of these impacts on epifaunal organisms will depend on the mineralogy of the epizoan macrofauna (Smith et al. 2013; Byrne and Fitzer 2019; Ye et al. 2019), the nature of mineralization (Barclay et al. 2020; Fordyce et al. 2020; Grenier et al. 2020) and on animal physiology (Goethel et al. 2017; Diaz-Castaneda et al. 2019; Fitzer et al. 2019; Devens et al. 2020; Sokolowski et al.2020). Based on that, it is possible that climate change impacts on CWCR will be more severe than previously thought.

Hosts with diverse epifaunal communities

The bivalves *Pododesmus squama*, *Heteranomia squamula*, the tunicate *Polycarpa pomaria*, serpulid and eunicid tubes hosted the most diverse epifaunal communities. These observations agree with findings from shallow-water areas where mussels, oysters and serpulid polychaetes create complex biogenic habitats with high species richness (Sanderson et al. 2008).

Macrofauna hosting the most diverse epifaunal communities were species of relatively large size, horizontal and with smooth surfaces. These findings agree with previous studies which showed that the host's body size was

positively related to epifaunal biodiversity (Buhl-Mortensen et al. 2010). Erect species hosted less diverse communities than horizontally laid ones, but the drivers behind this are not clear. Experiments with ascidians have shown higher settlement in vertical surfaces suggesting greater mortality of newly settled individuals or larvae on horizontal surfaces (Gotelli 1987), while surface orientation did not have an impact in the early growth and survivorship of scleractinian coral larvae (Babcock and Mundy 1996). The lower diversity in erect species may be related to some kind of chemical defence or to their rough/spiny surfaces hindering larvae settlement (Parisi et al. 2020). Furthermore, studies have shown that settlement is shaped by textural differences. In barnacles, the settlement was higher in fine/medium-roughness surfaces than in coarse/smooth ones (Hills and Thomason 1998). Bryozoans seem to require a firm substratum for attachment, and many also prefer to settle on relatively smooth surfaces (McKinney and McKinney 1993).

Despite the role of hosts' body size and morphology in explaining epifaunal biodiversity, it is important to note that most of the variability remains unaccounted for. For example, there were organisms with relatively large size and smooth surfaces that hosted little epifauna (e.g. *Ascidia* and *Ascidiella* tunicates and the anthozoan *P. anguicomus*). There are several reasons that could explain this situation. First, it is well known that sessile invertebrates have developed mechanisms to protect themselves from biofouling, bacterial infection, and predators. Perhaps the most widespread mechanism is the production of chemically active compounds (e.g. secondary metabolites) which can be toxic for larvae and inhibit their settlement (Datta et al. 2015). A second explanation could be the presence of microbial films on the hosts with the relationships between host and biofilm varying from harmful to beneficial (Dobretsov and Rittschof 2020). Experimental studies have shown that bryozoan larvae had little success in the colonization of surfaces with bacterial biofilms probably due to bacterial extracellular materials (Maki et al. 1989). Low biodiversity on large-sized hosts with smooth surfaces may be also due to the fact that the first colonizers (e.g. encrusting bryozoans) are strong space competitors (Beaulieu 2001) and/or induce the further settlement of conspecific larvae through the production of chemical compounds (Zimmer et al. 2016). Evidence on successional dynamics is also available from the fossil record (Barclay et al. 2013; Schneider 2013). For example, studies on Carboniferous brachiopods showed that much of the spatial and temporal variation in their epibiont communities was attributed to shifts in the magnitude and selective nature of larval recruitment (Lescinsky 1997).

Habitat cascade and types of host-epifauna associations

The findings of the present study provide evidence for first time that habitat cascades known up to now mainly for forests, salt marshes, seagrass meadows, and seaweed beds (Thomsen et al. 2010), are also present in CWCRs. Here, the role of the basal habitat former is played by the *L. pertusa* framework on which intermediate habitat formers exist (e.g. the bivalves, the tunicates, the polychaete tubes examined here) that in turn create living space for the other organisms (e.g. bryozoans, brachiopods, anthozoans). Faunal associations recorded in the present study resemble closely to the type of habitat cascade seen in forests and some shallow-water ecosystems where the size of the intermediate habitat former is smaller than that of the basal habitat former (Thomsen et al. 2010). For example, at MRC Actiniidae specimens had colonized eunicid tubes (Fig. 2a) or the bryozoan *Disporella hispida* had colonized the brachiopod *Novocrania anomala* (Fig. 2b). On the contrary the presence of the type recorded in soft-bottom estuaries where a relatively small invertebrate (e.g. polychaete, bivalve) provides basal habitat for larger intermediate seaweeds that, in turn, generate habitat for focal invertebrates and epiphytes (Thomsen et al. 2010) does not seem to be the case in CWCRs.

The absence of epifaunal communities living attached on a specific taxonomic group at MRC pinpoint to the dominance of facultative relationships where the host supplies habitat to its epifauna. In their review on corals' epifauna, Buhl-Mortensen and Mortensen (2004a) mentioned that out of the 980 species found till then living on cold-water corals, 112 could be characterized as symbionts of which 30 species were obligate to various cnidarian taxa. 53% of the obligate deep-water coral symbionts were parasites, 47% were commensals. The prevalence of facultative relationships is supported also from more recent studies on pennatulaceans in the northwest Atlantic (Baillon et al. 2014), gorgonians and sea pens in the Norwegian continental margin (Buhl-Mortensen and Mortensen 2004b), scleractinian corals in the Mediterranean Sea (Rueda et al. 2019) and North Pacific (Du Preez et al. 2020), deep-sea sponges (Kazanidis et al. 2016; Kersken et al. 2014; Hawkes et al. 2019) and fish (Milligan et al. 2016; D'Onghia 2019).

The situation described above seems to be in contrast with the current perception about tropical reefs where large number of obligate symbionts has been recorded (Fautin 1986; Stella et al. 2011; Gilpin and Chadwick 2017). The mechanisms behind this sharp difference are not clear. In their review, Buhl-Mortensen and Mortensen (2004a) provided plausible explanations about this phenomenon elaborating on the time needed for the development of

obligate relationships, the frequency of disturbance, variability of nutrient supply and mode of larval development. On geological time scales, North Atlantic CWCRs have been subject to extensive changes leading to regional extinctions during glaciation (Dorschel et al. 2005; Frank et al. 2011). The MRC was glaciated and initiated 7–8 kya (Douarin et al. 2013). In contrast, the Mediterranean basin likely acted as a glacial refuge for cold-water corals (Henry et al. 2014). Based on this it could be expected that obligate relationships would be more prevalent in the Mediterranean than the North Atlantic.

Recent studies have shown, however, that facultative relationships are also the major pattern in Mediterranean CWCRs with a few commensal associations (Rueda et al. 2019). Variability in nutrient supply may also induce the lack of obligate relationships in CWCRs as cold-water corals and their epifauna rely on organic matter produced in upper ocean layers (Duineveled et al. 2007; Kazanidis and Witte 2016). Variability in nutrient supply may be even more pronounced in the bathyal zone than the continental shelf hindering obligate relationships in there; this suggestion is based on findings which have shown organic matter supplied to CWCRs in the continental shelf is higher in quantity and of greater quality compared to the organic matter supplied to CWCRs in the bathyal zone (Kazanidis and Witte 2016 and references therein). Another explanation offered by Buhl-Mortensen and Mortensen (2004a) was related to the direct development or very short planktonic larval development of several species associated with *L. pertusa*. Living in various habitats may be an adaptation for species with short larval periods to ensure successful dispersal in the long run. Scientific knowledge, however, about larval biology of organisms associated with cold-water corals is very limited (Larsson et al. 2014) and further work is needed. Here, it could also be mentioned that the limited presence of obligate relationships in CWCRs may be also due to strong currents found there (Duineveld et al. 2007; Mohn et al. 2014), which may hinder the establishment of stable associations over evolutionary timescales.

Resilience of marine biodiversity hotspots in the future ocean?

The bathyal zone where most of the CWCRs are found will suffer the most significant changes in pH in all oceans by 2100 (Puerta et al. 2020 and references therein). The habitat suitability for calcifying organisms in the deep sea will get severely decreased; > 80% reduction is predicted for scleractinians and octocorals (Morato et al. 2020). Research on the impacts of acidification on calcified organisms pinpoint to more fragile skeletons with greater porosity (Byrne and Fitzer 2019; Hennige et al. 2020) and

altered anchoring ability of bivalves (O'Donnell et al. 2013). Furthermore, ocean warming has been shown to destabilize the microbial symbionts in corals, sponges, and bivalves increasing their susceptibility to parasites (Baker et al. 2018). This deterioration of health status can have cascading effects on the geographic distribution of organisms (Gormley et al. 2013) and habitat provision (Bell et al. 2018). These findings are alarming considering that bivalves and serpulid polychaetes (i.e. major macrofaunal habitat suppliers as shown here) are found in several CWCRs in continental margins in the North Atlantic (Jensen and Frederiksen 1992; Duineveld et al. 2007; Henry and Roberts 2007; Cordes et al. 2008; Kenchington et al. 2017) and the Mediterranean (Rueda et al. 2019), while *Eunice norvegica* is a ubiquitous CWCR component from tropical to boreal latitudes (OBIS 2020—obis.org).

The present study has shown that macrofaunal species enhance CWCR biodiversity through habitat supply. Most of the species, however, that enhance CWCR biodiversity are calcified themselves or live closely with calcified species (e.g. the cold-water coral *L. pertusa*), and thus, it is possible that their health status will be negatively affected by the impacts of climate change (e.g. ocean acidification). These findings suggest that the impacts of climate change on the structure, functioning and ultimately on the health status of CWCRs can potentially be more severe than previously thought.

Declarations

Conflict of interest The authors declare no conflict of interest.

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