







Communication

Widespread Occurrence of a Rarely Known Association between the Hydrocorals *Stylaster roseus* and *Millepora alcicornis* at Bonaire, Southern Caribbean

Simone Montano ^{1,2,*} , James D. Reimer ^{3,4} , Viatcheslav N. Ivanenko ⁵ ,
Jaaziel E. García-Hernández ⁶ , Godfried W.N.M. van Moorsel ^{7,8} , Paolo Galli ^{1,2} and
Bert W. Hoeksema ^{9,10} 

¹ Department of Earth and Environmental Sciences (DISAT), University of Milan – Bicocca, Piazza della Scienza, 20126 Milan, Italy; paolo.galli@unimib.it

² MaRHE Center (Marine Research and High Education Center), Magoodhoo Island, 12030 Faafu Atoll, Maldives

³ Molecular Invertebrate Systematics and Ecology Laboratory, Graduate School of Engineering and Science, University of the Ryukyus, Okinawa 903-0213, Japan; jreimer@sci.u-ryukyu.ac.jp

⁴ Tropical Biosphere Research Center, University of the Ryukyus, Okinawa 903-0213, Japan

⁵ Department of Invertebrate Zoology, Biological Faculty, Lomonosov Moscow State University, 119992 Moscow, Russia; ivanenko.slava@gmail.com

⁶ Marine Genomic Biodiversity Laboratory, University of Puerto Rico - Mayagüez, La Parguera, PR 00667, USA; jaaziel.garcia@upr.edu

⁷ Ecosub, Berkenlaantje 2, 3956 DM Leersum, The Netherlands; vanmoorsel@ecosub.nl

⁸ ANEMOON Foundation, P.O. Box 29, 2120 AA Bennekom, The Netherlands

⁹ Taxonomy and Systematics Group, Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands; bert.hoeksema@naturalis.nl

¹⁰ Groningen Institute for Evolutionary Life Sciences, University of Groningen, P.O. Box 11103, 9700 CC Groningen, The Netherlands

* Correspondence: simone.montano@unimib.it; Tel.: +39-02-6448-2050

Received: 14 May 2020; Accepted: 29 May 2020; Published: 30 May 2020



Abstract: Among symbiotic associations, cases of pseudo-auto-epizoism, in which a species uses a resembling but not directly related species as substrate, are poorly documented in coral reef ecosystems. In the present study, we assessed the distribution of an association between the hydrocorals *Stylaster roseus* and *Millepora alcicornis* on about 50% of coral reef sites studied in Bonaire, southern Caribbean. Although previously thought to be uncommon, associations between the lace coral *S. roseus* and the fire coral *M. alcicornis* were observed at both the windward and leeward sides of Bonaire, mainly between 15 and 25 m depth, reaching a maximum occupation of 47 *S. roseus* colonies on a single *M. alcicornis* colony. Both species' tissues did not show any signs of injuries, while an in-depth inspection of the contact points of their skeletons revealed that both partners can partially overgrow each other. How it is possible that *S. roseus* is able to settle on the stinging tissue of *Millepora* as well as how, by contrast, the latter may facilitate the lace coral by offering a certain degree of protection are questions that deserve further investigations.

Keywords: Caribbean Netherlands; fire corals; Hydrozoa; pseudo-auto-epizoism; stony corals; substrate; symbiosis

1. Introduction

As one of the most species-rich marine ecosystems, coral reefs are renowned for their plethora of different interspecific associations [1]. Reef-building corals serve as home for diverse assemblages of macro- and micro-organisms from all kingdoms of life [2], which rely on them for food, shelter and substrate [3–5].

To date, reef-building corals belonging to the order Scleractinia account for the majority of host species studied [3], although other hosts of other benthic groups exist, such as anthozoans, bryozoans, sponges, ascidians and hydrocorals.

Regarding hydrocorals (Class Hydrozoa), the genus *Millepora* Linnaeus, 1758 (Suborder Capitata) occurs as a circumtropical component of shallow-water coral reefs [6–11]. Milleporids are found in depths of less than 1 m to about 40 m and provide substratum for sedentary organisms and food or shelter for mobile ones [12–16]. The three-dimensional structural complexity of the colonies generated by in particular branching *Millepora* species harbors a great diversity of organisms that includes crustaceans, worms, fishes and other organisms that live in close association [12–14].

Similar to *Millepora*, hydrocorals belonging to the family Stylasteridae (Suborder Filifera), commonly known as “lace corals”, are colonial hydroids characterized by a calcium carbonate skeleton, with 90% of the species occurring at depths over 50 m [17]. Their colonies are generally erect and branching with only the Pacific genus *Stylantheca* Fisher, 1931 having an encrusting morphology [18]. Most lace corals, including those of the genus *Stylaster* Gray, 1831, are known to form strict relationships with other invertebrates [18,19]. Stylasterids are host of a number of commensals such as polychaetes [20–22], nemerteans, pycnogonids, cirripids, barnacles, and bryozoans [23,24]. In addition to these, six species of gall living siphonostomatoid copepods of the family Asterocheridae [25,26] and tiny ovulid gastropods of the genus *Pedicularia* Swainson, 1840 are known to be obligate symbionts on various stylasterid species [27,28].

Among interspecific relationships involving hydrozoans, a minority includes a hydrozoan-hydrozoan association that has been classified as auto-epizoism, even though the two partners do not belong to the same species [29,30]. Indeed, several hydroids are known to live epizootically on other hydroids, usually using the other as a solid substratum, e.g., members of the genera *Hebella* Allman, 1888 and *Anthohebella* Boero, Bouillon & Kubota 1997 can be observed on the perisarc of other hydroid species [31,32].

Currently no information is present about a possible association between *Stylaster* and *Millepora*, although two earlier observations have been reported from the southern and eastern Caribbean [33,34]. Here we investigated the distribution and abundance of the association between *Stylaster roseus* (Pallas, 1766) and *Millepora alcicornis* Linnaeus, 1758 found during a biodiversity expedition conducted at Bonaire, in the Dutch Caribbean. In addition, an in-depth morphological analysis of the skeleton interactions between both partners is provided.

2. Materials and Methods

The study was conducted in the waters of Bonaire from October to November 2019. We explored 34 localities, chosen randomly among accessible sites (Figure 1; Table S1). The presence of the *Stylaster-Millepora* association was recorded by applying the roving diving technique with scuba, in which a 1-h dive served as the sampling unit, by starting at the maximum depth at each dive locality (15–35 m) and moving to shallower water from there [35]. Even though the information collected from this timed dive method does not result in quantitative data per site, it is particularly useful when the goal of the study is to compare biodiversity among site via finding as many species as possible, or when looking for small and/or cryptic species and symbiotic associations [36]. Moreover, to preliminarily assess the abundance and spatial distribution of this association, the total number of *Stylaster-Millepora* associations and their depth ranges were recorded for each site. In addition, the total numbers of colonies of *S. roseus* found to grow on each *M. alcicornis* colony were noted. For documentation purposes underwater photographs of the *Stylaster-Millepora* association were taken using a Canon GX7 Mark II camera in a Fantasea GX7 II underwater housing and a Nikon D7100 in a Hugyfot housing.

A branch fragment of about 10 cm in length of *M. alvicornis* colonized by *S. roseus* was collected for further analyses. Microphotographs ($\times 32$) of stylasterids growing on the coral skeletons of *M. alvicornis* were taken using a Leica EZ4 D stereo microscope equipped with a Canon GX7 Mark II camera. Several parts of the fragment were observed using the Zeiss Gemini SEM500 scanning electron microscope operating at beam energies of 5 kV (ZEISS, Oberkochen, Germany) in order to characterize the skeletal interface/interactions of the association.

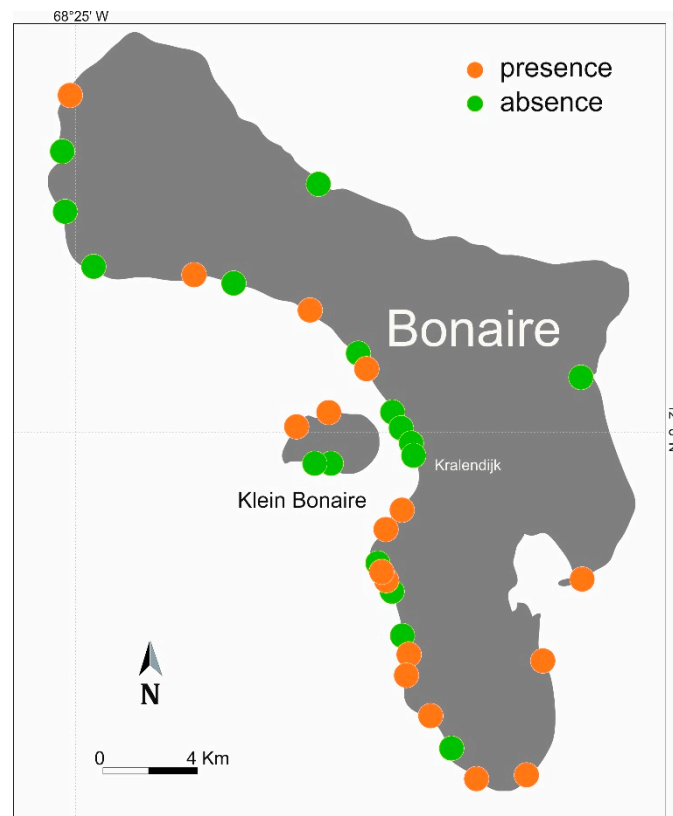


Figure 1. Map of Bonaire island showing locations where the *Stylaster-Millepora* association was found among all sites surveyed.

3. Results and Discussion

Bonaire is known for its rich coral reef ecosystem, considered as one of the healthiest and most resilient in the Caribbean [37], and therefore it serves as a major tourist destination for scuba divers and snorkellers. In spite of being one of the most popular diving spots in the Caribbean [38,39], this is the first time that the *Stylaster-Millepora* association has been reported. Moreover, to the best of our knowledge, this is the first report that preliminarily assesses abundance, depth distribution and skeleton interactions involving both partners.

Our biodiversity survey revealed that the *Stylaster-Millepora* association was found at 17 out of 34 (50%) of the sites explored (Figure 1; Table S1). Interestingly, this apparently uncommon association seems to be relatively abundant and widespread on Bonaire's coral reefs. In fact, it was observed at both the windward and leeward sides of Bonaire, despite the reefs along the island's windward shores being generally less developed compared to those of the leeward coast [40].

In particular, *S. roseus* and *M. alvicornis* were observed to form strict relationships (Figure 2a) in depths ranging from 13 to 32 m. In total we counted 55 colonies of *M. alvicornis* hosting *S. roseus* with the highest number of records ($n = 37$) between 15–25 m depths. Again, the density of *S. roseus* colonies on *M. alvicornis* colonies ranged from one to at least 47 for the largest fire coral colonies (Figure 2b; Table S1). The observed pattern is not surprising since a high diversity of associated

invertebrates has been reported from the complex structure of *M. alcicornis*, showing high numbers of individuals, which appear to be directly related to the volume of the host colony [14]. Moreover, additional observations made using a stereo microscope revealed the presence of newly settled single-cyclosystem colonies (Figure 2c), which were not observable with the naked eye. This suggests that the number of *S. roseus* colonies present on each single *M. alcicornis* coral is probably higher than observed. Because *Millepora* and *Stylaster* represent different families of hydrocorals, Milleporidae and Stylasteridae, that only resemble each other by forming a calcareous skeleton, while both belong to different suborders, their relation is not considered an example of auto-epizoism but the first case of what can be considered pseudo-auto-epizoism.

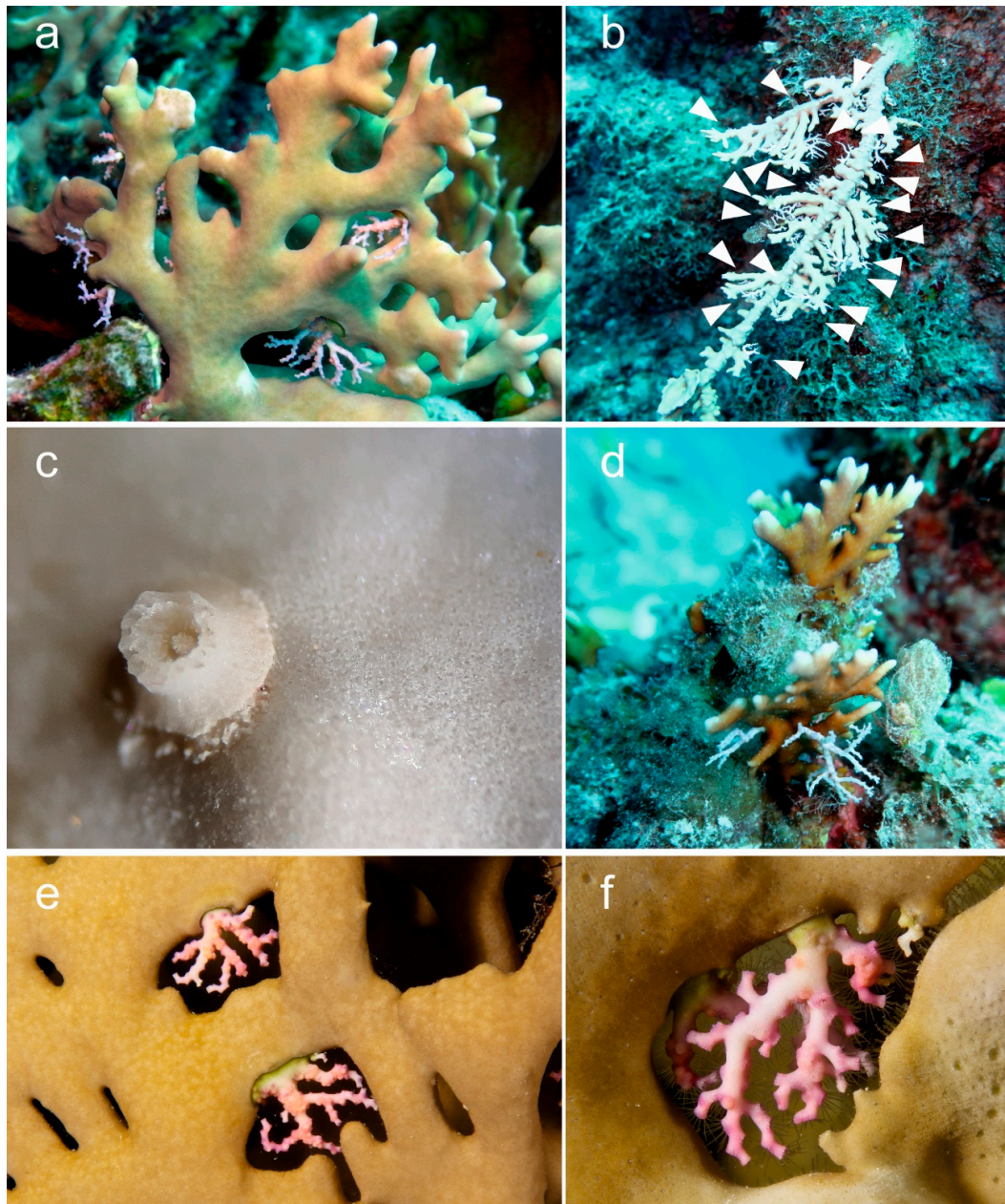


Figure 2. *Stylaster-Millepora* association. (a) Overview of field appearance; (b) high number of *S. roseus* colonies growing on a *M. alcicornis* colony; (c) a single *S. roseus* recruit on *M. alcicornis*; (d) exposure of *S. roseus* when overgrowing a fire coral colony; (e,f) peculiar pattern of *S. roseus* and *M. alcicornis* growth and close-up of both colonies with extended polyps.

Exploring the position of the association we noted that most *S. roseus* colonies were clearly located in the upper parts or in windows between the anastomose branches of *M. alcicornis*, while they were always abnormally exposed (Figure 2d). This is remarkable because, typically, *S. roseus* is a very cryptic species, inhabiting shaded crevices of the reef or the dead underside of foliaceous corals [33]. Occasionally they are found underneath overhangs or large rocks in shallow water (<3 m depth) where the colonies are more exposed to light and wave action (Figure S1). However, in these particular cases, when associated with *M. alcicornis*, the lace corals are completely exposed with colonies protruding upwards or toward the maximum exposition of water motion.

In addition, another interesting pattern was observed. In the portions of the colonies of *M. alcicornis* where *S. roseus* are located both species appear to grow in synchrony by creating a specular shape of the main three-dimensional structure of the colonies (Figure 2e). In this case, if it is *S. roseus* that limits the growth of *M. alcicornis* or, in contrast, if *S. roseus* simply fills the gaps between the anastomosing *Millepora* branches, both seem to be valid hypotheses. In this context, we highlight how, in the majority of the cases, the polyps of *S. roseus* and *M. alcicornis* were frequently observed extended at the same time (Figure 2f). However, in all our observations no evidence of injuries to either species were detected. In fact, in this scenario, both partners do not seem to trigger the stinging cells of polyps of their partner species despite potentially being in contact. It may be that the well-known stinging properties of *Millepora* fire corals may facilitate this association by conferring a certain degree of protection. This is currently unknown and worthy of further investigations.

The patterns observed at the edge of both tissues also deserve attention. In this case, no apparent inflammation status or stressed condition related to adjacent growth of the partner was found (Figure 3a). In contrast, on a macroscopic scale, the tissues of both partners seem to attach so tightly that the boundaries between them almost appear to have disappeared (Figure 3b).

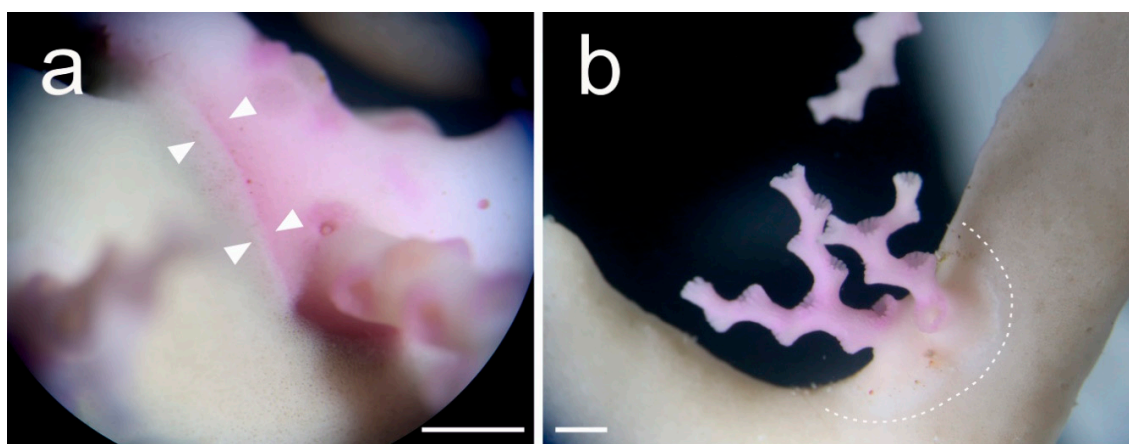


Figure 3. (a) Apparently healthy tissue of both partners when intimately close, and (b) the undefined borders/edges between the two hydrocorals' tissues. (Scale bars ~ 2 mm).

An in-depth inspection of the skeletons showed that the skeleton tissue of *M. alcicornis* can overgrow that of *S. roseus* and may limit its growth (Figure 4a,b). In contrast, in some other observations it was evident that the skeleton tissue of *S. roseus* also easily overgrows that of *M. alcicornis*, extending the colony above the *M. alcicornis* tissue and producing an enlarged basal disc from which new cyclosteams arise (Figure 4c,d). Although both mechanisms can be deduced by the observation of the growth patterns of the skeletons, we found also a portion of the interface between the two colonies that appeared literally fused, on which the edges of both species were almost undefined (Figure 4e,f).

In colonies of *M. alcicornis*, the stinging cells in the epidermis can form a barrier against the larval settlement [33], but this does not seem to prevent settlement of new *S. roseus* recruits. The early development stages of the new coenosteum after planulae settlement are known in only a few stylasterid species. Ostarello [41] studied the natural history of *Stylaster* sp. and observed that after release,

the planula generally crawled for a short time around the parental colony before settling close to it. How *S. roseus* larvae can settle on *M. alcicornis* in the present case is not understood.

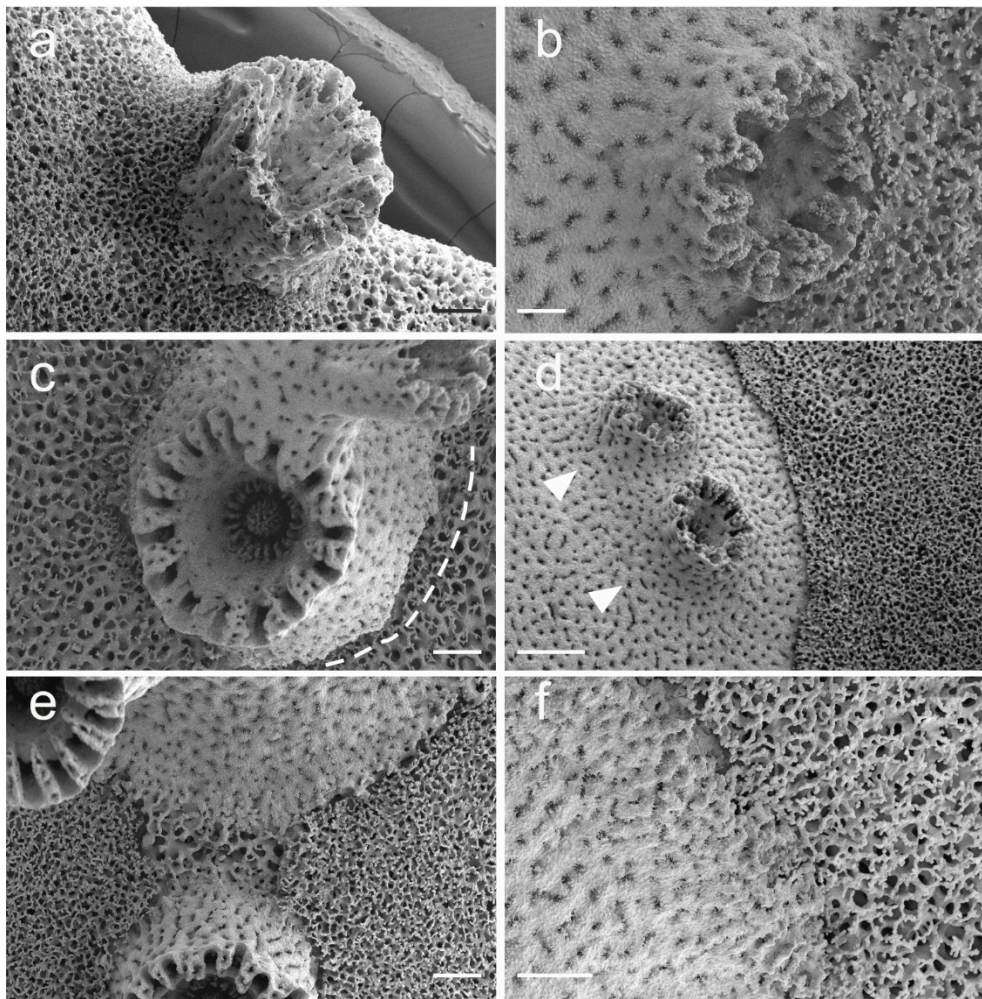


Figure 4. SEM analyses revealed (a,b) the capacity of *Millepora alcicornis* to overgrowth *Styaster roseus*; (c,d) the capacity of *S. roseus* to overgrowth on *M. alcicornis*; (e,f) the apparently intimately connection of both skeletons in some parts of the associations. (Scale bars: a–c ~100 μ m; d ~200 μ m; e–f ~100 μ m).

Furthermore, it would be intriguing to investigate the advantages of *S. roseus* in colonizing *M. alcicornis*. In fact, despite the fact that this fire coral species has many different growth morphologies [42,43] (Figure S2a,b), with branches often becoming anastomose (Figure S2c) and crucial in providing many different places where *S. roseus* may settle, the higher growth rate of *M. alcicornis* [44] may also results in a total overgrowth of *S. roseus* colonies (Figure S2d).

By contrast, the “sheet-tree” morphology of *M. alcicornis* (sensu [44]) appears to have a number of beneficial consequences as the role in competitive interactions, zooplanktivory, and asexual reproduction [45] that may be potentially vital for the lace coral. Thus, we cannot exclude that *S. roseus* may exploit *M. alcicornis* to increase its capture of zooplankton, taking advantages of the greater asexual reproduction of *M. alcicornis* in order to support its natural turnover, as well as to increase the spatial diffusion of the species and to reduce the conspecific competition.

In conclusion, it will be necessary to understand how this association affects both partners and how it is of benefit to both of them. Although elucidating the nature of the diverse types of symbiotic interactions is not always easy, it has already been demonstrated that symbionts may play an active role in protecting their hosts from various stresses [46–48]. Further investigations on the nature of

this *S. roseus* and *M. alcicornis* association will undoubtedly provide more insights into the nature of symbioses on coral reefs.

Moreover, since we cannot rule out the possibility that our results may not be representative of large-scale patterns valid for the whole Bonaire reef, we hope that our preliminary data will promote future in-depth ecological investigations focusing on this association.

Supplementary Materials: The following are available online at <http://www.mdpi.com/1424-2818/12/6/218/s1>, Figure S1. *Stylaster rosesus* in its natural habitat. Figure S2. Different growth morphologies of *M. alcicornis*. Table S1. List of locations and number of associations recorded for each site sampled.

Author Contributions: Conceptualization, S.M. and B.W.H.; methodology, S.M.; investigation, S.M., J.D.R., V.N.I., J.E.G.-H.; resources, B.W.H., P.G., G.W.N.M.v.M.; data curation, S.M.; writing—original draft preparation, S.M., B.W.H., J.D.R.; All authors have read and agreed to the published version of the manuscript.

Funding: The fieldwork in Bonaire was supported by a grant from the WWF-Netherlands Biodiversity Fund to BWH.

Acknowledgments: S.M., J.D.R., V.N.I., and J.E.G.-H. are grateful to Naturalis Biodiversity Center for supporting fieldwork in Bonaire (2019). We are grateful to STINAPA and DCNA at Bonaire for assistance in the submission of the research proposal and the research permit. S.M. would like to express his sincere gratitude to Morena Nava for the precious support provided.

Conflicts of Interest: The authors declare no conflict of interest.

References

- Gates, R.D.; Ainsworth, T.D. The nature and taxonomic composition of coral symbiomes as drivers of performance limit in scleractinian corals. *J. Exp. Mar. Biol. Ecol.* **2011**, *408*, 94–101. [[CrossRef](#)]
- Rohwer, F.; Breitbart, M.; Jara, J.; Azam, F.; Knowlton, N. Diversity of bacteria associated with the Caribbean coral *Montastraea franksi*. *Coral Reefs* **2001**, *20*, 85–91.
- Stella, J.S.; Pratchett, M.S.; Hutchings, P.A.; Jones, G.P. Coral-associated invertebrates: Diversity, ecological importance and vulnerability to disturbance. *Oceanogr. Mar. Biol. Annu. Rev.* **2011**, *49*, 43–116.
- Hoeksema, B.W.; van der Meij, S.E.T.; Fransen, C.H.J.M. The mushroom coral as a habitat. *J. Mar. Biol. Assoc. U. K.* **2012**, *92*, 647–663. [[CrossRef](#)]
- Hoeksema, B.W. The hidden biodiversity of tropical coral reefs. *Biodiversity* **2017**, *18*, 8–12. [[CrossRef](#)]
- De Souza, J.N.; Nunes, F.L.D.; Zilberberg, C.; Sanchez, J.A.; Migotto, A.E.; Hoeksema, B.W.; Serrano, X.M.; Baker, A.C.; Lindner, A. Contrasting patterns of connectivity among endemic and widespread fire coral species (*Millepora* spp.) in the tropical Southwestern Atlantic. *Coral Reefs* **2017**, *36*, 701–716. [[CrossRef](#)]
- Arrigoni, R.; Maggioni, D.; Montano, S.; Hoeksema, B.W.; Seveso, D.; Shlesinger, T.; Terraneo, T.I.; Tietbohl, M.D.; Berumen, M.I. An integrated morpho-molecular approach to delineate species boundaries of *Millepora* from the Red Sea. *Coral Reefs* **2018**, *37*, 967–984. [[CrossRef](#)]
- Takama, O.; Fernandez-Silva, I.; López, C.; Reimer, J.D. Molecular phylogeny demonstrates the need for taxonomic reconsideration of species diversity of the hydrocoral genus *Millepora* (Cnidaria: Hydrozoa) in the Pacific. *Zool. Sci.* **2018**, *35*, 123–133. [[CrossRef](#)]
- Boissin, E.; Pogoreutz, C.; Pey, A.; Gravier-Bonnet, N.; Planes, S. *Millepora platyphylla* (Cnidaria, Hydrozoa) range extended back to the Eastern Pacific, thanks to a new record from Clipperton Atoll. *Zootaxa* **2019**, *4668*, 599–600. [[CrossRef](#)]
- Rodríguez, L.; López, C.; Casado-Amezua, P.; Ruiz-Ramos, D.V.; Martínez, B.; Banaszak, A.; Tuya, F.; García-Fernández, A.; Hernández, A. Genetic relationships of the hydrocoral *Millepora alcicornis* and its symbionts within and between locations across the Atlantic. *Coral Reefs* **2019**, *38*, 255–268. [[CrossRef](#)]
- Boissin, E.; Leung, J.K.L.; Denis, V.; Bourmaud, C.A.F.; Gravier-Bonnet, N. Morpho-molecular delineation of structurally important reef species, the fire corals, *Millepora* spp., at Réunion Island, Southwestern Indian Ocean. *Hydrobiologia* **2020**, *847*, 1237–1255. [[CrossRef](#)]
- Lewis, J.B. Biology and ecology of the hydrocoral *Millepora* on coral reefs. *Adv. Mar. Biol.* **2006**, *50*, 1–55. [[PubMed](#)]
- García, T.M.; Matthews-Cascon, H.; Franklin-Junior, W. Macrofauna associated with branching fire coral *Millepora alcicornis* (Cnidaria: Hydrozoa). *Thalassas* **2008**, *24*, 11–19.

14. Garcia, T.M.; Matthews-Cascon, H.; Franklin-Junior, W. *Millepora alcicornis* (Cnidaria: Hydrozoa) as substrate for benthic fauna. *Braz. J. Oceanog.* **2009**, *57*, 153–155. [[CrossRef](#)]
15. Hoeksema, B.W.; Ten Hove, H.A. The invasive sun coral *Tubastraea coccinea* hosting a native Christmas tree worm at Curaçao, Dutch Caribbean. *Mar. Biodivers.* **2017**, *47*, 59–65. [[CrossRef](#)]
16. Hoeksema, B.W.; García-Hernández, J.E. Host-related morphological variation of dwellings inhabited by the crab *Domecia acanthophora* in the corals *Acropora palmata* and *Millepora complanata* (Southern Caribbean). *Diversity* **2020**, *12*, 143. [[CrossRef](#)]
17. Cairns, S.D. Deep-water corals: An overview with special reference to diversity and distribution of deep-water scleractinian corals. *Bull. Mar. Sci.* **2007**, *81*, 311–322.
18. Cairns, S.D. Global diversity of the Stylasteridae (Cnidaria: Hydrozoa: Athecatae). *PLoS ONE* **2011**, *6*, e21670. [[CrossRef](#)]
19. Pica, D.; Cairns, S.D.; Puce, S.; Newman, W.A. Southern hemisphere deep-water stylasterid corals including a new species, *Errina labrosa* sp. n. (Cnidaria, Hydrozoa, Stylasteridae), with notes on some symbiotic scalpellids (Cirripedia, Thoracica, Scalpellidae). *ZooKeys* **2015**, *472*, 1–25. [[CrossRef](#)]
20. Light, W.J. *Polydora allopuris*, new species, a commensal spionid (Annelida, Polychaeta) from a hydrocoral off Central California. *Proc. Cal. Acad. Sci.* **1970**, *37*, 459–472.
21. Pettibone, M.H. Polynoid commensals with gorgonian and stylasterid corals, with a new genus, new combinations, and new species (Polychaeta: Polynoidae: Polynoinae). *Proc. Biol. Soc. Wash.* **1991**, *104*, 688–713.
22. Martin, D.; Britayev, T.A. Symbiotic polychaetes revisited: An update of the known species and relationships (1998–2017). *Oceanogr. Mar. Biol. Ann. Rev.* **2018**, *56*, 371–448.
23. Zibrowius, H. Associations of Hydrocorallia Stylasterina with gall-inhabiting Copepoda Siphonostomatoidea from the South-West Pacific. Part 1. On the stylasterine hosts, including two new species, *Stylaster papuensis* and *Crypthelia cryptotrema*. *Bijdr Dierk* **1981**, *51*, 268–286.
24. Zibrowius, H.; Cairns, S.D. Revision of the Northeast Atlantic and Mediterranean Stylasteridae (Cnidaria: Hydrozoa). *Mém Mus Nat Hist Nat. Ser. A* **1992**, *153*, 1–136.
25. Stock, J.H. Associations of Hydrocorallia Stylasterina with gall-inhabiting Copepoda Siphonostomatoidea from the South-West Pacific. Part II. On six species belonging to four new genera of the copepod family Asterocheridae. *Bijdr. Dierk.* **1981**, *51*, 287–312.
26. Stock, J.H. On the presence of gall-inducing Copepoda on stylasterine corals.—Proceedings of the First International Conference on Copepoda. *Studies on Copepoda II. Crustaceana* **1984**, *7*, 377–380.
27. Goud, J.; Hoeksema, B.W. *Pedicularia vanderlandi* spec. nov., a symbiotic snail (Caenogastropoda; Ovulidae) on the hydrocoral *Distichopora vervoorti* Cairns and Hoeksema, 1998 (Hydrozoa; Stylasteridae), from Bali, Indonesia. *Zool. Verh.* **2001**, *334*, 77–97.
28. Wisshak, M.; López Correa, M.; Zibrowius, H.; Jakobsen, J.; Freiwald, A. Skeletal reorganisation affects geochemical signals, exemplified in the stylasterid hydrocoral *Errina dabneyi* (Azores Archipelago). *Mar. Ecol. Prog. Ser.* **2009**, *397*, 197–208. [[CrossRef](#)]
29. Millard, N.A.H. Auto-epizoism in South African hydroids. In: Recent trends in research in Coelenterate biology. Proceedings of the Second International Symposium on Cnidaria. *Publ. Seto Mar. Biol. Lab.* **1973**, *20*, 23–34. [[CrossRef](#)]
30. Galea, H.R.; Leclère, L. On some morphologically aberrant, auto-epizootic forms of *Plumularia setacea* (Linnaeus, 1758) (Cnidaria: Hydrozoa) from southern Chile. *Zootaxa* **2007**, *1484*, 39–49. [[CrossRef](#)]
31. Boero, F.; Bouillon, J.; Kubota, S. The medusae of some species of *Hebella* Allman, 1888, and *Anthohebella* gen. nov. (Cnidaria, Hydrozoa, Lafoeidae), with a world synopsis of species. *Zool. Verh.* **1997**, *310*, 1–53.
32. Bouillon, J.; Gravili, C.; Pagès, F.; Gili, J.M.; Boero, F. An introduction to Hydrozoa. *Mém. Mus. Nat. Hist. Nat.* **2020**, *194*, 1–591.
33. Sánchez, J.A.; Nava, G.R. Note on the distributions, habitat and morphology of *Stylaster roseus* (Pallas 1766) (Hydrozoa; Stylasterina) in the Colombian Caribbean. *Bol. Investig. Mar. Cost.* **1994**, *23*, 193–197.
34. Hoeksema, B.W.; van Moorsel, G.W.N.M. Stony corals of St. Eustatius. In *Marine Biodiversity Survey of St. Eustatius, Dutch Caribbean, 2015*; Hoeksema, B.W., Ed.; Naturalis Biodiversity Center: Leiden, The Netherlands, 2016; pp. 32–37.
35. Hoeksema, B.W.; Koh, E.G.L. Depauperation of the mushroom coral fauna (Fungiidae) of Singapore (1860s–2006) in changing reef conditions. *Raffles. Bull. Zool. Suppl.* **2009**, *22*, 91–101.

36. Reimer, J.D.; Wee, H.B.; García-Hernández, J.E.; Hoeksema, B.W. Zoantharia (Anthozoa: Hexacorallia) abundance and associations with Porifera and Hydrozoa across a depth gradient on the west coast of Curaçao. *Syst. Biodivers.* **2018**, *16*, 820–830. [[CrossRef](#)]
37. IUCN. *Coral Reef Resilience Assessment of the Bonaire National Marine Park, Netherlands Antilles*; International Union for Conservation of Nature: Gland, Switzerland, 2011; p. 51.
38. Parsons, G.; Thur, S. Valuing changes in the quality of coral reef ecosystems: A stated preference study of scuba diving in the Bonaire National Marine Park. *Environ. Resour. Econ.* **2008**, *40*, 593–608. [[CrossRef](#)]
39. Jackson, J.B.C.; Donovan, M.; Cramer, K.; Lam, V. (Eds.) *Status and Trends of Caribbean Coral Reefs: 1970–2012*; Global Coral Reef Monitoring Network, International Union for the Conservation of Nature Global Marine and Polar Program: Washington, DC, USA, 2014.
40. Bak, R.P.M. Ecological aspects of the distribution of reef corals in the Netherlands Antilles. *Bijdr. Dierk.* **1975**, *45*, 181–190. [[CrossRef](#)]
41. Ostarello, G.L. Natural history of the hydrocoral *Allopora californica* Verrill (1866). *Biol. Bull. Mar. Biol. Lab. Woods Hole* **1973**, *145*, 548–564. [[CrossRef](#)]
42. Boschma, H. The species problem in *Millepora*. *Zool. Verh.* **1948**, *1*, 1–115.
43. de Weerd, W.H. Taxonomic characters in Caribbean *Millepora* species (Hydrozoa, Coelenterata). *Bijdr. Dierk.* **1984**, *54*, 243–262. [[CrossRef](#)]
44. Edmunds, P.J. The role of colony morphology and substratum inclination in the success of *Millepora alcicornis* on shallow coral reefs. *Coral Reefs* **1999**, *18*, 133–140. [[CrossRef](#)]
45. Sebens, K.P.; Witting, J.; Helmuth, B. Effects of water flow and branch spacing on particle capture by the reef coral *Madracis mirabilis* (Duchassaing and Michelotti). *J. Exp. Mar. Biol. Ecol.* **1997**, *211*, 1–28. [[CrossRef](#)]
46. Glynn, P.W. Increased survivorship in corals harboring crustacean symbionts. *Mar. Biol. Lett.* **1983**, *4*, 105–111.
47. Hoeksema, B.W.; van Beusekom, M.; ten Hove, H.A.; Ivanenko, V.N.; van der Meij, S.E.T.; van Moorsel, G.W.N.M. *Helioseris cucullata* as a host coral at St Eustatius, Dutch Caribbean. *Mar. Biodivers.* **2017**, *47*, 71–78. [[CrossRef](#)]
48. Montano, S.; Fattorini, S.; Parravicini, V.; Berumen, M.L.; Galli, P.; Maggioni, D.; Arrigoni, R.; Seveso, D.; Strona, G. Corals hosting symbiotic hydrozoans are less susceptible to predation and disease. *Proc. R. Soc. B* **2017**, *284*, 20172405. [[CrossRef](#)]

