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Local Variability in Microbiome Composition and Growth Suggests Habitat Preferences for Two Reef-Building Cold-Water Coral Species

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Cold-water coral (CWC) ecosystems provide niches and nurseries for many deep-sea species. Lophelia pertusa and Madrepora oculata, two cosmopolitan species forming three dimensional structures, are found in cold waters under specific hydrological regimes that provide food and reoxygenation. There is now more information about their feeding, their growth and their associated microbiome, however, little is known about the influence of their habitat on their physiology, or on the composition of their bacterial community. The goal of this study was to test if the habitat of L. pertusa and M. oculata influenced the hosts associated bacterial communities, the corals’ survival and their skeletal growth along the slope of a submarine canyon. A transplant experiment was used, based on sampling and cross-redeployment of coral fragments at two contrasted sites, one deeper and one shallower. Our results show that M. oculata had significantly higher skeletal growth rates in the shallower site and that it had a specific microbiome that did not change between sites. Inversely, L. pertusa had the same growth rates at both sites, but its bacterial community compositions differed between locations. Additionally, transplanted L. pertusa acquired the microbial signature of the local corals. Thus, our results suggest that M. oculata prefer the shallower habitat.

**Keywords:** Lophelia pertusa, Madrepora oculata, DNA, bacteria, skeletal growth rates, Mediterranean canyon

**INTRODUCTION**

Scleractinian cold-water corals (CWC) such as Lophelia pertusa and Madrepora oculata, iconic engineer species of submarine canyons, are important frame-builders that provide shelter for a large diversity of associated fauna (Buhl-Mortensen et al., 2010). During the last decades, significant efforts have been dedicated to characterize CWC’s feeding, reproduction, growth, and
their associated coral microbiome (Waller and Tyler, 2005; Tsounis et al., 2010; Lartaud et al., 2014; Meistertzheim et al., 2016; Galand et al., 2020). However, due to the difficulty of sampling in the deep sea, a detailed knowledge of their ecology is still lacking when compared to their shallow water counterparts. Such knowledge is important as these animals with a great ecological value are threatened by trawling, pollution and climate change (Freiwald et al., 2004; Foley and Armstrong, 2010).

*Lophelia pertusa* (synonymized recently as *Desmophyllum pertusum* (Addamo et al., 2016) and *M. oculata* are the most abundant species forming reef frameworks in the North Atlantic, the Gulf of Mexico, and the Mediterranean Sea (Freiwald et al., 2004, 2009; Roberts et al., 2006). While *L. pertusa* dominates in many regions, *M. oculata* is often found as a secondary species together with *L. pertusa*. *M. oculata* have fragile branches and it is therefore thought that their framework building capacity is limited (Freiwald, 2002). The relative abundance and/or spatial distribution of *L. pertusa* and *M. oculata* change following geographical locations, which suggests different living strategies (Freiwald et al., 2004; Schröder-Ritzrau et al., 2005; Lartaud et al., 2019). The two species exhibit different responses to environmental changes (Naumann et al., 2014), different skeletal growth rates (Lartaud et al., 2014), reproductive cycles (Waller and Tyler, 2005), feeding strategies (Tsounis et al., 2010; Gori et al., 2014; Galand et al., 2020), and bacterial community associations (Hansson et al., 2009; Meistertzheim et al., 2016; Galand et al., 2018, 2020), with a more stable microbiome for *M. oculata*.

Coral sampling and transplant experiments have never been conducted for cold water coral microbiomes.

The general aim of this study was to test how the local habitat of *L. pertusa* and *M. oculata* impact their bacterial associations, together with other integrative parameters such as coral calcification and mortality. The study was based on *in situ* transplant experiments with sampling and redeployment of coral fragments at two contrasted sites, one deeper and one shallower, in the Lacaze-Duthiers canyon (LDC) where *L. pertusa* and *M. oculata* reefs are naturally abundant (Fiala et al., 2010; Gori et al., 2013; Lartaud et al., 2014). This multidisciplinary approach ultimately aimed at better understanding the adequacy between CWC and their surrounding environmental conditions, and thus to better assess their resilience to a changing ocean.

### MATERIALS AND METHODS

#### Study Sites

The Lacaze-Duthiers canyon, part of the Gulf of Lion Nature Marine Park, is located in the Gulf of Lion, in the northwestern part of the Mediterranean Sea. The present study focused on two different morpho-bathymetric sites of the canyon: the deeper “A” site (42°32.43N, 03°25.17E), at 530 m depth, is characterized by large colonies of *L. pertusa* and some smaller *M. oculata* colonies that grow on hard substrates outcropping the floor (Lartaud et al., 2017). The shallower “B” site (42°33.47N, 03°24.29E), is located closer to the head of the canyon, where numerous *M. oculata* colonies, together with *L. pertusa*, grow on vertical cliffs that extend from 300 to 480 m depth. This submarine canyon, is characterized by the presence of episodic dense water shelf cascade events driven by wind conditions (Canals et al., 2009).

Three different types of events are described, corresponding to autumnal storm events (stratified water masses with low intensity), winter storm events (large amount of particles), and winter cascading events (non-stratified water masses with high intensity) (Canals et al., 2006). These events lead to ventilation, changes in the temperature, current speed and transport of material such as organic matter and sediments. These events do not have the same strength at the deeper site compared to the shallow site.

#### Coral Sampling and Transplant Procedure

*Lophelia pertusa* and *M. oculata* were sampled from the deeper sites “A” at 530 m and the shallower site “B” at 380 m using a remotely operated vehicle (ROV) deployed form the R/V Minibex Vessel (COMEX SA). Coral fragments were collected in thermally insulated polypropylene boxes to maintain ambient seawater temperature (13°C) during transport to the surface. On board, colony fragments were transferred into aerated 30 L seawater tanks maintained at 13°C using a chiller. The same day, once in the laboratory, the apical parts of corals from both sites were cut with sharp pliers into different nubbins (nubbins with ~5 polyps for *L. pertusa* and ~10 polyps for
DNA Extractions and Sequencing

For Lophelia pertusa, DNA was extracted from the polyps of eight different colonies, and for M. oculata, from seven different colonies. In total, the study is based on 23 DNA samples for L. pertusa and 25 for M. oculata. For the DNA extraction, individual polyps were crushed using a hammer and the tissues were homogenized in tubes containing a garnet matrix without the large ball (Lysing Matrix A) and lysed mechanically using a FastPrep Instrument (MP, Biomedical, Santa Ana, CA, United States). DNA was extracted using the Maxwell Blood DNA Purification Kit LEV and the Maxwell 16 MDx Instrument (Promega, Madison, WI, United States). DNA concentrations were measured by spectrophotometry directly after extractions (NanoDrop ND-1000, Thermo Fisher Scientific, Waltham, MA, United States).

The V1–V3 region of the bacterial 16S rRNA genes were amplified using the primers 27F AGRGTTTGTACMTGGCTCAG modified from Lane (1991) and 519R GTNTTACNCGGCGGCGGTG modified from Lane et al. (1985) with a single step and 28 cycles of polymerase chain reaction (PCR), annealing at 53°C, using the HotStarTaq Plus Master Mix Kit (Qiagen, Valencia, CA, United States). Following the PCR, all the amplicon products from the different samples were mixed in equal concentrations and purified using Agencourt AMPure beads (Agencourt Bioscience Corporation, MA, United States). The purified PCR products were used to prepare a DNA library by following the Illumina TruSeq DNA library preparation protocol. All the samples were sequenced on the same MiSeq Illumina sequencer run (Illumina, San Diego, CA, United States) using MiSeq reagent kit V3 (Illumina) producing 2 × 300-bp long reads. PCR and sequencing were conducted in a commercial laboratory (MR DNA, Shallowater, TX, United States). All sequences were deposited in GenBank under SRA accession number PRJNA563840.

Sequence Analysis

Sequence analysis was performed with the open-source software package DADA2 (v. 1.12) in “R” to model and correct Illumina-sequenced amplicon errors (Callahan et al., 2016). We applied the standard pipeline with the following parameters: trimLeft = 20, truncLen = c(290,250), maxN = 0, maxEE = c(2.2), truncQ = 2. Thus, the sequences were filtered, dereplicated, denoised by removing sample inference and chimeras, and merged. Representative sequences were classified against the SILVA v.128 database (Quast et al., 2012) for the taxonomy assignment and to obtain amplicon sequence variants (ASVs). To produce a finer taxonomical resolution, an additional BLAST search (Altschul et al., 1990) was performed on the ASVs that were the most abundant under each transplant condition. We obtained a total of 843,483 sequences for the entire datasets, which is an average of 17,000 sequences per sample.

Statistical Analysis

Tests for normality of variance were performed using the Shapiro–Wilk test on R software (v3.4.3), which revealed that the data distribution was not normal for mortality and skeletal growth rates ($p < 0.05$). A multiple-comparison non-parametric Kruskal–Wallis test was used to analyze differences between the sites for each parameter investigated.

To compare the bacterial community composition and diversity, the sequence data were normalized by dividing counts by sample size to obtain a relative abundance. Possible differences in bacterial community composition were assessed by correspondence analysis (CA) with the vegan package in R (Oksanen et al., 2013). The Bray Curtis index (Bray and Curtis, 1957) and the Shannon diversity index (Shannon, 1948) were computed for all samples with the vegan package in R. To identify the ASVs that characterized the different samples, a simper test was applied with the plyr package in R.

RESULTS

Coral Mortality

For Madrepora oculata, polyp mortality was low when redeployed at their site of origin (Figure 1). For L. pertusa redeployed at their site of origin, there was no polyp mortality at site A, but some mortality at site B. There was no significant difference in mortality between species ($n = 66$, $p > 0.05$).

For Lophelia pertusa, there was no difference in mortality (average < 10%) between individuals that were cross transplanted from one site to another and those that were not ($n = 23$, $p > 0.05$). For M. oculata, there was a difference in mortality between the cross transplanted and non-cross transplanted corals.
The different bacterial community composition (ANOSIM, \(p < 0.001\)) of corals associated to Madrepora oculata transferred from site A to site B seemed to have a different microbiome composition, which could not be conclusive (Figure 3). Inversely, the bacterial communities of L. pertusa transferred from site A to B (AB) were composed of the phylum characterizing site B (Figure 4).

The Shannon diversity index (Shannon, 1948) showed no significant differences between the deeper and the shallower sites, but it was significantly higher in L. pertusa compared to M. oculata (\(p < 0.001\)) (Figure 5).

We further identified at the ASV level the main bacteria present in each species and at each site by SIMPER analysis (Figure 6). The four most abundant ASVs represented more than 75% of the sequences in L. pertusa and M. oculata. The ASV1 (Order Spirochetales) and ASV2 (Order Entomoplasmatales) were significantly more abundant in M. oculata while ASV3 (Order Rickettsiales) and ASV4 (Order Spirochetales) were more abundant in L. pertusa microbiomes (Figure 6). Looking at sites, ASV4 appeared relatively more abundant at site A while ASV3 was dominant in corals growing at site B. Some of these ASVs were highly similar to sequences previously retrieved from CWCs and others were distantly related to sequences found in tropical corals (Supplementary Table S1). The ASV8 (Order Rickettsiales) was typical of the site B in both coral species (88% similarity to database sequences). The ASV19 (Order Spirochetales) was characteristic of M. oculata living at site A. ASV51 (Order Rickettsiales) and ASV16 (Order Rickettsiales) were mostly present in the transplanted corals (AB) in both species. ASV16 was 100% similar to a sequence previously detected in L. pertusa (Supplementary Table S1). Finally, Endozoicomonas, a typical coral symbiont, was observed only in L. pertusa and M. oculata redeployed at their original site (Supplementary Figure S1).

Coral Bacterial Communities

The in situ experiment showed that L. pertusa and M. oculata had different bacterial community composition (ANOSIM, \(p < 0.001\)) (Figure 3). M. oculata’s bacterial communities did not differ between the two sites A and B (ANOSIM, \(p > 0.05\)). The M. oculata transferred from site A to site B seemed to have a different microbiome composition, but as only two samples were available, it could not be conclusive (Figure 3). Inversely, the bacterial communities associated to L. pertusa differed between the sites A and B (ANOSIM, \(p < 0.05\)). The coral microbiome composition of L. pertusa transferred from site A to site B (AB) was similar to the bacterial community composition of the corals growing at site B (ANOSIM, \(p > 0.05\)) (Figure 3).

At the phylum level, the M. oculata bacterial communities were mostly dominated by Spirochetae (ASV1) and Tenericutes (ASV2) with no significant differences observed between sites (ANOVA, \(p > 0.05\)) (Figure 4). Inversely, there was a difference between sites for L. pertusa. The deeper site A coral microbiome was characterized by the phylum Spirochetae (ASV4) and the shallower site B by Alphaproteobacteria (ASV3). Interestingly, the bacterial communities of L. pertusa transferred from site A to B (AB) were composed of the phylum characterizing site B (Figure 4).

Coral Growth Rates

For each coral fragment, the budding rates and the linear extension were measured (Figure 2). Overall, M. oculata had a significantly higher budding rate than L. pertusa (\(p < 0.001\)).

For Lophelia pertusa, there was no significant difference between corals growing at the two sites, although the highest budding rate values (average of 104 ± 124%) were observed for corals that originated and remained at the deeper site A (Figure 2). For M. oculata, the corals that grew on the shallower site B (averages of 200 ± 80% and 170 ± 50% for BB and AB, respectively) had significantly higher budding rates than corals at site A (averages of 100 ± 90% and 36 ± 23% for AA and BA, respectively, \(p < 0.001\)) (Figure 2).

For the linear extensions, there was overall no significant differences between species. For L. pertusa, there was no significant difference between sites but the highest values (12 ± 13 mm y\(^{-1}\)) were found at AA. For M. oculata, the non-cross transplanted corals at site B (mean of 10 ± 5 mm y\(^{-1}\) at BB) had significantly higher linear extension compared to corals from site A (mean of 6 ± 5 mm y\(^{-1}\) at AA, \(p < 0.05\)). However, there were no differences between cross transplanted and non-cross transplanted corals (Figure 2).

Our results cast a new light on the strength of the host-microbiome relationship in CWCs. Madrepora oculata, conserved overall its bacterial community composition at the ASV level across habitats, although some bacteria were only present at one of the sites. Inversely, L. pertusa had a more variable bacterial community composition that changed with habitat. Interestingly, cross transplanted L. pertusa microbiomes became similar in composition to the bacterial communities of the local L. pertusa corals. Differences in bacterial community composition have been observed earlier for L. pertusa and M. oculata at large geographical scale (Jensen et al., 2019) but also between L. pertusa from the Mediterranean Sea and a Norwegian fjord (Yakimov et al., 2006; Neuling et al., 2008). At a smaller geographical scale, there were differences in bacterial communities.
composition within the Trondheimsfjord, but they were not related to the distance between sites (Neulinger et al., 2008). The present observations of the acquisition of a local microbial signature by *L. pertusa* is new, and it opens new hypothesis about the corals’ acquisition of a microbiome. The geographical differences could result from a horizontal transfer of the bacterial community. Such transfer could give a plasticity to some coral microbiomes, which could change according to environmental conditions. This has been shown with the comparison of *Eugachipsamnia fistula* microbiomes between in situ and aquarium samples (Röthig et al., 2017). Aquarium conditions were also recently shown to transform *L. pertusa* microbiome within a day (Galand et al., 2018). Inversely, *M. oculata*’s microbiome was maintained for at least 6 months in aquaria (Galand et al., 2018). Here we thus validate in situ the previous observations made in aquaria, showing that *L. pertusa*’s bacterial community can quickly change with a changing environment. The acquisition of new microbes by *L. pertusa* may also be due to differences in nutrition that may lead to biochemical and/or metabolic differences, which in turn influence the selection of different microbial communities (Dodds et al., 2007; Schöttner et al., 2012; Meistertzheim et al., 2016). The difference in bacterial community observed between *L. pertusa* and *M. oculata* sharing the same habitat agrees with former observations for these coral species (Hansson et al., 2009; Meistertzheim et al., 2016).

Among the bacterial taxa detected in the present study, the *Entomoplasmatales* (phylum Tenericutes), which are characterized by the lack of cell walls, were previously observed in association with gorgonian corals where they dominate the assemblage (Gray et al., 2011). These bacteria were also observed in Atlantic *L. pertusa* and are supposed to play a major role for the coral (Neulinger et al., 2008; Kellogg et al., 2009). For *M. oculata*, we detected *Spirochetes*, which have not been seen earlier in this coral species. This bacterial association has already been observed with *L. pertusa* (Kellogg et al., 2009; Meistertzheim et al., 2016), *E. fistula* (Röthig et al., 2017) and with gorgonian corals from the deep sea (Gray et al., 2011; Lawler et al., 2016; van de Water et al., 2016).

Here, we also report that *L. pertusa* acquired the coral-associated *Rickettsiales* when transferred to the shallower geographic location (B site). This bacterial order has already
FIGURE 3 | Correspondence analysis (CA) of bacterial community composition based on 16S rRNA gene for L. pertusa and M. oculata. AA, coral originating from site A and redeployed at site A; AB, coral from site A and redeployed to B; BB, coral from site B and redeployed to B.

FIGURE 4 | Bacterial community composition at the phylum/class level for L. pertusa and M. oculata from different transfer sites. AA, coral originating from site A and redeployed at site A; BA, coral from site B and redeployed to A; AB, coral from site A and redeployed to B; BB, coral from site B and redeployed to B. The 10 most abundant phyla are shown and the others are grouped as “Other.”
been observed in different gorgonian and coral species (Casas et al., 2004; Gray et al., 2011; Klinges et al., 2019). This microbe was also widespread in both healthy and diseased tropical corals and may induce white band disease (Gignoux-Wolffsohn and Vollmer, 2015). Moreover, this Rickettsiales-like prokaryote from the Alphaproteobacteria group, is a Gram-negative microbe and can cause disease in invertebrates (Antonio et al., 2000). Thus, we can make the hypothesis these Rickettsiales may be opportunistic bacteria, with potential pathogens, that affect the coral development. However, considering that we are at the taxonomic level of the Order, this hypothesis has to be carefully considered.

Our work based on an in situ transplant experiment revealed difference between species following habitats. Combining microbiome results with measures of coral mortality and skeletal growth, we can suggest that M. oculata has a habitat preference, the shallower B site. In contrast, the versatile microbiome and the stable skeletal growth suggested that L. pertusa may not have such a strict habitat preference. M. oculata showed higher growth rates (i.e., budding rate and linear extension) at site B compared to site A, and its transplantation to site A reduced its growth and increased mortality. This is in accordance with field observations showing that site A (deeper) is dominated by L. pertusa reefs whereas the site B (shallower) is dominated by M. oculata reefs (personal observations). Lophelia pertusa did not show significant difference in growth rate between sites, even though the highest values were always observed at site A.

The different habitat preferences may be associated to the different physiological characteristics of the two species coupled to the different hydrological features defining the two sites in the canyon. Lophelia pertusa and M. oculata exhibit distinct physiological functions, including skeletal growth rates (Lartaud et al., 2014), feeding behavior and preferences (Tsounis et al., 2010; Galand et al., 2020), reproduction cycles (Waller and Tyler, 2005), but also distinct associated microbial communities (Meistertzheim et al., 2016). Different patterns of distribution between L. pertusa and M. oculata have been reported in the Atlantic and Mediterranean regions where M. oculata is the dominant species in the mid slope while L. pertusa is more abundant in the down slope (Foubert et al., 2011; Fabri et al., 2017; Boolukos et al., 2019). Gori et al. (2013) also reported that M. oculata was more abundant at depths shallower than 500 m in the Mediterranean canyons Cap de Creus and Lacaze-Duthiers. These previous results together with our new data suggest that M. oculata has a strong preference for shallower habitats. This may be linked to different temperature range tolerance between species with a higher sensitivity of M. oculata to lower temperatures (Naumann et al., 2014).

Both Lophelia pertusa and Madrepora oculata feed mostly on zooplankton, but it has been demonstrated that they do not share the same metabolism (Gori et al., 2014). Analyses of lipid compositions, and their nitrogen isotopic signatures, suggest that the two species adopt different feeding strategies (Kiriakoulakis et al., 2005; Galand et al., 2020). Lophelia pertusa is a more opportunistic suspended feeder, so its capacity to catch enough prey to sustain growth may be higher compared to M. oculata (Mueller et al., 2014). This could explain the more widespread occurrence of L. pertusa reefs. In addition, it has been shown that CWC capture rates depend on current regimes (Purser et al., 2010). The hydrology of the Lacaze Duthiers canyon is driven by episodic dense water shelf cascades that overflow the slope and provide food to sessile organisms as the CWCs (Ulses et al., 2008; Canals et al., 2009). However, the different morpho-bathymetric sites of the canyon are not influenced by the same water currents, and thus, the availability of food transported from the surface varies following the slope (Sanchez-Vidal et al., 2008). The current regimes in the Lacaze...
Duthiers canyon also resuspend sediments that can cover the living polyps (Durrieu de Madron et al., 2005). *Lophelia pertusa* has a great tolerance to sediments and drill cuttings (Larsson et al., 2013), and may thus thrive in impacted sites. Inversely, *M. oculata* may be more sensitive to suspended materials and may better develop at the head of the canyon on vertical cliffs, where strong currents wash away sediments. This is in accordance with earlier reports suggesting that *M. oculata* settles preferentially on areas with high topography and strong but irregular water current (Fabri et al., 2017).
CONCLUSION

We identified, through a transplant experiment, changes in L. pertusa's coral microbiome composition between two sites and the acquisition of a local coral microbial signature after transplant. This transplantation did not affect L. pertusa's skeletal growth rates but the transfer induced the acquisition of bacteria in the shallower site. Inversely, M. oculata's microbiome did not change with transplantation, but its skeletal growth was reduced. Our results suggest a higher plasticity of L. pertusa microbiome, which could explain its success across sites contrary to M. oculata which seem to harbor a habitat preference. Thus, in the context of ongoing climate change in Mediterranean Sea, both species may show different responses to changing environmental conditions.

DATA AVAILABILITY STATEMENT

The datasets generated for this study can be found in the PRJNA563840.

AUTHOR CONTRIBUTIONS

LC, NL, FL, and PG designed the study. LC, FL, and PG analyzed the data. LC, PG, NL, EP, and FL wrote the manuscript.

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SUPPLEMENTARY MATERIAL

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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