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High Diversity and Abundance of Foraminifera Associated with Mediterranean Benthic Red Algae Mats

Felix Ivo Rossbach *, Benedikt Merk and Christian Wild

Marine Ecology Department, Faculty of Biology and Chemistry, University of Bremen, 28359 Bremen, Germany; bmerk@uni-bremen.de (B.M.); christian.wild@uni-bremen.de (C.W.)
* Correspondence: felix.rossbach@uni-bremen.de

Abstract: The Mediterranean Sea comprises habitats such as *Posidonia oceanica* seagrass meadows that exhibit high associated biodiversity of sessile organisms. Recent pilot research indicates that benthic mats formed by the scarcely investigated fleshy red alga *Phyllophora crispa* also host a high diversity of benthic fauna. Among the key taxa found in these mats in the recent pilot studies are benthic foraminifera that live as epiphytes on the red algae thalli. Knowledge about their abundance and species richness associated with this habitat in relation to reference habitats is missing. We thus carried out a comparative assessment focusing on foraminifera within samples from *P. crispa* mats and neighboring *P. oceanica* meadows on five different sampling sites around Giglio Island in the Tuscan Archipelago (Tyrrhenian Sea, Italy). A total of 104 different foraminiferal taxa were identified, of which a total of 85 taxa were found in *P. crispa* samples (46 exclusively in this habitat). This biodiversity was higher compared to other studies on phytal habitats in the Mediterranean Sea. The number of foraminiferal taxa associated with *P. crispa* was significantly higher (average 27.5 ± 8.1 taxa) compared to *P. oceanica* (leaves average 7.0 ± 3.6, shoots average 7.9 ± 3.4 taxa). The abundance of foraminifera (12,000 individuals m^{-2} surface area of *P. crispa* mat) was also higher than in the neighboring *P. oceanica* meadows (7792 individuals m^{-2} leaf and 8171 individuals m^{-2} shoot surface area). The most frequently found taxa across habitats were *Miniacina miniacea*, *Lobatula lobatula*, and *Sejunctella* sp. (24%, 20%, and 6% of the total population, respectively). Our results imply that *P. crispa* mats host an exceptional diversity of associated foraminifera that is even higher than those associated with seagrass meadows. Red algae mats built by *P. crispa* may thus be considered as potential refuge habitats and biodiversity reservoirs in management and conservation.

Keywords: *Phyllophora crispa*; phytal habitat; hard-bottom communities; ecosystem engineer; Mediterranean Sea; epibionts

1. Introduction

The Mediterranean Sea harbors almost 17,000 described eukaryotic species [1], a high amount of biodiversity that is accompanied by a high rate of endemism (estimated 20%) resulting from its somewhat enclosed geographical position [2]. Together with this high rate of endemism, this high biodiversity marks the region as a "biodiversity hotspot" [1,3,4]. On a smaller scale, the structural complexity of many Mediterranean habitats (e.g., *Posidonia oceanica* seagrass meadows) facilitates their role as biodiversity hotspots by providing spawning grounds, nurseries, and permanent settling space for a variety of sessile and mobile species across habitat borders [5–9]. The ecological niches required for this high biodiversity are often created by spatial or temporal gradients (e.g., light and temperature, as recently described for *P. crispa* mats [10]) formed by an engineering species [11]. Engineering species may alter their environment by their growth, while others actively change local conditions to favor inhabiting species. The resulting modification of the habitat may result in shifts of ecological zonation (e.g., algae accumulating debris as a food source for detritivores) by mitigating stressors for depending species [12]. Often, the

inhabitant also mitigates stress for the engineer, e.g., by fending off predators or cleaning out competitors [13,14].

Well-known habitats of high diversity in the Mediterranean Sea are *Posidonia oceanica* (L.) Delile, 1813 meadows, and coralligenous habitats. The seagrass species *P. oceanica* is a refuge for exceptional biodiversity and holds commercial value, e.g., by providing nursery grounds for important fish species [15]. The structural complexity of the meadow facilitates diverse communities of sessile invertebrates by providing secondary settling grounds and enhancing the settlement of planktonic life stages [5,16]. The calciferous bioconstructions of coralligenous habitats are mainly built by encrusting red algae and secondarily by calcifying invertebrate species, building a structurally complex matrix, and providing biogenic substrate for a wide range of associated biota [7]. Both are thus habitat-forming species and can be considered ecosystem engineers.

Recently, the mats of the red macroalgae *Phyllophora crispa* (Hudson) P.S.Dixon, 1964 have gained some attention as engineering species and potential hotspots of sessile epifauna biodiversity in the Mediterranean Sea [17–22]. In the Black Sea, these habitats facilitate prosperous communities and have led to establishing a marine reserve in the Bay of Odesa [23]. In the Mediterranean Sea, assemblages of different macroalgae have been shown to host diverse epiphytic foraminiferal communities [24,25].

In the Mediterranean Sea, dense mats of *P. crispa* have been reported to form hardbottom communities in the Tyrrhenian Sea, around the islands Giglio [19,20] and Sardina [17,18]. However, only a few studies describe the associated biodiversity in these mats, even though the composition of associated biodiversity differs between classical hotspots (i.e., *P. oceanica* meadows) and sciaphilic (shade-loving) hardbottom communities [26,27].

Foraminifera are unicelled protists with a high taxonomic diversity and cosmopolitan distribution across all marine ecosystems, brackish, and rarely freshwater habitats [28,29]. Foraminifera inhabit pelagic and benthic environments; the latter may be colonized by recent offspring or settlement of pelagic propagules [30]. In particular, vegetated bottoms form suitable habitats for epiphytic foraminifera, and primarily seagrass meadows have been studied for their foraminiferal assemblages [31–37]. Some studies have also shown the importance of macro-algae as particular habitat for epiphytic foraminifera [38,39]. Many taxa of foraminifera host different symbionts, such as red-/green algae, diatoms, or dinoflagellates [40]. Long-lived, symbiont-bearing benthic species larger than 3 mm^3 are summarized as larger benthic Foraminifera (LBF) [41,42]. In particular, LBF species are important calcifiers [43] and have been recognized as essential indicators for water quality and healthiness of marine ecosystems [44–46]. Key features for this function are their relatively short lifespan and reproductive cycle compared to benthic epifauna, their ubiquity, and sensitivity to biotic and abiotic perturbations, leading to rapid community composition changes after environmental disturbances [47–49]. The distribution patterns and role of foraminiferal communities in Mediterranean *P. crispa* mats are relatively unstudied to date. With this work, we aim to answer the following research questions:

1. What is the abundance and diversity of epiphytic foraminifera in *P. crispa* mats in relation to *P. oceanica* meadows?
2. What is the composition of epiphytic foraminifera morphotypes in *P. crispa mats*?

To answer these questions, we conducted a comparative field study of *P. crispa* mats and *P. oceanica* meadows along the coast of Giglio Island in the Tuscan Archipelago (northwestern Mediterranean Sea). We assessed the quantity of foraminifera occurrence and species composition at five different sampling sites.

2. Materials and Methods

2.1. Sampling Activities

The study area is located along the northeastern and northwestern coasts of Giglio Island, in the Tuscan Archipelago National Park (42°21′19.4″ N 10°54′06.1″ E, Tyrrhenian Sea) (Figure 1). Granite slopes characterize the benthic infralittoral around the island, alternating with sand bottoms, where *P. oceanica* meadows, *P. crispa* mats, and coralligenous

habitats colonize the sea bed. Five sampling sites were chosen where *P. crispa* mats and *P. oceanica* meadows occur at similar target water depths. SCUBA divers conducted sampling at a water depth of 30 m, where previous observations confirmed dense occurrences of *P. crispa*. Samples of *P. oceanica* were taken randomly between 20 and 30 m depth, a few meters above the lower boundary, to avoid bias by sampling at the ecological limit of the plant. The sampling sites included three locations with *P. crispa* mats (Site PC1, 2, and 3; Figure 1), two with only *P. oceanica* meadows (Site PO and 6), and another site (Site mix) with both habitats being present. Sampling activities took place on a timely randomized schedule between May and July 2019. Mats of dense *P. crispa* stands with a minimum thickness of five cm were chosen randomly. A handful of whole algae was carefully removed with the holdfast from the rock surface using a spatula. Each site was sampled four times, resulting in 16 *P. crispa* mat samples. All sampling was done with a spatula or scissors to avoid dropping of the specimen due to shaking movements (e.g., by just ripping off material) before immediately transferring the material into a sampling jar as described in previous studies [24,33]. We decided for this method to focus on the living, epiphytic foraminifera and avoid loss of fragile taxa by drying or sieving methods.
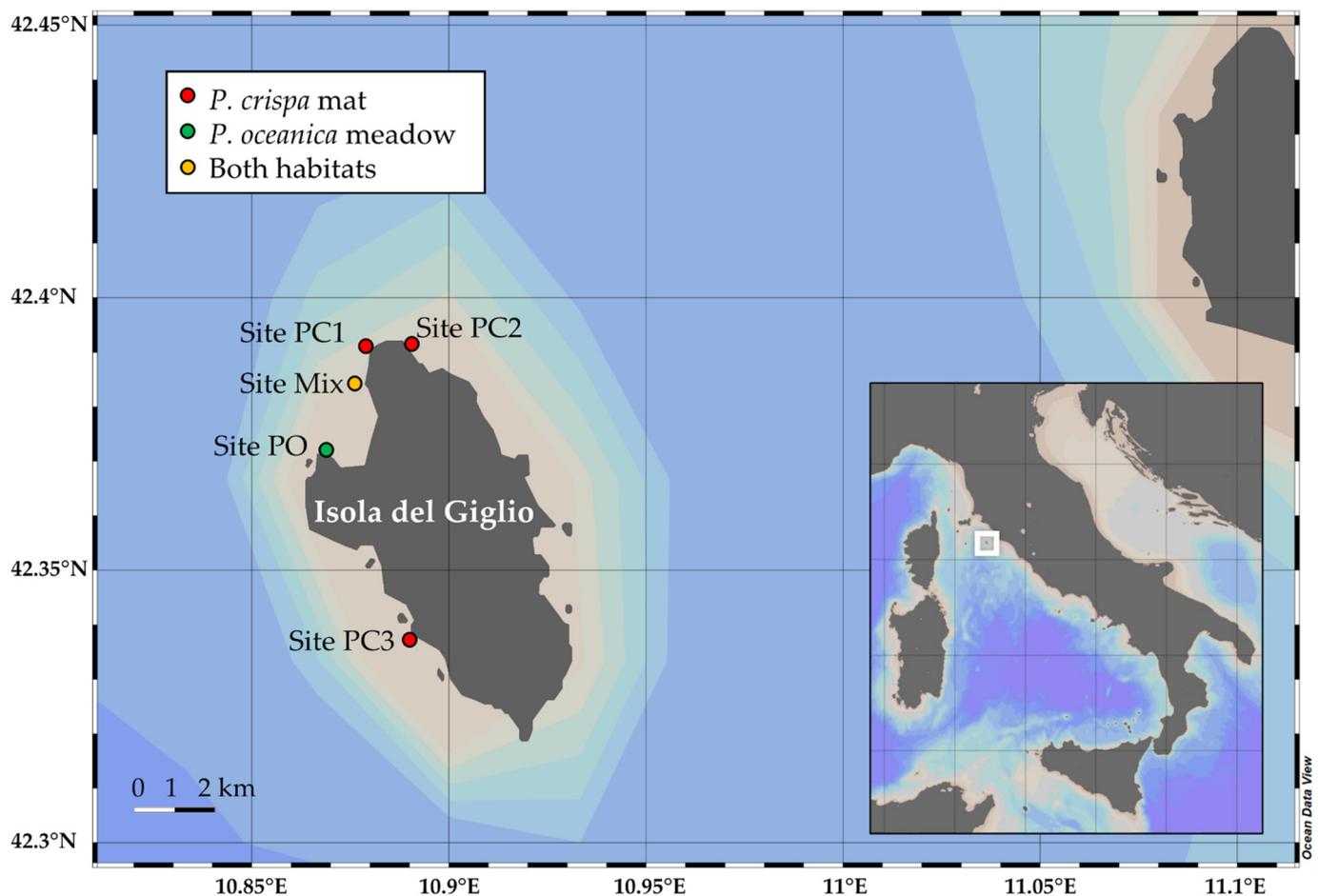

Figure 1. Location of the study area in the Tyrrhenian Sea with sampling sites around Giglio Island marked in red for *Phyllophora crispa* mats, green for *Posidonia oceanica* meadows, and yellow where both habitats were sampled, made with OceanDataView [50].

In total, 20 *P. oceanica* shoots and 18 leaves (site PO: 10 shoots and 9 leaves; Site Mix: 10 shoots and 9 leaves) were sampled at the respective sites. Shoots were cut at the lowest point to the rhizome node, and leaves were cut off at the sheath. All samples were transferred into one-liter PVC containers, allowing enough water inside to keep a constant temperature and sufficient oxygen supply for the biota (approximately 1/3 sample material

and 2/3 seawater). After each dive, samples were directly transferred into husbandry basins at the Institute for Marine Biology (IfMB, Campese, Italy) and kept at constant temperature (18 °C, equivalent to in situ temperature), with bubbling stones for oxygen supply. Processing of samples took place within three days after sampling. Shoots and leaves were treated separately because they are widely recognized as two sub-habitats with different ecological traits [51,52]. The sample completeness was confirmed with the rarefaction and interpolation method described by Chao et al. (Appendix A Figure A1) [53]. We also opted for this sampling approach to examine a similar surface area for each habitat and site (see results section).

In addition to the biodiversity assessments, we measured daily cycles of environmental parameters (i.e., oxygen and pH) on site PC2, where *P. oceanica* meadow (*n* = 12), *P. crispa* mat (*n* = 22), and bare rock bottom (*n* = 12) were found in close vicinity (<10 m distance). Oxygen concentration (mg/L) and pH were measured at the bottom of each habitat using Eureka Manta loggers (GEO Scientific Ltd.), set to one-minute measuring intervals. The obtained data were plotted as average values per hour $\pm$ SD.

2.2. Species Identification

All samples were examined as a whole in water bowls containing seawater under stereo magnifiers (maximum 45× magnification) or microscope (maximum 400× magnification) as needed. The leaves of *P. oceanica* were cut into pieces of 8 cm for easier handling under the stereomicroscope and to avoid double-counting. The shoots were analyzed as a whole. Algae thalli of *P. crispa* were carefully separated into single phylloids for the analysis. This study focused on living epiphytic foraminifera >300 μm to avoid juveniles and abundance bias due to short-lived, opportunistic species.

All foraminiferal specimens found in the samples were counted and identified to the lowest possible taxonomic level using relevant identification literature [32,36,54,55] and on-line resources (marinespecies.org, mindat.org, accessed on 16 June 2021) as a cross-reference. Species were then further categorized into morphotypes regarding their ecological features. We followed the categories proposed by Mateu-Vicens et al. in adaptation for the Mediterranean Sea, based on the original concept of Langer [35,37]. In this adaptation, five morphotypes were used: A* and SB for long-lived (lifespan of 1 year or more) and sensitive species, where A* are mostly flat and encrusting forms and SB species bear symbionts (e.g., *Miniacina* spp. and *Peneroplis* spp., respectively). Opportunistic species with an upright aperture were categorized as D* (e.g., *Textularia* spp). Small, heterotrophic species were categorized as B or C, where B comprises species with wide apertures and pseudopodal networks, and B encompasses species with multiple apertural openings, attached to the substrate via pseudopods.

Numbers of foraminifera were then related to the surface area of the substrate (*P. crispa*, respectively *P. oceanica* material as subsequently described). For *P. crispa* samples, all algae material was placed on top of laminated millimeter paper in a dissection dish with seawater and flattened with an acrylic glass pane. Using a tripod, pictures were taken from the top at a constant 90° angle. The surface area of the algae material was then calculated with ImageJ (version 1.52o) and multiplied by two to account for both sides of the phylloids. To calculate the *P. oceanica* shoot surface, a cylindrical shape was assumed and calculated after measuring the length and diameter of each sample. The straight leaves of *P. oceanica* were measured for length and width to calculate the surface area. This area was then doubled to account for both sides of each leaf.

2.3. Diversity Descriptors

The diversity of the epiphytic foraminiferal community was assessed with five descriptors: The total number of taxa per site and habitat, the Shannon diversity index (Appendix A Formula (A1)) [56], the Pielou index for evenness (Appendix A Formula (A2)) [57], plus the FORAM index and the lifespan index [35,37]. Additionally, we assessed the total density of individual foraminifera per m^2 of seafloor. We calculated the FORAM index [46] and

the lifespan index, as previously described for the Mediterranean Sea [35], based on the aforementioned morphotype categories. The FORAM index considers the proportions of small, heterotrophic taxa, larger, symbiont-bearing taxa, and stress-tolerant taxa. The index increases with higher abundances of symbiont-bearing taxa, and decreases with higher abundances of stress-tolerant taxa. The lifespan index emphasizes differences in the foraminiferal community regarding opportunistic vs. persistent taxa dominance—with lower values for high abundances of opportunistic taxa (D*), and higher values for longer living forms (A* and SB). A detailed figure of the morphotype classification and explanation of the calculations can be found in the original publication [35].

All results were plotted as boxplots and reported as means per site with the respective standard error.

To further analyze the functional composition of the community, all found taxa were pooled according to their test material, and the relative composition of each site was plotted.

2.4. Statistical Analysis

Differences in the structure of foraminiferal communities among sites and habitats were tested using multivariate permutational ANOVA (PERMANOVA) [58]. Differences in the diversity descriptors among sites and habitats at the site mix were tested using pairwise Wilcoxon–Mann–Whitney tests. Data were not transformed in order to minimize potential bias. The Foraminiferal assemblages were hierarchically clustered with Spearman ranked correlation (average linkage) using the software 'heatmapper' [59] to reveal differences in the taxonomic (Families) and ecological (test material) composition among sites and visually highlight variances in the assemblages among habitats. Analyses and boxplots were made with R (version 4.0.2) [60].

3. Results

3.1. Daily Cycles of Water Parameters

Our measurements showed higher pH values inside the *P. crispa* mat (average 8.36 ± 0.01) than inside the *P. oceanica* meadow (average 8.21 ± 0.01) and on a hardbottom reference habitat (average 8.32 ± 0.02; Figure 2A). Inside the *P. crispa* mat, the values fluctuated more (0.11 units) compared to *P. oceanica* meadow (0.05 units) and hardbottom (0.08 units).

The measured oxygen concentrations showed similar patterns for the *P. crispa* mat and hardbottom habitat (average 8.17 ± 0.10 mg L^{-1}, and average 8.20 ± 0.07 mg L^{-1}, respectively), compared to the *P. oceanica* meadow (average 7.90 ± 0.14 mg L^{-1}; Figure 2B). Here, the variation was highest inside the *P. oceanica* meadow (0.47 mg L^{-1}) compared to the *P. crispa* mat (0.33 mg L^{-1}) and the hardbottom habitat (0.24 mg L^{-1}).

3.2. Diversity of the Foraminiferal Community

We examined a total surface of 0.215 m^2 of *P. crispa* material (average 0.054 m^2 per site). The examined surface of *P. oceanica* was 0.086 m^2 of shoots (average 0.043 m^2 per site) and 0.054 m^2 of leaves (average 0.053 m^2 per site). A total of 3.639 foraminiferal specimens were counted, and 104 taxa were examined, out of which 81 were found on *P. crispa* phylloids (46 exclusively on *P. crispa*). While the abundance of single taxa showed no significant differences among *P. crispa* sites, the communities differed significantly among *P. oceanica* sites and sub-habitats (shoots and leaves, Table 1). We thus consolidated the data of *P. crispa* mats for further assessment of differences in the diversity among the different habitats (Figure 3).
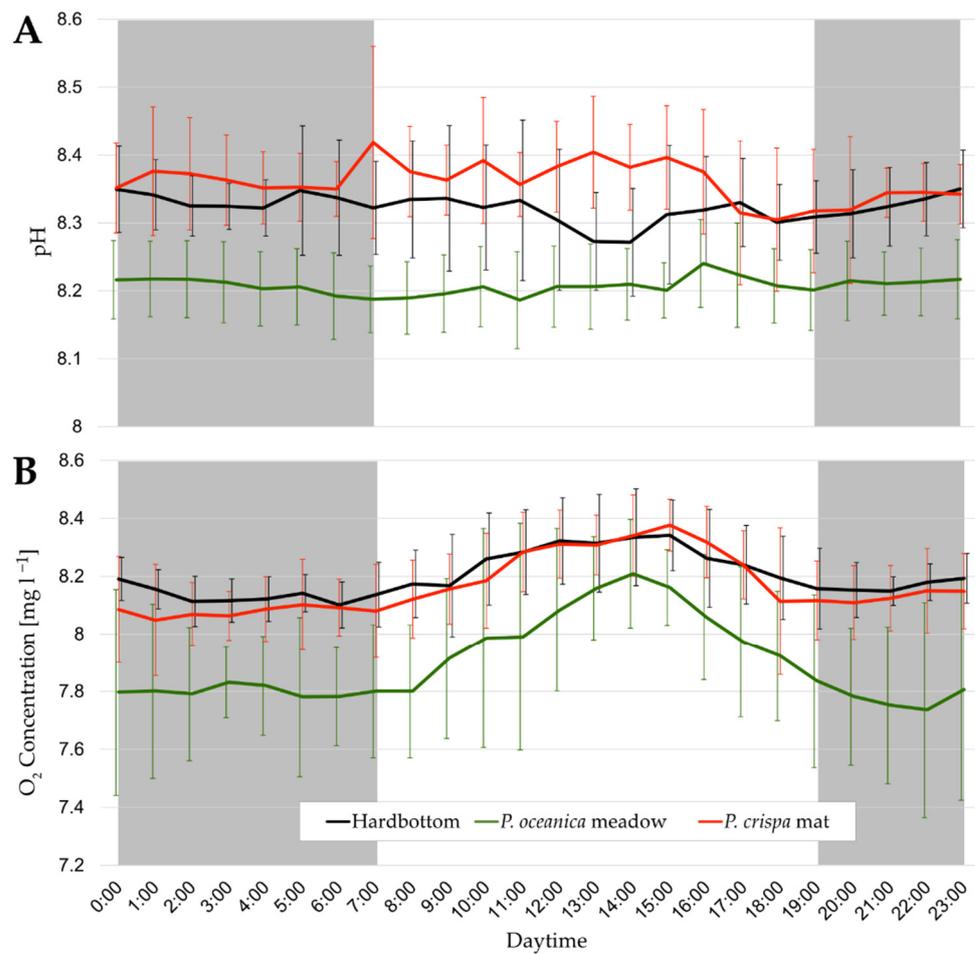
Figure 2. Daily cycles of water parameters measured on Site PC2 in *Phyllophora crispa* mat (red), *Posidonia oceanica* meadow (green), and bare rock bottom as reference (black). (**A**) pH and (**B**) oxygen concentration (mg L^{-1}), measured at the bottom of the respective habitat. Error bars indicate standard deviation, grey areas indicate dark phases.

Table 1. Results of permutational ANOVA tests for differences among sites and habitats. *Posidonia oceanica* sub-habitats resemble leaves and shoots. Significant results ($p > 0.05$) are indicated in bold.

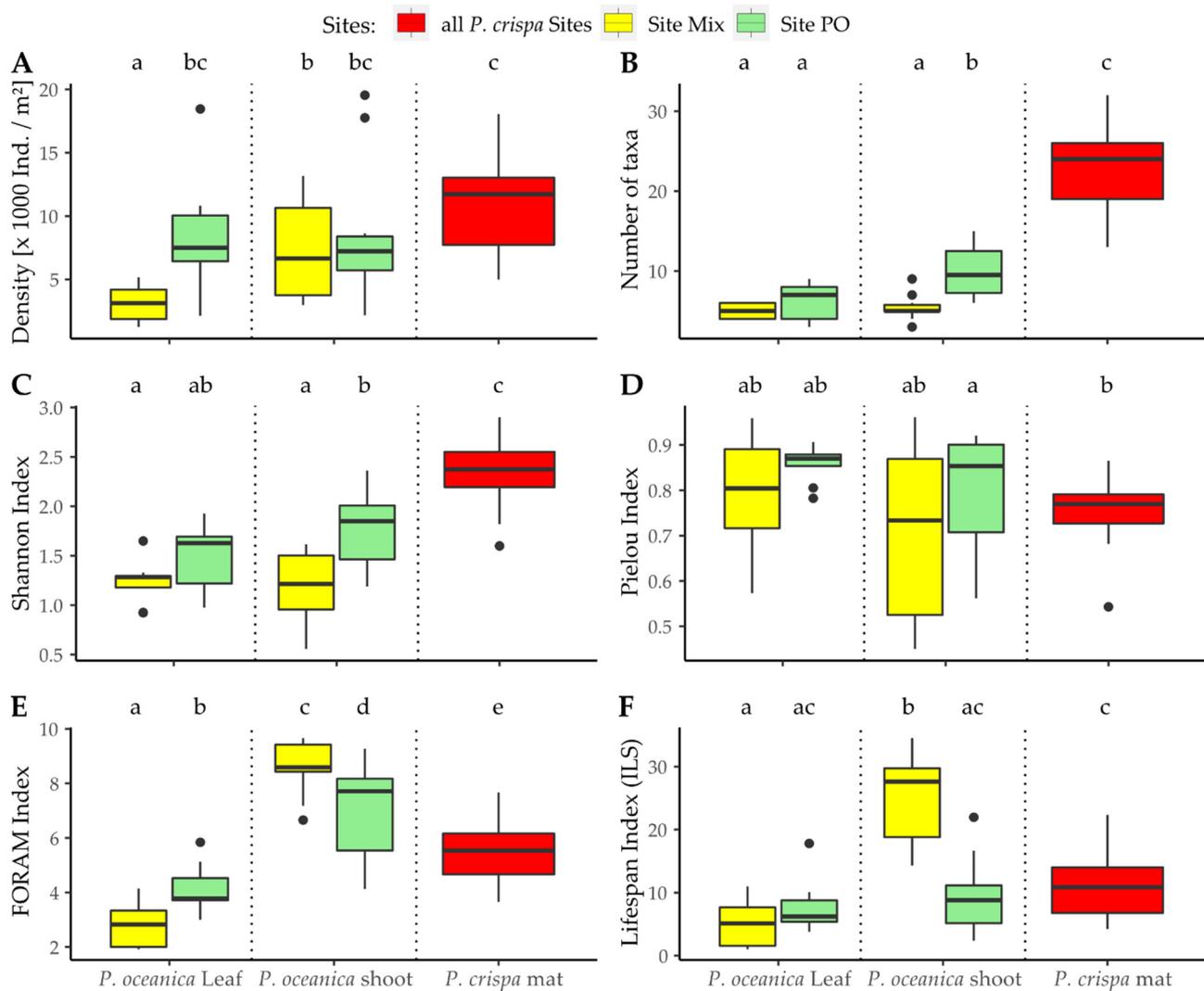| Foraminiferal Assemblages of *P. crispa* Mats					
Source	**Df**	**SS**	**R2**	**F**	***p***
site	3	0.3898	0.2161	1.1028	0.313
residual	12	1.4138	0.7839		
total	15	1.8036	1.0000		
Foraminiferal Assemblages of *P. oceanica* Meadows					
Source	**Df**	**SS**	**R2**	**F**	***p***
sub-habitat	1	4.5640	0.3886	25.7381	**0.001**
site	1	0.6696	0.0570	3.7759	**0.006**
sub-habitat:site	1	0.4833	0.0411	2.7252	**0.024**
residual	34	6.0291	0.5133		
total	37	11.7459	1.0000		

Figure 3. Abundance and diversity of foraminifera in *P. crispa* mats and *P. oceanica* meadows. (**A**) mean densities of foraminifera per m^2 substrate per site, (**B**) total numbers of identified taxa, (**C**) Shannon diversity indices, (**D**) Pielou evenness indices, (**E**) FORAM indices, and (**F**) lifespan indices reported for the investigated *Phyllophora crispa* sites in comparison to *Posidonia oceanica* shoots and leaves. Compact letter displays show significance levels resulting from Wilcoxon–Mann–Whitney pairwise comparison, boxes with different letters differed significantly ($p < 0.05$). Black dots resemble outliers.

The most frequently found species across all samples was *Miniacina miniacea* (average 2081 ± 2848 individuals m^{-2} surface area), which was most abundant on the shoots (average 4117 ± 3602 individuals m^{-2} surface area; Table 2) and *P. crispa* mats (average 1877 ± 1366 individuals m^{-2} surface area), but not found on *P. oceanica* leaves. The most frequent species on both leaves (average 2128 ± 1783 individuals m^{-2} surface area) and *P. crispa* (average 3147 ± 1590 individuals m^{-2} surface area) was *Lobatula lobatula*. Both species develop calcareous perforate tests and resemble some of the larger species of Foriminiferans in this study. While *M. miniacea* and *L. lobatula* show the highest values across all *P. crispa* sites, site PC2 also showed a high amount of *Sejunctella* sp. (average 1100 ± 303 individuals m^{-2} surface area). Total LBF (*Peneroplis* spp., *Sorites* sp. and *Vertebralina* sp.; Table 2) counts and diversity were highest in *P. crispa* samples (3 species, average 183 ± 239 individuals m^{-2} surface area) compared to *P. oceanica* shoots (2 species, average 119 ± 143 individuals m^{-2} surface area) and *P. oceanica* leaves (1 species, average 37 ± 123 individuals m^{-2} surface area). One LBF species (*Peneroplis planatus*) was only found on *P. crispa*.

Table 2. The five most abundant species per habitat (top) and average abundance of LBF species (bottom). Numbers are average abundance per m^2 substrate (AVG) $\pm$ standard deviation (STDEV); the most abundant species per habitat are indicated in bold. [1] according to Mateu-Vicens et al. and Langer [35,37]. No LBF were among the most abundant species.

	Family	Species	Ecotype [1]	*P. crispa* Mats		*P. oceanica* Leaves		*P. oceanica* Shoots	
				AVG	STDEV	AVG	STDEV	AVG	STDEV
Most abundant	Cibicididae	*Lobatula lobatula*	B	**3147**	1590	**2127**	1783	129	218
	Homotrematidae	*Miniacina miniacea*	A*	**1877**	1366	0	0	**4117**	3602
	Hauerinidae	Unknown	A*	**1245**	855	716	1330	0	0
	Discorbinellidae	*Discorbinella bertheloti*	B	472	338	**931**	1076	249	362
	Spirillinidae	*Sejunctella* sp.	A*	465	505	15	62	**912**	899
	Planorbulinida	*Planorbulina mediterranensis*	A*	365	266	353	484	132	252
	Hauerinidae	*Miliolinella subrotunda*	D*	169	285	25	67	**360**	506
	Hauerinidae	*Quinqueloculina seminula*	D*	163	201	0	0	281	388
	Ammoniidae	*Ammonia beccari*	B	86	275	**723**	605	119	248
	Trochamminidae	*Lepidodeuterammina ochracea*	A*	71	161	28	82	357	580
LBF	Peneroplidae	*Peneroplis pertusus*	SB	**153**	239	0	0	**66**	143
	Peneroplidae	*Peneroplis planatus*	SB	17	37	0	0	0	0
	Soritidae	*Sorites orbiculus*	SB	13	41	**37**	123	0	0
	Fischerinidae	*Vertebralina striata*	SB	0	0	0	0	53	122

The density of foraminifera was lowest at *P. oceanica* leaves on site mix (average 3183 $\pm$ 671 individuals m^{-2} surface area), with a significant difference between the two leaf sites (site mix and site PO). The highest density was found on *P. crispa* site PC1 (average 12,647 $\pm$ 1017 individuals m^{-2} surface area). Comparing the density among habitats revealed significantly higher values for *P. crispa* compared to *P. oceanica* shoots and leaves on site Mix ($p = 0.0198$ and $p < 0.0001$, respectively; Figure 3A).

The number of taxa was lowest on the *P. oceanica* leaves at site mix (average 5.0 $\pm$ 0.3) and highest on *P. crispa* phylloids at site PC1 (average 28.0 $\pm$ 0.7). Significant differences were found among *P. oceanica* shoot sites and all habitats (Figure 3B). The number of taxa found on *P. crispa* was significantly higher compared to *P. oceanica* leaves and shoots on both *P. oceanica* sites (all values for $p < 0.0213$).

The lowest Shannon diversity index was found on *P. oceanica* shoots (average 1.2 $\pm$ 0.1) and highest on *P. crispa* phylloids (average 2.5 $\pm$ 0.2), both at site mix. Both *P. oceanica* sub-habitats differed significantly, with higher values for site PO (Figure 3C). Among all habitats, *P. crispa* showed significantly more diversity than *P. oceanica* leaves and shoots (all values for $p < 0.0039$).

The evenness was similar across all comparisons. The lowest average value was found on *P. oceanica* shoots at site mix (average 0.7 $\pm$ 0.06), and the highest on *P. oceanica* leaves at site PO (average 0.9 $\pm$ 0.01). The pairwise comparison between *P. crispa* and *P. oceanica* shoots on site PO showed the only significant effect ($p = 0.0002$; Figure 3D).

The FORAM index was highest for the *P. oceanica* shoots, with a significantly higher value for site mix (8.6 $\pm$ 1.0) and lowest for the leaves, with a significantly lower value for site mix (2.8 $\pm$ 0.8). The values for all *P. crispa* samples ranged between the two *P. oceanica* sub-habitats (Figure 3E).

The lifespan index (ILS) was highest in the *P. oceanica* shoot samples from site mix (25.4 $\pm$ 7.0) and lowest in the leaf samples from the same site (7.9 $\pm$ 4.0). The *P. crispa* community showed similar values compared to *P. oceanica* site PO, while it ranged between both sub-habitats on site mix (Figure 3F).

The relative abundances of foraminiferal taxa sorted by test material show differences among the two *P. oceanica* sites in the higher abundance of the porcellaneous Hauerinidae (mainly *Milionella* spp. and *Quinqueloculina* spp.) at site PO. In contrast, the composition across *P. crispa* sites is more homogenous (Figure 4). The phylloids of *P. crispa* host more porcelaneous foraminifera than both *P. oceanica* sub-habitats on the same site (site mix),

mainly driven by an unidentified Hauerinidae species (Table 2). On the other hand, while agglutinated species were scarce in the whole study, they were relatively more abundant on *P. oceanica* sub-habitats (mainly *Trochammina inflata* and *Lepidodeuterammina ochracea*, Figure 4). The leaves of *P. oceanica* on the site mix did not host any porcelaneous foraminifera. The two *P. oceanica* sub-habitats mainly differ in the higher abundance of *Sejunctella* sp. (Spirillinidae; average 913 ± 196 individuals m^{-2} surface area; Figure 4).
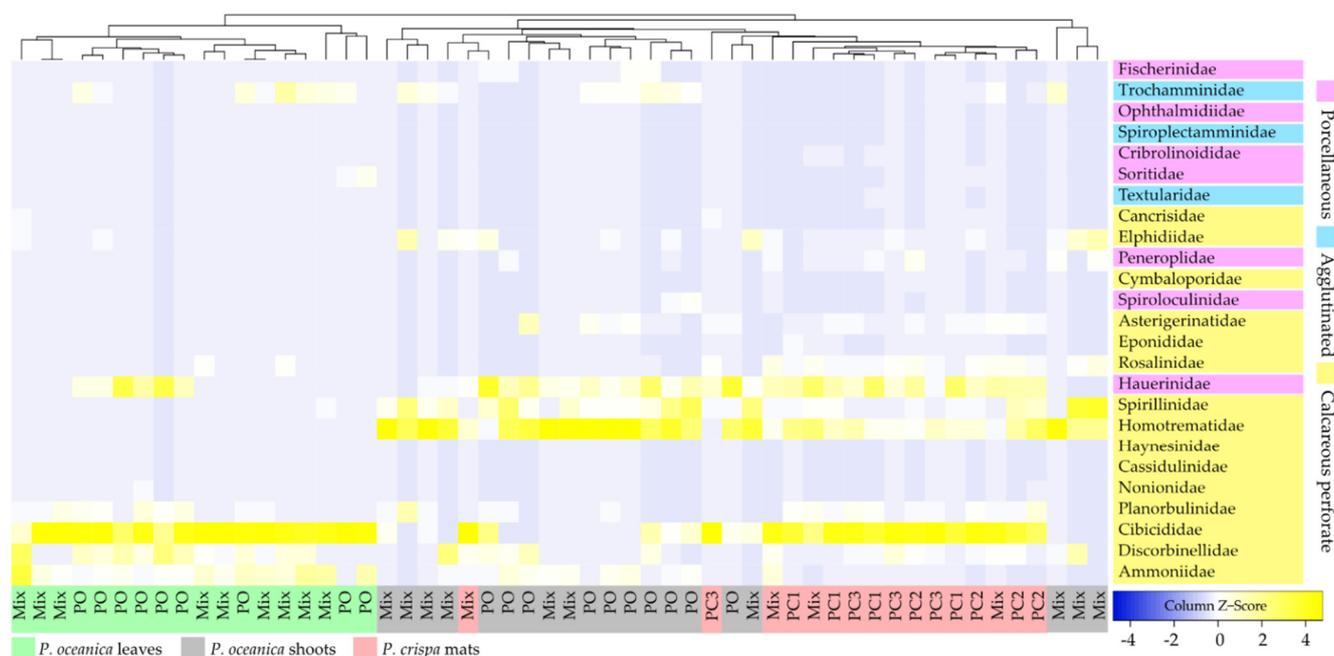
Figure 4. Hierarchical clustering (average linkage, Spearman ranked correlation) of family abundances among sites (individuals per m^2) found in *Phyllophora crispa* (red) and *Posidonia oceanica* habitat sites (green = leaf; grey = shoot). Test types are indicated as purple (porcellaneaus), blue (agglutinated) and yellow (calcareous perforate). The Z-score indicates the distance to the mean, which is indicated as "0".

Differences among sites for *P. crispa* were reflected in the lower abundances of Hauerinidae (unknown species) and Homotrematidae (i.e., *M. miniacea*) on site PC3 compared to all other sites (Figure 4). Among *P. oceanica* sites, differences were driven by the high abundance of an unknown Hauerinidae species on site PO (Figure 4).

4. Discussion

4.1. Environmental Parameters inside P. crispa Mats

The pH and oxygen concentrations inside the *P. crispa* mats differed from the environment inside *P. oceanica* meadows, mainly regarding the magnitude of their daily cycles (Figure 2). While the oxygen concentrations inside the *P. crispa* mat were similar to the bare rock reference habitat, the pH values showed more substantial fluctuations than the *P. oceanica* meadow. The lower oxygen concentrations inside the *P. oceanica* meadow were likely due to the measurements close to the rhizome layer, where more respiration occurred [61]. This effect also explains the lower pH values measured inside the *P. oceanica* meadow. A reason could be the spatial proximity of the photosynthetically active thalli of the red algae with the epiphytic respiring community, in contrast to the spatially more detached situation in the *P. oceanica* meadow. The resulting small-scale gradients of environmental parameters inside *P. crispa* mats were also recently described for water movement, temperature, and light conditions [10].

4.2. Abundance and Diversity of Epiphytic Foraminifera in P. crispa Mats

Overall, the foraminiferal assemblages represent a typical composition for carbonated shelf environments [61]. Our results showed that the abundance of foraminifera was higher in *P. crispa* mats than in both *P. oceanica* sub-habitats. A similar, but more pronounced trend was confirmed for the species richness (Figure 3). This observation is strengthened by the fact that previous studies found lower values for foraminiferal diversity on seagrass [62]. Additionally, the analysis of species incidences showed that our sampling efforts might even underestimate the total diversity of foraminiferal communities in *P. crispa* mats (see Appendix A Figure A2).

Interestingly, the leaf sites differed in density, while the shoot sites differed in species richness. This observation supports that *P. oceanica* sub-habitats provide different ecological traits (e.g., water movement, particle supply, light availability), especially for foraminiferal species. The high individual count on site PO leaves could have resulted from a recent reproduction event in that area, which usually occurs during summer [62]. The relative abundance of foraminiferal orders shows that the lack of porcelaneous taxa and differences in the composition of calcareous perforate taxa were the main drivers for the observed differences. Additionally, the relatively short-lived *P. oceanica* leaves favor small species (ecotype B, mainly *L. lobatula*) with high turnover rates compared to the long-lived shoots and *P. crispa* mats, where LFB (e.g., *Peneroplis* spp.) occur in persistent habitats [30]. This observation is confirmed by the higher lifespan index values (ILS) for *P. oceanica* shoots and *P. crispa* mats. Shannon indices support the at least comparably high foraminiferal diversity in *P. crispa* mats and higher consistency among sites in this habitat. While no statistical differences in the evenness were confirmed, the data scattering in *P. oceanica* samples shows high dispersion across replicates (Figure 3), pointing towards small-scale variations in the resilience of foraminiferal communities across *P. oceanica* meadows. Although there is no significant effect, we observe a trend to lower values on the southernmost site (site PC3, Figure 3) while, in contrast to *P. oceanica*, the sites within the north-western bay (bay of Campese), overall values are more similar. Our findings are consistent with previous studies on epiphytic foraminifera, where 55 living taxa were found on *Cystoseira* sp. (Phaeophyta) mats [25] and 62 taxa in shallow algae assemblages [24]. Adding to the results of Langer (1988) [38], who found lower diversities of foraminifera in green algae (*Udotea peticolata*) and brown algae (*Ectocarpus* sp.) compared to seagrass (*P. oceanica*), we confirm here that red algae mats of *P. crispa* have the potential to host even higher diversities than *P. oceanica*.

4.3. Composition of Epiphytic Foraminifera Morphotypes in P. crispa Mats

The test type comparison shows a similar trend to a more homogenous community across sites in *P. crispa* mats, while foraminiferal groups of different test types are more abundant on few *P. oceanica* samples (e.g., Trochaminidae, Hauerinidae, Discorbinellidae; Figure 4). The higher abundance of porcelaneous LBF taxa reflects the long-term stability of *P. crispa* mats (similar to *P. oceanica* shoots), accompanied with higher light regimes (similar to *P. oceanica* leaves) as species of porcelaneous LBF are often multichambered species, bearing photosymbionts [61,63]. Because of their calcified test, porcelaneous species are more sensitive to ocean acidification processes [64]. This is further supported by the low number of agglutinated, typically opportunistic species, favoring more unstable, physically controlled environments [65]. High abundances of agglutinated species also indicate carbonate undersaturation [66]. The low values (average 38 ± 62 individuals m^{-2} surface area) in this study suggest a relatively high nutrient availability and water mixture inside the *P. crispa* habitat. These traits are generally provided by *P. crispa* mats, where we found the highest numbers of LBF. However, these high numbers were mainly driven by *Peneroplis pertusus*, which was also abundant on *P. oceanica* shoots. The lack of porcelaneous foraminifera on both *P. oceanica* sub-habitats on site mix compared to site PO (Appendix A Table A1) indicates local factors (i.e., disturbances or pollution). Another explanation could be a lack of larval supply; however, the high amount of porcelaneous species in *P. crispa* mats on the same site (Appendix A Table A2) implicates local factors inside

the *P. oceanica* meadow as the main drivers. This observation underlines the function of *P. crispa* mats as refuge habitat and potential mitigating mechanisms for environmental disturbances accompanied with the mats. A recent study suggests that diel pH fluctuations in *P. oceanica* meadows foster the resistance of epiphytic forams (*Rosalina* sp.) towards ocean acidification [67]. Our study found higher diel pH fluctuations within *P. crispa* mats (0.11 units) than in *P. oceanica* meadows (0.05 units, Figure 2). This observation conforms with a higher abundance and diversity of *Rosalina* sp. in *P. crispa* habitats (6 species, average 27 ± 53 individuals m^{-2} surface area) compared to *P. oceanica* habitats (1 species, average 3 ± 22 individuals m^{-2} surface area leaves and average 0 ± 4 individuals m^{-2} surface area shoots). This observation supports the hypothesis that *P. crispa* mats could also foster the resistance of epiphytic forams against acidification scenarios as observed in *P. oceanica* [67]. These higher pH regimes could result from an accumulation of organic particles and thus higher net respiration in combination with elevated water holding capacities of *P. crispa* mats [10] and lower rates of photosynthesis, as shown by lower oxygen concentrations inside the algae mats (Figure 2B).

While *P. crispa* was dominated by a combination of type B (*L. lobatula*) and type A* (*M. miniacea*, and unknown Hauerinidae), the leaves and shoots of *P. oceanica* were dominated by one very abundant type (B—*L. lobatula* and A*—*M. miniacea*, respectively, Table 2). This difference indicates that *P. crispa* mats offer various traits for long-lived, encrusting species (A*) and short-lived and temporary motile species (B), but on the other hand, offer suitable conditions for species from both *P. oceanica* sub-habitats. The high abundance and diversity of porcellaneous LBF species confirm the function of *P. crispa* mats as persistent habitats.

Notably, LBF species were overall scarce in this study and absent in some samples across habitats, resulting in high standard deviations (Table 2, Appendix A Tables A1 and A2). For example, *S. orbiculus* was only found in two leaf samples, with relatively high abundances. A reason for this aggregation of LBF species in some samples could be local asexual reproduction, previously described for LBF species [68]. However, while LBFs were present in 11 *P. crispa* samples across all sites, they were found in 2 samples of *P. oceanica* leaves from site PO, and 8 samples of *P. oceanica* shoots from both sites.

5. Conclusions

We conclude that the community of epiphytic foraminifera >300μm is of higher diversity in *P. crispa* mats (Appendix A Figure A2) and is more homogeneously distributed across sites and replicates than *P. oceanica* sub-habitats. The fact that *P. crispa* mats are a suitable habitat for many foraminiferal species of both *P. oceanica* sub-habitats leads to the hypothesis that *P. crispa* mats may act as refuge habitats harboring biodiversity in times of loss and degradation of neighboring diversity hotspots. It underlines the relevance of this habitat in the Mediterranean Sea and justifies further assessments of *P. crispa* mat distribution along the Mediterranean coastline to confirm our results on a regional scale. We suggest further investigating the supraregional distribution and diversity of this vital rhodophyte habitat across the Mediterranean coastline to prove further its role as a vital habitat of high biodiversity. The recently adopted EU Biodiversity strategy for 2030 aims to protect and restore habitats of significant biodiversity to mitigate effects of e.g., regional human impact and climate change in terms of biodiversity loss. Our results in line with previous studies on *P. crispa* mats [17–22], as well as the successful implementation of a marine protected area covering "Zernov's *Phyllophora* field" in the Black Sea [23] suggest that this habitat hosts considerably high diversity of invertebrate taxa and should thus be considered in future conservation efforts.

Appendix A

Formula (A1): Calculation of the Shannon index (H'), using the proportion of each individual taxon $p_i = n/N$, where n = the number of individuals of a given taxon and N = the total number of individuals per sample:

$$H' = \sum_{i=0}^{R} p_i \ln p_i \tag{A1}$$

Formula (A2): Calculation of the Pielou index (J), using the Shannon index (H'), and the total number of taxa (S):

$$J = H'/\ln S \tag{A2}$$

Table A1. Abundance of LBF species in *P. oceanica* sites and sub-habitats. Numbers are average abundance per m^2 substrate (AVG) $\pm$ standard deviation (STDEV).

Species	Leaves Site Mix		Leaves Site PO		Shoots Site Mix		Shoots Site PO	
	AVG	STDEV	AVG	STDEV	AVG	STDEV	AVG	STDEV
Vertebralina striata	0	0	0	0	0	0	105	151
Peneroplis pertusus	0	0	0	0	92	177	41	82
Sorites orbiculus	0	0	73	160	0	0	0	0

Table A2. Abundance of LBF species in *P. crispa* sites. Numbers are average abundance per m^2 substrate (AVG) $\pm$ standard deviation (STDEV).

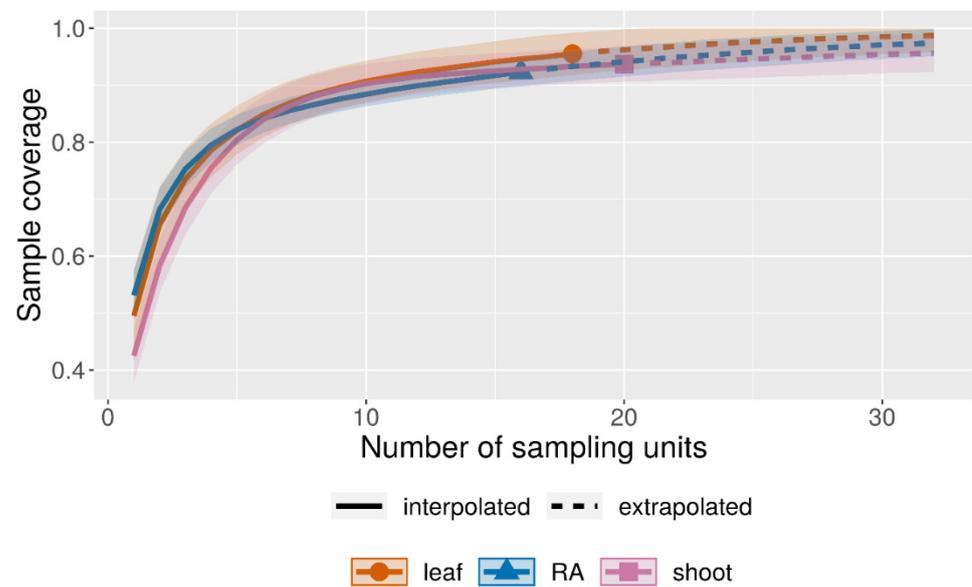| Species	Site PC1		Site PC2		Site PC3		Site Mix	
	AVG	STDEV	AVG	STDEV	AVG	STDEV	AVG	STDEV
Peneroplis pertusus	92	132	272	272	49	49	200	324
Peneroplis planatus	0	0	17	30	31	54	20	34
Sorites orbiculus	0	0	41	72	0	0	10	17

Figure A1. Sample completeness based on species incidence data according to Chao et al. [53]. Number of bootstraps used: 500; level of confidence: 0.95. Habitats with sample coverage (*C. hat*): "leaf" = *Posidonia oceanica* leaves (0.95), "RA" = *Phyllophora crispa* mats (0.92), "shoot" = *Posidonia oceanica* shoots (0.94).
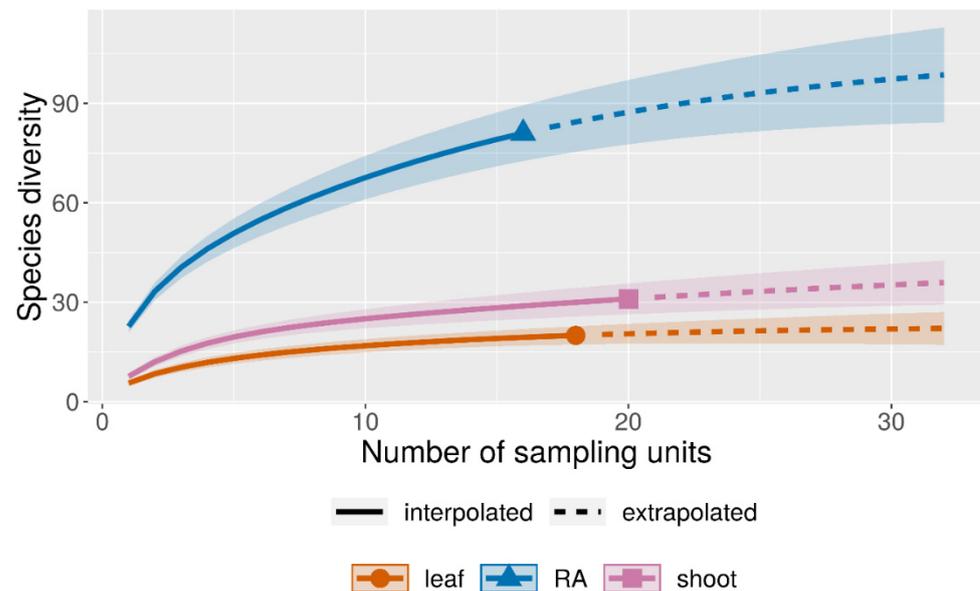

Figure A2. Species diversity extrapolated on number of sampling units, following the method of Chao et al. [53]. Number of bootstraps used: 500; level of confidence: 0.95. Habitats: "leaf" = *Posidonia oceanica* leaves, "RA" = *Phyllophora crispa* mats, "shoot" = *Posidonia oceanica* shoots.

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