New Insights into a Mediterranean Sea Benthic Habitat: High Diversity of Epiphytic Bryozoan Assemblages on *Phyllophora crispa* (Rhodophyta) Mats

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Abstract: With its geographically isolated location and geological history, the Mediterranean Sea harbors well-known biodiversity hotspots, such as *Posidonia oceanica* seagrass meadows. Recently, long-living mats formed by the fleshy red alga *Phyllophora crispa* have been described to be associated with a high diversity of sessile invertebrates in the Tyrrhenian Sea. One of the key taxa among these sessile invertebrates are bryozoans: their abundance, diversity, and spatial distribution in *P. crispa* mats represent a gap in scientific knowledge. Thus, we conducted a pilot study on bryozoan assemblages associated with *P. crispa* mats around Giglio Island (Tuscan Archipelago, Italy) in 2018, followed by a comparative study on four sites distributed around the island in the subsequent year, 2019. We compared these findings to bryozoan abundance and diversity on *P. oceanica* shoots and leaves during the second expedition. The findings revealed more than 46 families, with a significantly higher number of taxa identified in *P. crispa* mats (33) than in *P. oceanica* meadows (29). The Shannon diversity index was similar between *P. crispa* and *P. oceanica* shoots, while Pielou's evenness index was lower in *P. crispa* mats. The most abundant families reported across all habitats were Crisiidae, Aetidae, and Lichenoporidae; but the most abundant family on *P. crispa* was Chlidoniidae (*Chlidonia pyriformis*). The assemblages associated with *P. crispa* differed among sites, with higher abundances but lower diversity on the exposed southernmost site. The total bryozoan abundance was significantly higher on *P. crispa* (average $2.83 \times 10^6 \pm 1.99 \times 10^6$ colonies per m^2 seafloor) compared to *P. oceanica* meadows (average $0.54 \times 10^6 \pm 0.34 \times 10^6$ colonies per m^2 seafloor). Our results show a high diversity of bryozoans on *P. crispa* thalli compared to *P. oceanica* meadows, which was consistent throughout the study. These findings confirm the value of the red alga-generated habitat for associated bryozoans and may have implications for future biodiversity assessments and conservation measures.

Keywords: phytal habitat; epiphytic communities; engineering species; sessile invertebrates

1. Introduction

Understanding the patterns of variability of benthic assemblages represents one of the main goals for ecologists and has a pivotal role in managing and conserving marine habitats [1]. This information might help scientists predict or understand organisms' responses to global environmental changes. Hotspots of biodiversity in the Mediterranean Sea are often created by key engineering species that provide structurally complex habitats for associated communities [2]. Some of the most-studied engineered habitats in the Mediterranean Sea are seagrass meadows of the endemic angiosperm *Posidonia oceanica* (L.) Delile, 1813 (Figure 1C), and coralligenous reefs, mainly formed by the accumulation of crustose Rhodophytes thalli [3–6]. The rooted, flowering plants of *P. oceanica* build up dense meadows consisting of two sub habitats: a canopy of up to 50 cm long leaves that grows

from a dense network of stems and roots [7]. The crustose structures of coralligenous reefs provide a rigid substrate, characterized by systems of canals and crevices [5]. Both of these ecosystems promote high biodiversities of sessile invertebrates, as they provide different environmental gradients (e.g., light intensity, water movement, food availability), as well as shelter and space for larval settlement [8–10] (Figure 1D,E).
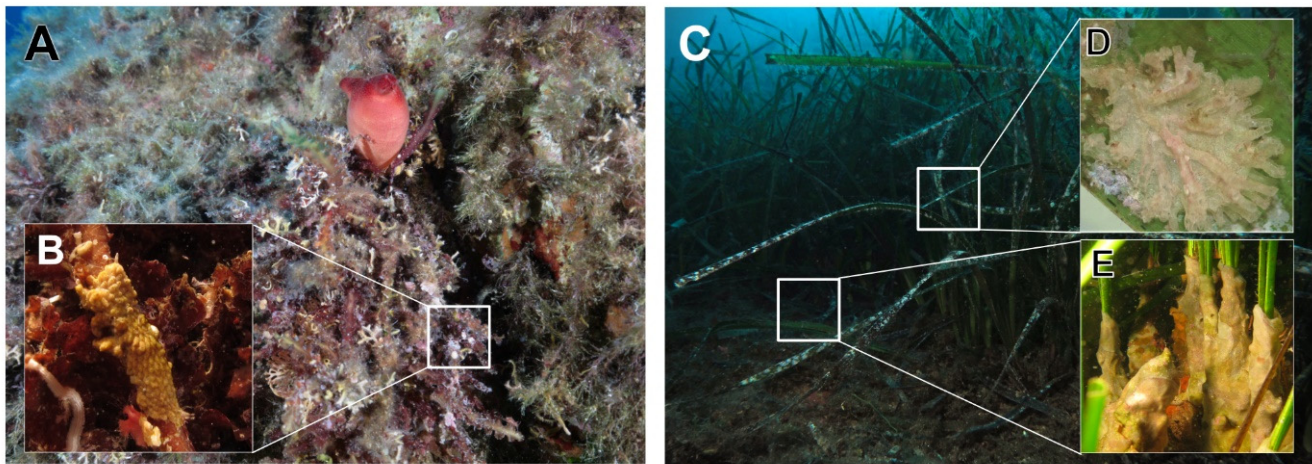

Figure 1. Edge of a *Phyllophora crispa* mat (**A**) with details on epiphytic fauna (**B**), including bryozoans, serpulids, and foraminiferans. Overview of *Posidonia oceanica* meadow (**C**), with details on the leaves (**D**) and shoots (**E**). Pictures: E.C. (**A**); F.R. (**B,C,E**); N.S. (**D**)).

Bryozoans are filter feeders and form one of the most abundant and diverse groups of epiphytic invertebrates on host organisms, such as seagrass (i.e., *P. oceanica*) and macroalgae [10–15]. In particular, the richest bryozoan diversity in the Mediterranean Sea has been reported on coralligenous reefs and marine caves due to the availability of several microhabitats that enhance the presence of bryozoans characterized by different shapes and ecological traits [16–18]. Their typical colonial structures consist of often highly specialized zooids and may vary between thin crusts, erect and branched forms, or larger rigid structures [19,20]. Many species are considered bioindicators for environmental changes, as they often respond faster to environmental and human-mediated pressures [21–23]. Because of their calcium carbonate hulls, they are sensitive to ocean acidification [24–26] and hold an essential part in fossil records [27]. Some bryozoan species have been reported as habitat-forming organisms playing a pivotal role in promoting biodiversity [24], e.g., by overgrowing *P. oceanica* shoots and preventing the settlement of other species [28] (Figure 1D). Furthermore, bryozoans play an essential role as primary consumers by transferring particulate organic matter from the water column into the benthic community [29,30].

The red macroalgae *Phyllophora crispa* ((Hudson) P.S.Dixon, 1964) is known for forming dense mats and hosting a diverse community of epiphytic invertebrates in the Black Sea [31]. In the north-western Mediterranean Sea, *P. crispa* forms dense mats [32–34] (Figure 1A), which have recently been shown to host high diversities of invertebrate fauna. Especially epiphytic filter feeders (e.g., Bryozoa, Serpulidae), which benefit from the algal thalli as a substrate and accumulated food particles from the water column, have been identified to contribute to the associated biodiversity [34–36] (Figure 1B). However, little is known about the variations of bryozoan diversity inside *P. crispa* mats over space and time or their diversity compared to other Mediterranean habitats (e.g., *P. oceanica* meadows).

To address this knowledge gap, we carried out a comparative field study on the abundance and diversity of bryozoans at four locations of *P. crispa* mats around Giglio Island (Tuscan Archipelago, Italy, Tyrrhenian Sea) in two consecutive seasons (2018 and 2019) and on a *P. oceanica* meadow as a reference habitat (2019). We decided on *P. oceanica* as a reference habitat because its biodiversity has been well studied during the last decades, and the structure is more similar to the fleshy *P. crispa* thalli than, e.g., the calcareous substrate of

coralligenous reefs. Additionally, extensive coralligenous reefs are generally found deeper, and other mat-forming macroalgae are not present at the same depth as *P. crispa* mats within the study area. With this work, we aim to answer the following research questions:

1. What are the abundances and diversity of bryozoans inside *P. crispa* mats compared to *P. oceanica* meadows?
2. Which are the most abundant families in the investigated habitats, and which families are unique to *P. crispa* mats?
3. What is the spatial variability of the bryozoan assemblages inside *P. crispa* mats?

2. Materials and Methods

2.1. Location and Sampling Procedure

The study area is located at the island of Giglio (42°21′19.4″ N 10°54′06.1″ E, Figure 2) and is characterized by steep granite slopes alternating with sandy bottoms. The infralittoral seabeds are colonized by *Posidonia oceanica* meadows, *Phyllophora crispa* mats, and coralligenous reefs [35]. Scientific SCUBA divers collected all samples at water depths of 30 ± 4 m at four sites around the island. Sampling took place between May and June 2018 (21 *P. crispa* samples on Site Mix) and between May and July 2019 (4 *P. crispa* samples per site, resulting in 16 total samples; 9 *P. oceanica* leaves, and 10 *P. oceanica* shoots on Site Mix). The sampling sites were chosen for their similar topography and occurrences of *P. crispa* mats of at least 90% coverage (by visual census; Appendix A Figure A1) at the target depth of 30 m. In 2018, we sampled *P. crispa* material from Site Mix. In 2019, all four sites (site PC1, PC2, PC3, and Site Mix) were sampled for *P. crispa* mats, and Site Mix was additionally sampled for *P. oceanica* material. Site Mix was the only site with a continuous *P. oceanica* meadow present at the target depth.
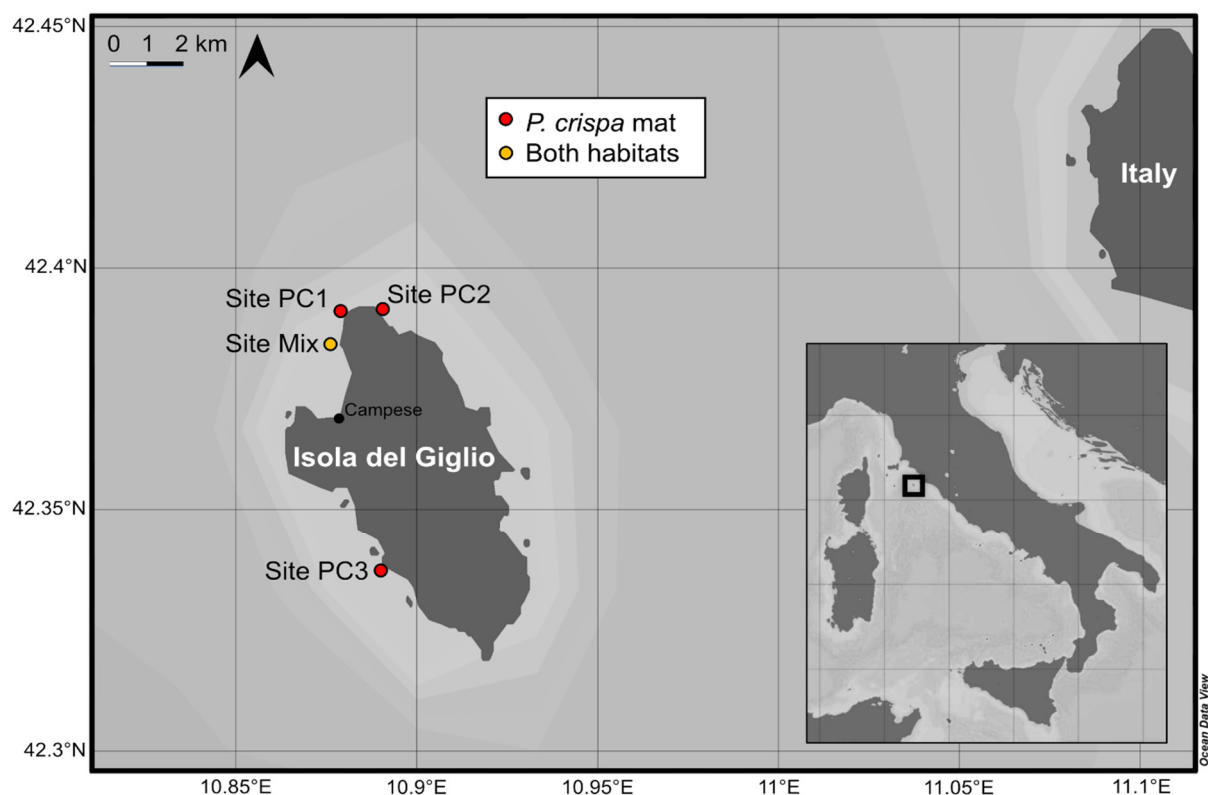

Figure 2. Locations of the sampling sites in the study area (Isola del Giglio, Italy). Red dots mark sampling sites of *Phyllophora crispa* in 2019, the yellow dot marks the site of comparative sampling in both years (2018 and 2019), and *Posidonia oceanica* reference habitat (2019).

The *P. crispa* mats were sampled using a metal quadrat (size 30 × 30 cm) that was placed randomly inside a continuous mat of at least 5 cm thickness to define the exact sampling area. All material of these main samples was then carefully scraped off the rock surface with a spatula directly under the holdfast to avoid breaking or removing epiphytic organisms.

The *P. oceanica* leaves and shoots were cut with scissors, directly on the sheath or rhizome branching point, on meadows close to the sampling depth of *P. crispa* mats (30 ± 4 m). Additionally, we counted the number of *P. oceanica* shoots per m^2 (n = 16 counts) and the number of leaves per shoot (n = 32 counts) for later extrapolating bryozoan colonies per m^2 seafloor. These density measures were carried out by counting the number of shoots within a 40 × 40 cm frame. Shoots and leaves were treated as separate sub-habitats considering their different ecological traits, particularly regarding their longevity as a fundamental trait for larval settlement [37,38].

All main samples were carefully transferred into plastic jars immediately after sampling. Every jar contained approximately one-third of sampled material and two-thirds of seawater to avoid oxygen depletion during the transport to the holding facilities in the Institute for Marine Biology (IfMB, located in the near bay of Campese). The main samples were then kept in aerated seawater tanks at constant temperature (18 °C; equivalent to in situ temperature) before they were analyzed within three days after sampling.

2.2. Species Identification and Abundance Assessment

From the *P. crispa* main samples, subsamples between 20 and 100 g wet weight were extracted, roughly 20% of the respective main sample. The span of different wet weights resulted from the different amounts of main samples due to the randomly picked sampling area. The remaining material of the main samples was analyzed for other taxonomic groups that are not within the frame of this study. The shoots and leaves of *P. oceanica* were analyzed as a whole under stereo magnifiers (maximum 40× magnification). Bryozoan colonies were identified to the lowest possible taxonomic level using the relevant literature (Appendix A, Table A2). The abundance was assessed by counting the number of colonies. In the case of branching, stolonal taxa—e.g., *Chlidonia pyriformis* (Bertoloni, 1810)—all parts connected by stolons were considered one colony. We opted to work with the family level for further analysis to reduce observer bias and increase work efficiency. Previous studies have shown that this method may not result in a significant loss of information [39]. Furthermore, the taxonomic sufficiency hypothesis applied to Mediterranean peculiar habitats revealed that surrogate taxonomic levels higher than species could be used to highlight the diversity pattern of benthic assemblages [40].

The surface area of all subsamples was assessed as follows. For *P. oceanica* shoots, the length and diameter were measured, and surface area calculations were based on an assumed cylindrical shape. For *P. oceanica* leaves, the length and width were measured to calculate the rectangular surface (times two, to account for both sides of the leaf). The *P. crispa* subsamples were flattened with a glass pane on laminated graph paper before being photographed from above with a fixed tripod. The surface area was then determined using ImageJ (version 1.52o, https://imagej.nih.gov/ij/, accessed on 23 April 2019) and multiplied by two to account for both sides of the thalli. The wet weight of all *P. crispa* main samples and subsamples was assessed after shaking off excess water to extrapolate the abundances from the subsamples to the main sample and finally to the surface of the seafloor. Bryozoan abundance was then calculated as the number of colonies per m^2 of seafloor ± standard deviation (SD) (Appendix A, Formulas (A1)–(A3)).

2.3. Diversity Descriptors and Statistical Analysis

Bryozoan diversity was assessed using four descriptors: total numbers of families per site and habitat, Shannon diversity index [41], and Pielou's evenness index [42]. The descriptors were calculated as means per site and habitat and were reported with the respective SD.

Differences in the composition of bryozoan assemblages in *P. crispa* mats among sites were tested using multivariate permutational analysis of variance (PERMANOVA [43]). The source of significant results ($p < 0.05$) was tested using Tukey's honestly significant difference (HSD) test. Based on the results of the multivariate analysis, the data of the northern sites were pooled for further comparison among habitats (Appendix A, Table A1).

Statistical differences in the diversity descriptors among sites and (sub-) habitats were assessed with pairwise Wilcoxon–Mann–Whitney tests. The comparison among habitats on the northern sites was visualized using non-metric multidimensional scaling (NMDS). In addition, the bryozoan assemblages were clustered with a Spearman ranked correlation (average linkage) on a family level to visualize the composition of the bryozoan assemblages using the software' heatmapper' [42]. Analyses and plots were made with R (version 4.0.5) [44].

To avoid potential variability between the observer and different sampling efforts in the two subsequent seasons, we decided against a direct statistical comparison on a temporal scale.

3. Results

3.1. Bryozoan Richness and Abundance

A total of 17,822 bryozoan colonies were found (2018 = 10,312; 2019 = 7510) and 46 taxa identified to at least the family level. The highest number of families was identified in *Phyllophora crispa* mats in 2019 (33), while *Posidonia oceanica* meadows held 29 families (Figure 3). A similar amount was found in *P. crispa* mats during the pilot study in 2018 (28). In the comparative study of 2019, the two habitats shared 21 families, while this number was higher for *P. crispa* and *P. oceanica* shoots (20) than for *P. crispa* and *P. oceanica* leaves (13). A significantly higher number of families ($p < 0.05$) was reported in *P. crispa* compared to *P. oceanica* sub-habitats (Figure 4F).
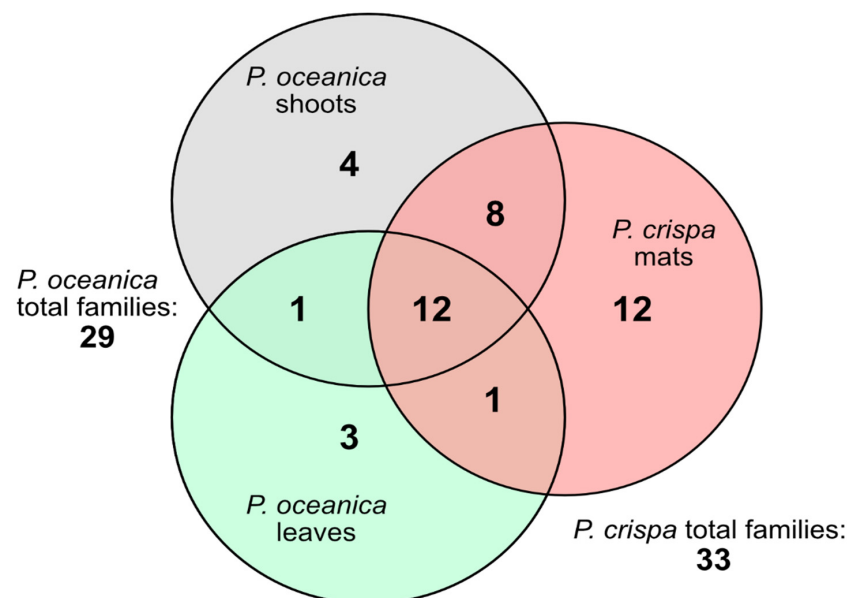

Figure 3. Number of families found per habitat during the second sampling season (2019), showing shared families between the respective habitats.
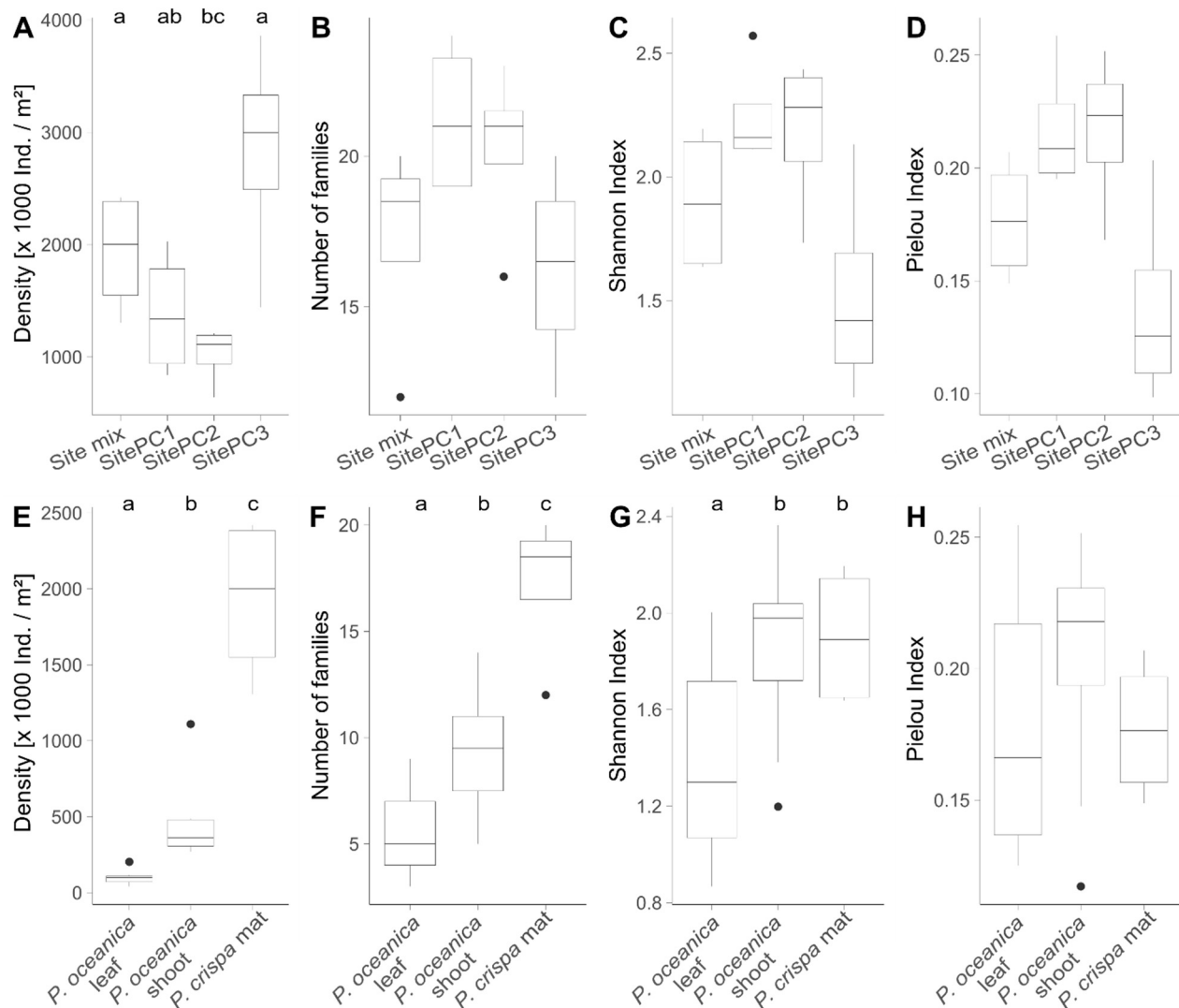
Figure 4. Comparison of abundance and diversity descriptors among sites and habitats. First row (**A**–**D**): all four investigated *Phyllophora crispa* sites in 2019. Second row (**E**–**H**): all three (sub-) habitats on the northern sites (Site Mix, site PC1, site PC2) in 2019. Columns show the density of colonies per m^2 seafloor, number of identified taxa, Shannon index, and Pielou's index. Statistical differences ($p < 0.05$; Wilcoxon–Mann–Whitney test) are indicated by small letters (a–c) where significant results occurred. Black dots resemble outliers.

The most abundant families across all habitats were Crisiidae, Aetidae, and Lichenoporidae (Table 1). The highest density of bryozoan colonies was found in *P. crispa* mats in 2018 (average 2,827,762 ± 1,984,965 colonies per m^2 seafloor). Among *P. crispa* sites, the density was highest on the southernmost site (site PC3) and lowest on the northernmost site (site PC2, Figure 4A). This observation was the only significant effect among sites in the diversity descriptors of *P. crispa* mats and confirmed the results of the multivariate analysis (Appendix A, Table A1). Based on these results, the data of the northern *P. crispa* sites were pooled for further comparison among (sub-) habitats. The lowest abundance was recorded on *P. oceanica* leaves (average 177,912 ± 104,999 colonies per m^2 seafloor, Figure 4E). The most abundant family contributing to the measured densities was Chlidoniidae (*Chlidonia pyriformis*) in *P. crispa* mats and *P. oceanica* shoots, with a higher abundance on *P. crispa*. Candidae were abundant on *P. crispa* mats and *P. oceanica* shoots as well. On the leaves of *P. oceanica*, Haplopomidae and Tubuliporidae were most abundant (Table 1). It is also notable that *P. crispa* mats host additional growth types,

such as petraliform (e.g., *Beania hirtissima* (Heller, 1867)), encrusting (e.g., *Watersipora* sp.), and creeping (e.g., *Aeta* sp.), while *P. oceanica* leaves mainly support encrusting forms (e.g., *Haplopoma* sp.).

Table 1. Most abundant families of every (sub-) habitat and both years of *Phyllophora crispa* sampling (top 5 indicated in bold for each habitat) and *Posidonia oceanica* sampling in 2019. Numbers show the mean number of colonies per m^2 seafloor $\pm$ standard deviation (SD).

Family	*P. crispa* 2018		*P. crispa* 2019		*P. oceanica* Leaves 2019		*P. oceanica* Shoots 2019	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Aetidae	15,976	5887	**112,140**	13,312	**52,535**	12,360	**45,064**	5863
Candidae	**268,368**	93,217	5183	2343	0	0	**37,916**	5463
Chlidoniidae	**1,287,926**	276,738	**1,250,665**	445,419	0	0	**131,954**	46,711
Crisiidae	**192,089**	22,353	**347,948**	54,644	**48,945**	14,288	**64,743**	9896
Haplopomidae	4674	1652	56,640	20,818	**155,149**	36,106	0	0
Tubuliporidae	**240,495**	33,541	**200,127**	31,551	**63,966**	19,210	**33,656**	7157
Watersiporidae	**212,608**	37,342	24,788	5333	0	0	0	0
Unknown	113,593	50,098	**130,742**	22,592	**183,536**	36,544	3628	1166

3.2. Diversity Indices

The Shannon index was highest in *P. crispa* mats in 2019 at sites PC1 and PC2 ((mean 2.2 $\pm$ 0.1), Figure 4C), while in the direct comparison of the northern *P. crispa* sites to *P. oceanica* on Site Mix, the *P. oceanica* shoots showed slightly higher values (mean 2.3 $\pm$ 0.4) than *P. crispa* ((mean 2.1 $\pm$ 0.2) Figure 4C).

The evenness (Pielou's index) was similar on *P. oceanica* leaves and shoots (mean 0.20 $\pm$ 0.01, and 0.18 $\pm$ 0.01, respectively), compared to *P. crispa* (mean 0.20 $\pm$ 0.01) on the northern sites. The northern sites showed slightly higher values, while the southern site was lower, without significant effects (Figure 4D).

3.3. Structure of Bryozoan Assemblages

The diversity inside the *P. crispa* mats consisted of many taxa unique to this habitat. Out of the 46 families identified during this study, 18 were exclusively found on *P. crispa*. In the *P. oceanica* samples, we found 3 families not present on *P.crispa* (Figure 5). Most of the taxa solely found on *P. crispa* belonged to Watersiporidae (212.608 $\pm$ 37.342 and 24.788 $\pm$ 5.333 colonies per m^2 in 2018 and 2019, respectively).

The cluster analysis highlights the differences between *P. oceanica* sub-habitats and *P. crispa* and between sampling years (Figure 5). It also shows the dominance of *C. pyriformis* (the only species of Chlioniidae found) and Crisiidae (mainly *Filicrisia geniculate* and *Crisia* sp.) in *P. crispa* mats and on *P. oceanica* shoots. The family of Tubuliporidae was abundant across samples and habitats. Between the two years of *P. crispa* sampling, Watersiporidae and Candidae showed higher abundances in 2018, while Aetidae were more abundant in 2019 (Figure 5, Table 1).

The non-metric multidimensional scaling (NMDS) further highlights the differences in the composition of bryozoan families among the (sub-) habitats in 2019 (only northern sites; Figure 6). While all three (sub-) habitats form distinct clusters, the *P. oceanica* sub-habitats samples show a higher degree of scattering than the *P. crispa* samples.
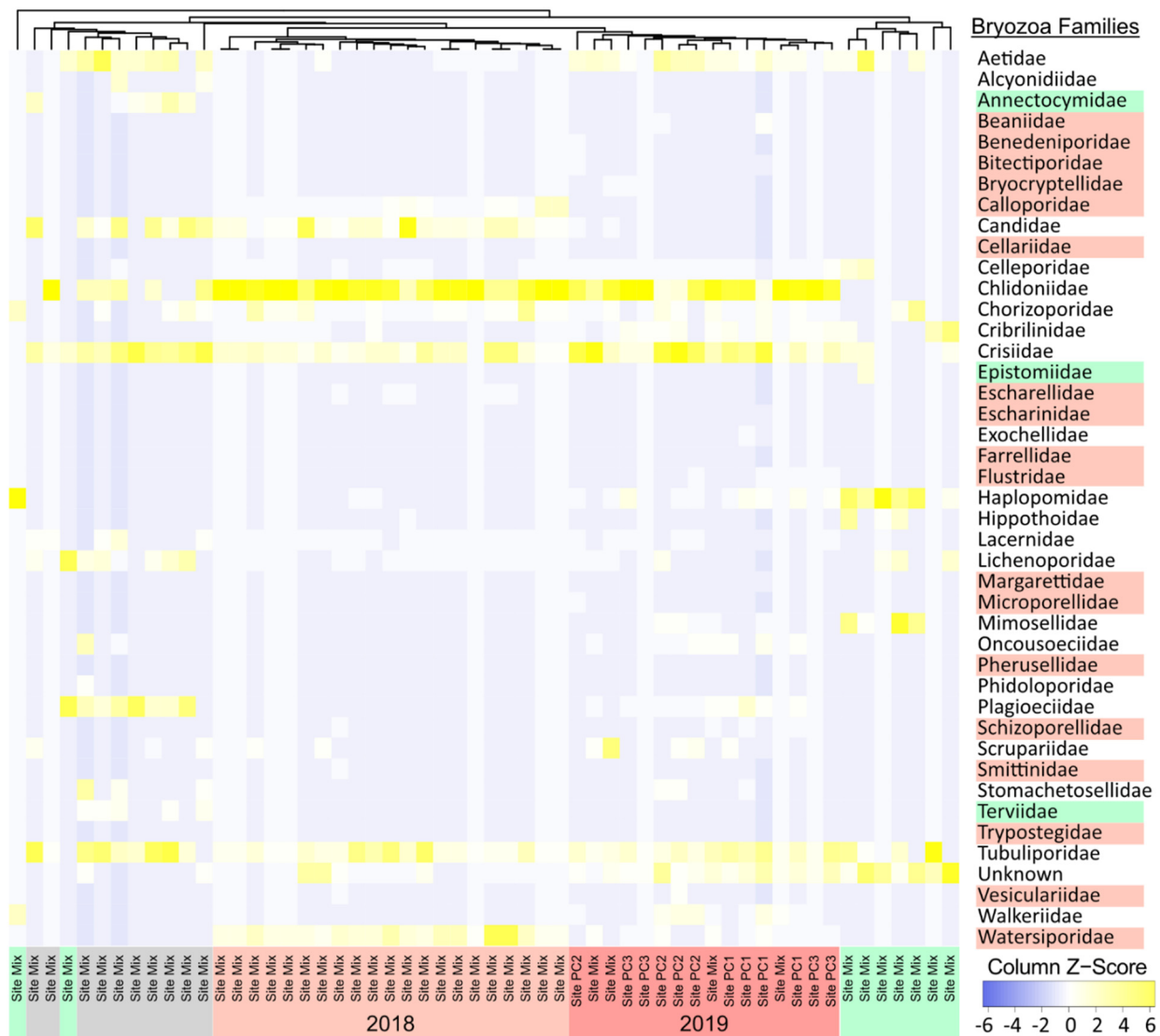
Figure 5. Visualization of Spearman ranked correlation of the abundances (colonies per m^2 seafloor) of bryozoan families. Samples of *Posidonia oceanica* leaves and shoots are indicated in green and grey, respectively. *Phyllophora crispa* samples are indicated in light red (2018) and dark red (2019). Bryozoa families highlighted in green were exclusive to *Posidonia oceanica*, highlighted in red were exclusive to *Phyllophora crispa*.
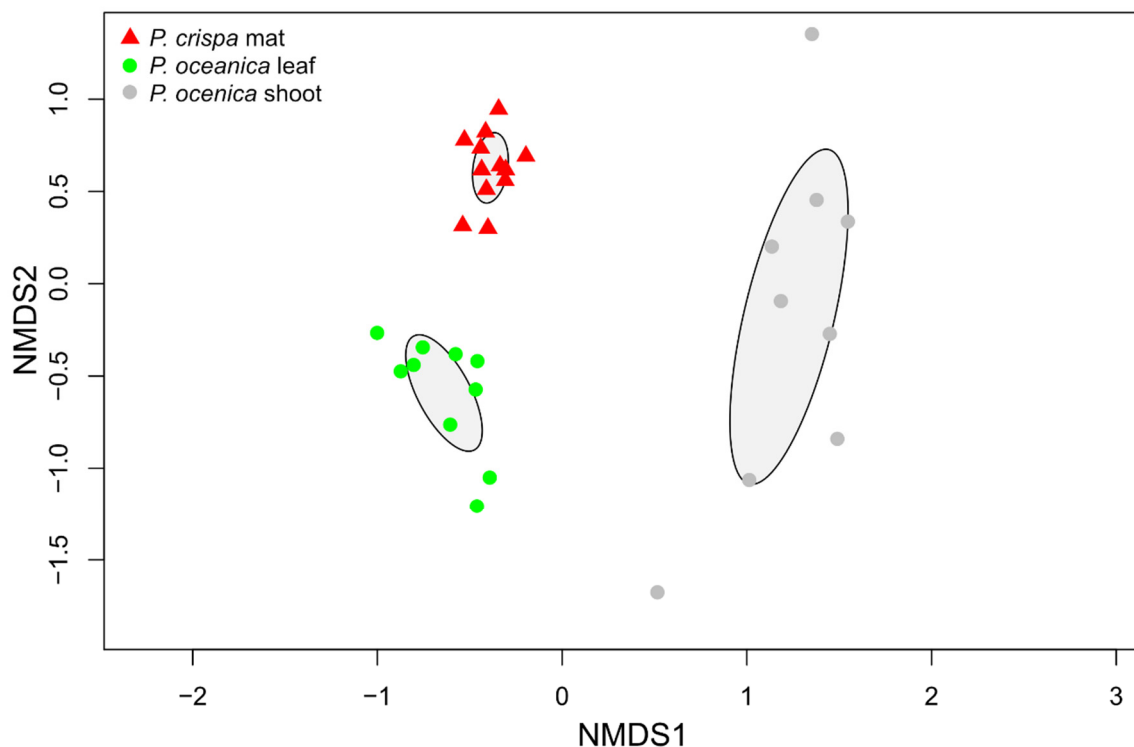
Figure 6. Non-metric multidimensional scaling (NMDS) plot comparing the bryozoan communities found on the three (sub-) habitats across the northern sites (Site Mix, site PC1, site PC2) during the second sampling season (2019).

4. Discussion

4.1. Differences in Bryozoan Abundances and Diversity between Phyllophora crispa Mats and Posidonia oceanica Sub-Habitats

Our results show differences among the three (sub-) habitats, with a clear trend of higher abundances and diversity of the bryozoan community inside the *P. crispa* mats (Figure 4E–H). The results have shown that the bryozoan assemblages in *P. crispa* mats and on *P. oceanica* shoots are similar concerning the chosen diversity descriptors (Figure 4G,H), whereas the distinct clusters in the NMDS analysis (Figure 6) highlight the differences according to the structure of the assemblages. While the quantitative diversity (abundance and number of taxa) was significantly higher in *P. crispa* mats, the diversity indices were similar to *P. oceanica* meadows. The relatively low indices for *P. crispa* compared to the indices on *P. oceanica* are likely due to the high abundance of one species (*Chlidonia pyriformis*, Chlionidae), while the diversity on *P. oceanica* is more evenly distributed (Figures 4H and 5). The erect colonies of *C. pyriformis* are typical for calm water conditions and are often associated with macro-algae [45]. High abundances of erect and branching colonies (e.g., *C. pyriformis*, *Scrupocellaria* sp., *Crisia* sp.) on *P. crispa* and *P. oceanica* shoots are likely related to water current gradients inside *P. crispa* mats [46], as demonstrated before for *P. oceanica* meadows [47–49]. This is further supported by an experimental study that has confirmed negative phototaxis for the larvae of some erect bryozoan species [50], since strong light gradients are present in both habitats [46]. These traits, accompanied by the higher longevity of *P. crispa* and *P. oceanica* shoots compared to the relatively short-lived *P. oceanica* leaves, could be the main reason for the higher similarity of the two habitats in bryozoan families' composition (Table 1) and diversity (Figure 4G). A richer diversity on *P. oceanica* shoots compared to the leaves has also been reported before in the Mediterranean Sea [51]. While the leaves of *P. oceanica* mainly host encrusting forms, *P. crispa* hosted additional growth types (petraliform and creeping), further underlining the structural diversity of the bryozoan community. As demonstrated above for *P. oceanica* meadows, this structural diversity is likely linked to gradients in water currents and light intensity, which have recently been confirmed for *P. crispa* mats [46].

Further investigations are needed to identify the mechanisms of these gradients and their influence on the epiphytic community in this specific habitat.

The high amount of rare bryozoan taxa found exclusively on *P. crispa* during this study further emphasizes the relevance of *P. crispa* for the quantitative diversity and its role as an essential habitat besides classically known hotspots, such as *P. oceanica* meadows. Furthermore, a high diversity of filter feeders potentially supports a diverse and productive food web by transferring biomass from the water column into benthic communities [29]. Previous studies have shown that other sessile filter feeders are abundant inside *P. crispa* mats [34–36,39]. Bryozoans attract a wide range from invertebrates to fish and from incidental to specialized predators [52]. Some predators are highly specialized on bryozoans (e.g., nudibranchs [53,54] or pycnogonids [55]). We also thus expect to find high abundances and diversities of mobile benthic predators inside these mats in the future.

Some characteristic species for the *P. oceanica* leaf assemblages, such as the endemic *Electra posidoniae* (Electridae; Gautier, 1954), were not found. This absence can be explained by the depth limitations and seasonality of these species [56].

4.2. Spatio-Temporal Variability of the Bryozoan Community inside Phyllophora crispa Mats

The high diversity and abundance of bryozoans found in the pilot study in 2018 were confirmed in the comparative study in 2019 (Figure 5, Table 1). Because sampling took place within the same period (May–July) in both years, we can not evaluate seasonal changes during the year. The differences in the taxa composition (higher abundance of Watersiporidae and Candidae in 2018; higher abundance of Aetidae in 2019; Figure 5) are consistent with a previous study carried out on the eastern side of the island [34], where *Watersipora* sp. (Watersiporidae) was the most abundant species at depths between 25 and 35 m. Assemblages of cheilostome bryozoans (such as Candidae, Aeteidae, and Watersiporidae) have been shown to follow seasonal and depth-related variations [10]. Our study focused on the same depth range and season during both years to avoid impacts on the results. However, satellite data from both years show differences in the Mediterranean Sea surface temperature, with relatively high values for 2018 and lower values for the first half of 2019 [56]. This effect has potentially shifted the natural seasonal variations and could have caused the observed effect.

Among the sampling sites of *P. crispa* during the 2019 campaign, our analysis showed higher diversity but lower abundance values for the northern sites (PC1 and PC2, Figure 4A–D). The high abundance accompanied by low diversity indices at Site PC3 was mainly driven by an exceptionally high density of *C. pyriformis*. The larvae of cheilostomate bryozoans (such as *C. pyriformis*) are often selective for suitable settling grounds [57]. The observed differences at Site PC3 could result from alterations in the environmental conditions due to the more exposed location towards the prevalent southern currents in the area [58], and thus an enhanced larval supply of this generalistic species. It remains unclear to what extent these differences could be explained by the relatively sheltered western site (Site Mix) from prevalent southern currents [58], resulting in different hydrodynamic patterns inside the bay. In addition, Campese bay is known for extensive touristic usage during the summer months, which might result in changes in the water quality. Physical disturbances and changes in water quality have been reported to affect bryozoan abundance and diversity [22,59,60]. Recent studies highlight the effects of local temperature and salinity changes in intertidal areas [61,62]. In the context of reoccurring temperature anomalies [63–65] and impacts on the thermohaline circulation [63], these effects are potentially also becoming relevant for sublittoral coastal habitats in the Mediterranean Sea. Further research is needed to describe hydrodynamic patterns and potential disturbances on these algal mats inside the bay.

5. Conclusions

We conclude that *P. crispa* mats provide an essential habitat for bryozoan diversity, harboring a high density of bryozoan colonies and a large number of families that were not present in the *P. oceanica* reference habitat. The Mediterranean "bryodiversity" (bryozoan

diversity) has been recently estimated to 556 species, representing 9.6% of global bryozoan diversity [17]. About 79% of the bryozoan species in the Mediterranean Sea colonize coralligenous and dark and semi-dark cave habitats (219 and 220 species, respectively). Nevertheless, as recently highlighted by [66] for the mesophotic reefs in the Adriatic Sea, the understanding of bryozoans' diversity and ecological roles in Mediterranean habitats is still far from being thoroughly investigated. Our results further strengthen the significance of *P. crispa* mats as a habitat harboring an exceptional bryozoan diversity, along with previous studies on epiphytic epifauna [34–36,67]. Regional human impacts and climate change threaten biodiversity in the Mediterranean Sea [68–70]. Therefore, identifying, protecting, and enhancing highly diverse habitats have become central parts of conservation strategies [71]. We suggest further investigations on the distribution of *P. crispa* mats along the Mediterranean coastline to confirm previous results on a larger scale and gain knowledge on the distribution of significant *P. crispa* aggregations. Furthermore, it is essential to understand how *P. crispa* mats are threatened by local and regional environmental impacts.

Appendix A

Figure A1. Diver assessing *Phyllophora crispa* mat on site PC2. The picture shows the typical closed coverage of *Phyllophora crispa* across the rocky surface of all sampling sites (Picture: F. I. Rossbach).

Table A1. Results of permutational multivariate analysis of variance (PERMANOVA) of bryozoan communities among *P. crispa* sites, and pairwise comparison (Tukey's honestly significant difference (HSD) test) of sites and (sub-) habitats. Significant results ($p < 0.05$) are indicated in bold.

PERMANOVA broyzoan assemblages *P. crispa* all sites					
Source	**Df**	**SS**	**R2**	**F**	***p***
Site	3	0.9441	0.40007	2.6674	**0.018**
Residual	12	1.4158	0.59993		
Total	15	2.3599	1		
PERMANOVA broyzoan assemblages *P. crispa*, northern sites					
Source	**Df**	**SS**	**R2**	**F**	***p***
Site	2	0.35393	0.2497	1.4976	0.192
Residual	9	1.06348	0.7503		
Total	11	1.41741	1		

Table A1. *Cont.*

Pairwise comparison all sites							
pairs		**Df**	**SS**	**F**	**R2**	**p**	**p adj**
SiteMix	SitePC3	1	0.258842	2.391555	0.284995	0.097	0.582
SiteMix	SitePC2	1	0.295435	2.6252	0.304364	0.109	0.654
SiteMix	SitePC1	1	0.127757	1.11843	0.157118	0.359	1
SitePC3	SitePC2	1	0.685668	5.632692	0.484212	**0.029**	0.174
SitePC3	SitePC1	1	0.412804	3.344677	0.357923	0.09	0.54
SitePC2	SitePC1	1	0.107701	0.843212	0.123219	0.444	1
Pairwise comparison (sub-) habitats, northern sites							
pairs		**Df**	**SS**	**F**	**R2**	**p**	**p adj**
P. oceanica shoot	*P. oceanica* leaf	1	3.10581	14.89658	0.287044	0.001	**0.003**
P. oceanica shoot	*P. crispa* mat	1	1.654007	9.524627	0.24098	0.001	**0.003**
P. oceanica leaf	*P. crispa* mat	1	1.923498	10.44726	0.264841	0.001	**0.003**

Table A2. Literature used for species identification.

Authors	Year	Title
Ryland, J. S. & Hayward, P. J.	1977	British Anascan Bryozoans
Hayward, P. J. & Ryland, J. S.	1979	British Ascophoran Bryozoans
Hayward, P. J. & Ryland, J. S.	1985	Cyclostome Bryozoans
Hayward, P. J.	1985	Ctenostome Bryozoans
Zabala, M. & Maluquer, P.	1988	Treballs del museu de zoologia–illustrated keys for the classification of Mediterranean Bryozoa
Hayward, P. J. & Ryland, J. S.	1995	Handbook of the Marine Fauna of North-West Europe
Hayward, P. J. & Ryland, J. S.	1998	Cheilostomatous Bryozoa: Part 1 Aeteoidea-Cribrilinoidea
Hayward, P. J. & Ryland, J. S.	1999	Cheilostomatous Bryozoa: Part 2 Hippothooidae - Celleporoidae
Bedini, R.	2003	Gli animali delle praterie a Poseidonia oceanica: dai macroinvertebrati ai pesci

Formula (A1): Calculation of bryozoan colonies on *P. crispa* per m^2 seafloor (Col_{SF}) from colonies per m^2 substrate (Col_{SS}), using wet weights of the main sample (WW_{MS}) and subsample (WW_{SS}), and surface area of the subsample (SA_{SS}) (0.09 m^2 corresponds to the size of the sampling frame):

$$Col_{SF} = \frac{\frac{WW_{MS} \times SA_{SS}}{WW_{SS}}}{SA_{SS}} \times Col_{SS} \times \frac{1 \text{ m}^2}{0.09 \text{ m}^2} \tag{A1}$$

Formula (A2): Calculation of bryozoan colonies on *P. oceanica* leaves (Col_{SF}) per m^2 seafloor using the mean leaf surface area ($SA_{leafAVG}$), the mean number of leaves per m^2 (162), the surface area of investigated leaf sample (SA_{leafSS}), and colony count per m^2 substrate (Col_{SS}):

$$Col_{SF} = \frac{162 \times SA_{leafAVG}}{SA_{leafSS}} \times Col_{SS} \tag{A2}$$

Formula (A3): Calculation of bryozoan colonies on *P. oceanica* shoots per m² seafloor (Col_{SF}) using the shoot surface area ($SA_{shootSS}$), the mean number of shoots per m² (40.5), and colony count per m² substrate (Col_{SS}):

$$Col_{SF} = \frac{40.5 \times SA_{shootSS}}{SA_{shootSS}} \times Col_{SS} \tag{A3}$$

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