


A mesophotic hotel: the octocoral *Bebryce* cf. *grandicalyx* as a host

DAVIDE MAGGIONI ^{1,2,4} SIMONE MONTANO,^{1,2}
OLIVER VOIGT,³ DAVIDE SEVESO^{1,2} AND PAOLO GALLI^{1,2}

Manuscript received 22 August 2019; revised 10 October 2019; accepted 12 November 2019. Corresponding Editor: John Pastor.

¹Dipartimento di Scienze dell'Ambiente e della Terra (DISAT), Università degli Studi di Milano-Bicocca, 20126 Milano, Italy.

²Marine Research and High Education (MaRHE) Center, Università degli Studi di Milano-Bicocca, 12030 Faafu Magoodhoo Island, Republic of Maldives.

³Department of Earth and Environmental Sciences, Palaeontology and Geobiology, Ludwig-Maximilians-Universität München, 80333 München, Germany.

⁴E-mail: davide.maggioni@unimib.it

Citation: Maggioni, D., S. Montano, O. Voigt, D. Seveso, and P. Galli. 2019. A mesophotic hotel: the octocoral *Bebryce* cf. *grandicalyx* as a host. *Ecology* 00(00):e02950. [10.1002/ecy.2950](https://doi.org/10.1002/ecy.2950)

Key words: *Maldives*; *mesophotic coral ecosystem*; *Suberitidae*; *symbiosis*; *Zanclaea timida*.

Mesophotic coral ecosystems are widespread and harbor rich coral reef communities below 30 m and down to 150-m depth (Puglise et al. 2009). Although in recent years the knowledge of these charismatic ecosystems has increased (Khang et al. 2014), many aspects are still to be explored, including, for instance, symbiotic associations. Sessile reef invertebrates are known to host a multitude of organisms in shallow waters (e.g., Hoeksema et al. 2012), and this may be likewise extended to mesophotic organisms. For instance, both shallow and deep-water octocorals are known to form a large variety of associations with micro-organisms, invertebrates, and vertebrates (Goh et al. 1999, Buhl-Mortensen and Mortensen, 2004), including host-specific relationships (e.g., Montano et al. 2017a). In a few cases, these associations include commensalistic, mutualistic, and parasitic interactions (Watling et al. 2011).

During surveys of the upper mesophotic reef of Faafu Dharanboodhoo Island, Republic of Maldives (3.059 N, 72.927 E), in February 2016 and January 2017, a previously unreported association was discovered. The organisms involved in the association were identified, through combined morphological and molecular analyses

(European Nucleotide Archive accession numbers: LR732019–LR732022), as the octocoral *Bebryce* cf. *grandicalyx*, a sponge belonging to the family Suberitidae, and the hydrozoan *Zanclaea timida*. The three species were not found at shallower depths in the investigated area, alone or in association, suggesting that the upper distributional limit of these organisms is represented by the sampling depth, that is, the upper mesophotic.

The octocoral was commonly found along the reef at depths ranging from 40 to 50 m, perpendicular to the prevailing currents (Fig. 1a). A closer inspection of the colonies revealed the presence of two common associates. In all cases ($n = 50$), the octocoral colony was overgrown by the demosponge. Usually, the sponge fully covered the octocoral, reaching the rim of the calyces and leaving only the polyps uncovered (Fig. 1b); sporadically, small portions of the octocoral surface remained free of the poriferan (Fig. 1c). In over 70% of the observed octocoral–sponge associations, hydrozoan polyps were found as additional epibionts on the octocoral (Fig. 1d). *Zanclaea timida* appeared as colonies of stolonal polyps, interconnected through a creeping hydrorhiza running over the octocoral surface (Puce et al. 2008). Hydroids reached high densities, covering almost all the available space, except for octocoral polyps. The hydrorhiza, as well as the proximal portion of hydroids, were embedded in the sponge, which covered up to half of the hydranths (Fig. 1e, Appendix S1: Fig. S1). *Zanclaea timida* colonies were observed to bear medusa buds on their basal part, below the sponge layer (Fig. 1f). A few medusae were released during laboratory observations, indicating that they can set themselves free from the sponge.

Intimate associations involving octocorals, sponges, and hydrozoans two by two have been already described in previous works (e.g., Calcinaï et al. 2013, Maggioni et al. 2016, 2017), but never forming the three-way relationship observed herein. The three organisms seem here well integrated with each other in a stable way, given the high prevalence of the association, especially for octocorals and sponges. A parasitic interaction seems to be excluded, because no detrimental effect for any of the associates could be observed. Indeed, octocoral colonies did not show any association-related damage and the polyps were able to extend without being hampered by the sponge and hydroids. Instead, both the sponge and hydroids may provide their host with additional defense from predators. For instance, sponges associated with the octocoral *Carijoa riisei* in Hawai'i suppress nudibranch predation, probably because of the production of toxic compounds (Wagner et al. 2009), and *Zanclaea* polyps associated with scleractinian corals likely protect their hosts from gastropod and fish predation, thanks to their

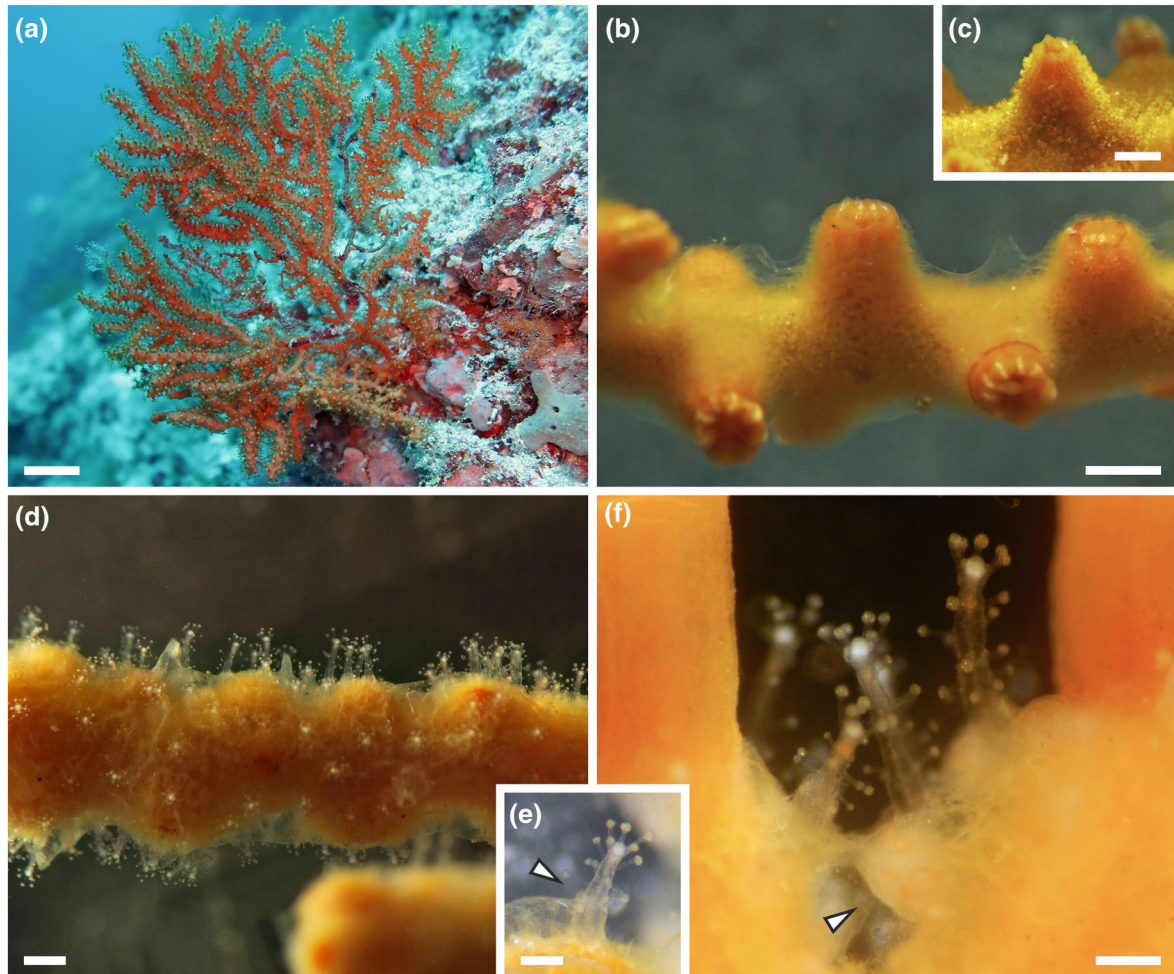


FIG. 1. Three-way association between *Bebryce* cf. *grandicalyx*, a suberitid sponge, and *Zanclea timida*. (a) General view of the octocoral colony. (b, c) Portion of the octocoral (b) covered and (c) not covered by the sponge. (d) Hydroids growing on the octocoral and partially embedded in the sponge. (e) Closeup of a hydroid surrounded by the sponge (arrowhead). (f) Hydroids bearing medusa buds below the sponge layer (arrowhead). Scale bars: (a) 3 cm, (b-d) 1 mm, (e, f) 0.3 mm.

additional nematocyst complement (Montano et al. 2017b). In the association reported here, these two acquired defensive mechanisms may act in synergy to protect the octocoral and each of its associates from multiple sources of predation and overgrowth by other organisms.

Furthermore, because colonies of *Z. timida* were only found in association with *B. cf. grandicalyx* and the suberitid sponge in the investigated area, the relationships may be obligate for the hydroid. This hydrozoan species has been previously reported only once, from Indonesia, and associated with the octocoral *Paratelesto* sp. but not with sponges (Puce et al. 2008), supporting the hypothesis of its obligate association at least with octocorals. The hydroids may exploit the position of the octocoral to increase their access to planktonic preys and they may take advantage of locally generated currents that are produced by the filtering activity of the sponge. Additionally,

the poriferan may protect the hydroids, allowing their withdrawal within the sponge layer, and may give shelter to immature medusa buds before their release.

Because the sponge was always found overgrowing the octocoral, it is likely taking advantage from this association. By growing on the octocoral, the sponge results in a hydrodynamically favorable position, away from the sluggish currents of the bottom and exposed to a higher water flow that could enhance its filtration efficiency (Buhl-Mortensen and Mortensen 2004). The position of the sponge may also result in a reduced competition by algae or other benthic invertebrates and in a lower impact of sedimentation.

The association herein described seems therefore to be mutualistic for all three partners. Mutualistic overgrowth has been proposed for many benthic organisms, but the cost-benefit of these associations is still poorly

known and often challenging to define, especially in organisms with complex life cycles. According to our observations and the literature, the possible advantages can be related to escape from reduced space on the substratum (McKinney et al. 1990), increased ability to overgrow competitors (Osman and Haugsness 1981), expanded chemical or physical defense from predators (Osman and Haugsness 1981, Wulff 1997, Montano et al. 2017b), increased ability to hold to the substratum (Wulff 1997), and enhanced food supply (Buhl-Mortensen and Mortensen 2004). Interestingly, in our case one of the octocoral's epibionts (the hydroid) was in turn partially overgrown by another epibiont (the sponge). Moreover, the medusa buds of the hydrozoan were embedded in the sponge when immature and set free only when maturity was reached. This mechanism of protection by the sponge may benefit the hydrozoan

polyps and directly and positively influence the release, survival, and persistence of *Zanclaea* medusae in the water column, therefore influencing the benthos-plankton networks and the plankton dynamics.

Peculiar relationships like these are often specific, and investigating the mechanisms that rule the onset of the association between one organism and the larval stage of the other is particularly challenging. For instance, it would be interesting to understand whether the hydrozoan larvae settle on yet uncovered parts of the octocoral and are later overgrown by the sponge or they settle on the sponge and grow through it. One general hypothesis is that associated bacteria may play a major role in the early stages of the association between hydroids and specific living substrates (see, for instance, Müller and Leitz 2002), and variations in this system may also cause ecological speciation by host shift.

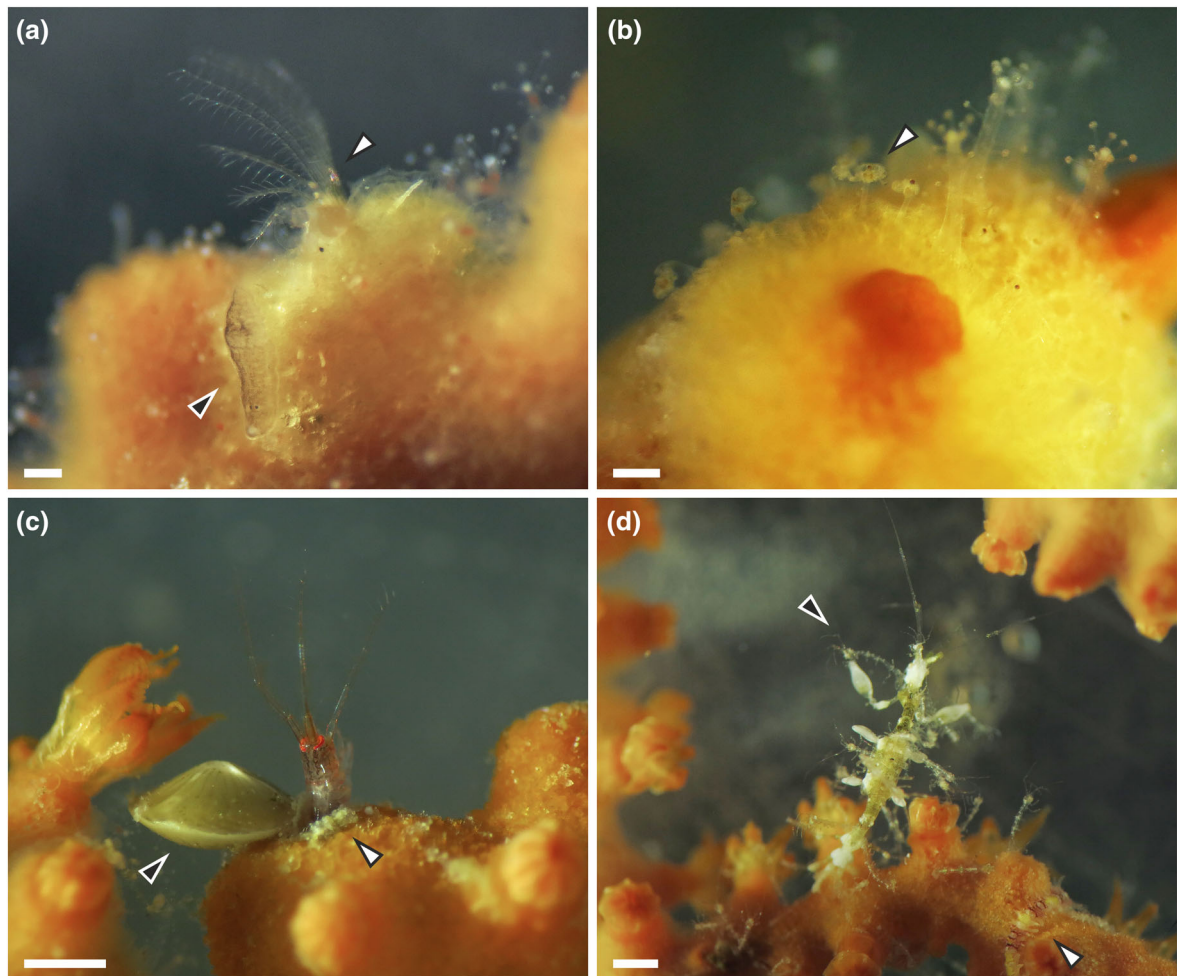


FIG. 2. Invertebrates associated with the octocoral and sponge. (a) A barnacle (white arrowhead) and a triclad flatworm (black arrowhead). (b) Entoproct (white arrowhead). (c) A gammarid amphipod (white arrowhead) and a rotaliid foraminiferan (black arrowhead). (d) A caprellid amphipod with its offspring (black arrowhead) and the arm of an ophiuran (white arrowhead). Scale bars: (a, b) 0.3 mm, (c, d) 1 mm.

In addition to the recurring three-way association, some other invertebrates were found dwelling on the octocoral and sponge surface. In particular, sessile organisms such as barnacles (Fig. 2a) and entoprocts (Fig. 2b) were embedded in, or attached to, the sponge layer. Similarly, gammarid amphipods were settled in the sponge or octocoral, extruding only their heads, antennae and first pairs of pereopods (Fig. 2c). Other observed organisms were triclad flatworms (Fig. 2a), rotaliid foraminiferans (Fig. 2c), caprellid amphipods with their offspring (Fig. 2d), and ophiurans (Fig. 2d).

The presence of these organisms may be related to an increased habitat availability provided by the stable association between the octocoral and the sponge. This may be the case, for instance, of gammarids and barnacles living partially embedded in the sponge growing on the octocoral surface. The ecological interactions among all these organisms are difficult to define, but we cannot exclude their reciprocal influence. We may be dealing with a situation similar to that of scleractinian corals, in which all the associates can contribute, positively or negatively, to the overall fitness of the coral symbiome (Gates and Ainsworth 2011).

The finding of the herein-reported association highlights the still scarce knowledge of the ecological interactions in mesophotic coral ecosystems and the possible existence of other so-far-unknown similar associations, including mutualistic overgrowth in these environments. Therefore, this and other multitaxa associations need further investigation to characterize their taxonomic composition and the possible detrimental and positive effects on the whole associated system, especially in threatened ecosystems such as coral reefs at both shallow and mesophotic depths.

LITERATURE CITED

- Buhl-Mortensen, L., and P. B. Mortensen. 2004. Symbiosis in deep-water corals. *Symbiosis* 37:33–61.
- Calcinai, B., G. Bavestrello, M. Bertolino, D. Pica, D. Wagner, and C. Cerrano. 2013. Sponges associated with octocorals in the Indo-Pacific, with the description of four new species. *Zootaxa* 3617:1–61.
- Gates, R. D., and T. D. Ainsworth. 2011. The nature and taxonomic composition of coral symbiomes as drivers of performance limits in scleractinian corals. *Journal of Experimental Marine Biology and Ecology* 408:94–101.
- Goh, N. K., P. K. Ng, and L. M. Chou. 1999. Notes on the shallow water gorgonian-associated fauna on coral reefs in Singapore. *Bulletin of Marine Science* 65:259–282.
- Hoeksema, B. W., S. E. Van der Meij, and C. H. Franssen. 2012. The mushroom coral as a habitat. *Journal of the Marine Biological Association of the United Kingdom* 92:647–663.
- Kahng, S. E., J. M. Copus, and D. Wagner. 2014. Recent advances in the ecology of mesophotic coral ecosystems (MCEs). *Current Opinion in Environmental Sustainability* 7:72–81.
- Maggioni, D., S. Montano, D. Seveso, and P. Galli. 2016. Molecular evidence for cryptic species in *Pteroclava krempfi* (Hydrozoa, Cladocorynidae) living in association with alcyonaceans. *Systematics and Biodiversity* 14:484–493.
- Maggioni, D., P. Galli, M. L. Berumen, R. Arrigoni, D. Seveso, and S. Montano. 2017. *Astrocoryneabela*, gen. nov. et sp. nov. (Hydrozoa: Sphaerocorynidae), a new sponge-associated hydrozoan. *Invertebrate systematics* 31:734–746.
- McKinney, F. K., T. W. Broadhead, and M. A. Gibson. 1990. Coral-bryozoan mutualism: Structural innovation and greater resource exploitation. *Science* 248:466–468.
- Montano, S., D. Maggioni, P. Galli, and B. W. Hoeksema. 2017a. A cryptic species in the *Pteroclava krempfi* species complex (Hydrozoa, Cladocorynidae) revealed in the Caribbean. *Marine Biodiversity* 47:83–89.
- Montano, S., S. Fattorini, V. Parravicini, M. L. Berumen, P. Galli, D. Maggioni, R. Arrigoni, D. Seveso, and G. Strona. 2017b. Corals hosting symbiotic hydrozoans are less susceptible to predation and disease. *Proceedings of the Royal Society B* 284:20172405.
- Müller, W. A., and T. Leitz. 2002. Metamorphosis in the Cnidaria. *Canadian Journal of Zoology* 80:1755–1771.
- Osman, R. W., and J. A. Haugsness. 1981. Mutualism among sessile invertebrates: a mediator of competition and predation. *Science* 211:846–848.
- Puce, S., C. G. Di Camillo, and G. Bavestrello. 2008. Hydroids symbiotic with octocorals from the Sulawesi Sea, Indonesia. *Journal of the Marine Biological Association of the United Kingdom* 88:1643–1654.
- Puglise, K. A., L. M. Hinderstein, J. C. Marr, M. J. Dowgiallo, and F. A. Martinez. 2009. Mesophotic Coral Ecosystem Research Strategy: International Workshop to Prioritize Research and Management Needs for Mesophotic Coral Ecosystems, Jupiter, Florida, 12–15 July 2008. Silver Spring, Maryland, USA. Page 24.
- Wagner, D., S. E. Kahng, and R. J. Toonen. 2009. Observations on the life history and feeding ecology of a specialized nudibranch predator (*Phyllodesmium poindimiei*), with implications for biocontrol of an invasive octocoral (*Carijoa riisei*) in Hawaii. *Journal of Experimental Marine Biology and Ecology* 372:64–74.
- Watling, L., S. C. France, E. Pante, and A. Simpson. 2011. Biology of deep-water octocorals. Pages 41–122 in *Advances in marine biology*. Volume 60. Academic Press, Cambridge, UK.
- Wulff, J. L. 1997. Mutualisms among species of coral reef sponges. *Ecology* 78:146–159.

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2950/supinfo>