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SHORT COMMUNICATION

Colonies of the fire coral *Millepora platyphylla* constitute scleractinian survival oases during *Acanthaster* outbreaks in French Polynesia

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Abstract Outbreaks of the predator crown-of-thorns starfish *Acanthaster planci* cause widespread coral mortality throughout the Indo-Pacific. Identifying mediating processes that promote coral survival during *Acanthaster* outbreaks can help support reef resilience. During surveys in French Polynesia, large colonies of the calcifying hydrozoan *Millepora platyphylla* appeared to be avoided by the starfish, providing predator-free sanctuaries to scleractinian corals in their proximity during an intense *Acanthaster* outbreak. Such refuges particularly benefited susceptible taxa such as *Acropora* and *Pocillopora*, whose populations were normally targeted by the starfish. These biological sanctuaries provided by *Millepora* to scleractinians are newly identified forms of associational refuges that can increase coral resistance to predation by *Acanthaster*. Our observations thus identify a key ecological role in reef resilience for *Millepora*, which is a ubiquitous component of tropical reefs usually seen as a strong competitor of scleractinians.

Keywords Predator outbreak · Crown-of-thorns starfish · Scleractinian coral · Associational refuge · Biological sanctuary

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Introduction

Outbreaks of the corallivorous predator crown-of-thorns starfish *Acanthaster planci* cause mass coral mortality and constitute major disturbances to coral reefs (Pratchett et al. 2014). Over the last decade, a recrudescence of *Acanthaster* outbreaks has been observed throughout the Indo-Pacific, including in Polynesia (Kayal et al. 2012; Timmers et al. 2012), Micronesia (Houk et al. 2014), Melanesia (Pratchett et al. 2009; Houk and Raubani 2010; Clements and Hay 2015), Australia (Wooldridge and Brodie 2015), Southeast Asia (Bos 2010; Lane 2012; Baird et al. 2013), East Asia (Nakamura et al. 2015), the Indian Ocean (Saponari et al. 2015), and around the Arabian Peninsula (Mendonça et al. 2010; Riegl et al. 2013). These events have sparked heightened interest in better understanding these disturbances and identifying mediating processes that can promote coral survival.

A variety of factors are known to influence coral susceptibility to predation during *Acanthaster* outbreaks. First, while *Acanthaster* preys on coral species, this predator shows marked feeding preferences for fast-growing taxa from the families Acroporidae and Pocilloporidae (Kayal et al 2012; Pratchett et al. 2014). In addition, different coral symbionts are known to affect *Acanthaster*'s choice of prey and efficiency of predation (DeVantier et al. 1986; Pratchett 2001; Bergsma 2012; McKeon and Moore 2014; Rouzé et al. 2014). Furthermore, various forms of associational refuges that prevent *Acanthaster* from detecting, accessing, or targeting specific prey have recently been identified (Kayal et al. 2011; Bulleri et al. 2013; Clements and Hay 2015). In this context, we document a newly discovered form of associational refuge provided by a calcifying hydrozoan species of the genus *Millepora*, which promotes survival of coral taxa susceptible to *Acanthaster*.

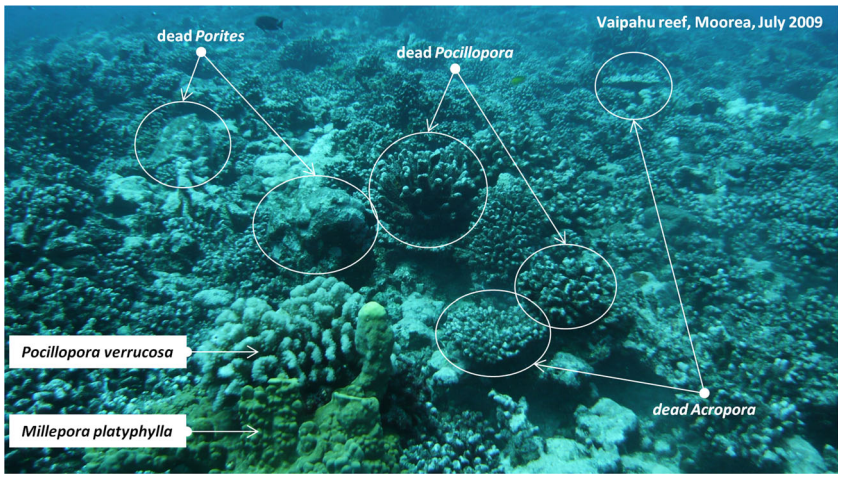

Fig. 1 Adult *Pocillopora* coral associated with a large colony of *Millepora* and standing as the only surviving scleractinian in a reefscape of dead coral skeletons following predation by swarms of starfish *Acanthaster* during an outbreak. Here the coral cover had dropped to 3 %

Millepora corals are a ubiquitous component of the tropical reefscape (Veron 2000; Lewis 2006). Although not a scleractinian, *Millepora* is usually considered both a member and a natural enemy of reef-building coral communities, given its contribution to the reef framework and at the same time its formation of large colonies that pre-empt space and compete with other corals (Andréfouët et al. 2014; Dubé et al. 2015). *Millepora* species share many features with scleractinians in their ecology and susceptibility to various sources of regulation and disturbance, with the exception that they are rarely preyed upon by *Acanthaster* (Lewis 2006). To date, *Millepora platyphylla* is the only species of this genus documented in French Polynesia (e.g. Andréfouët et al. 2014; Dubé et al 2015).

Material and methods

Our observations were performed on the outer reefs surrounding the island of Moorea, French Polynesia, during one of the most devastating *Acanthaster* outbreaks ever documented

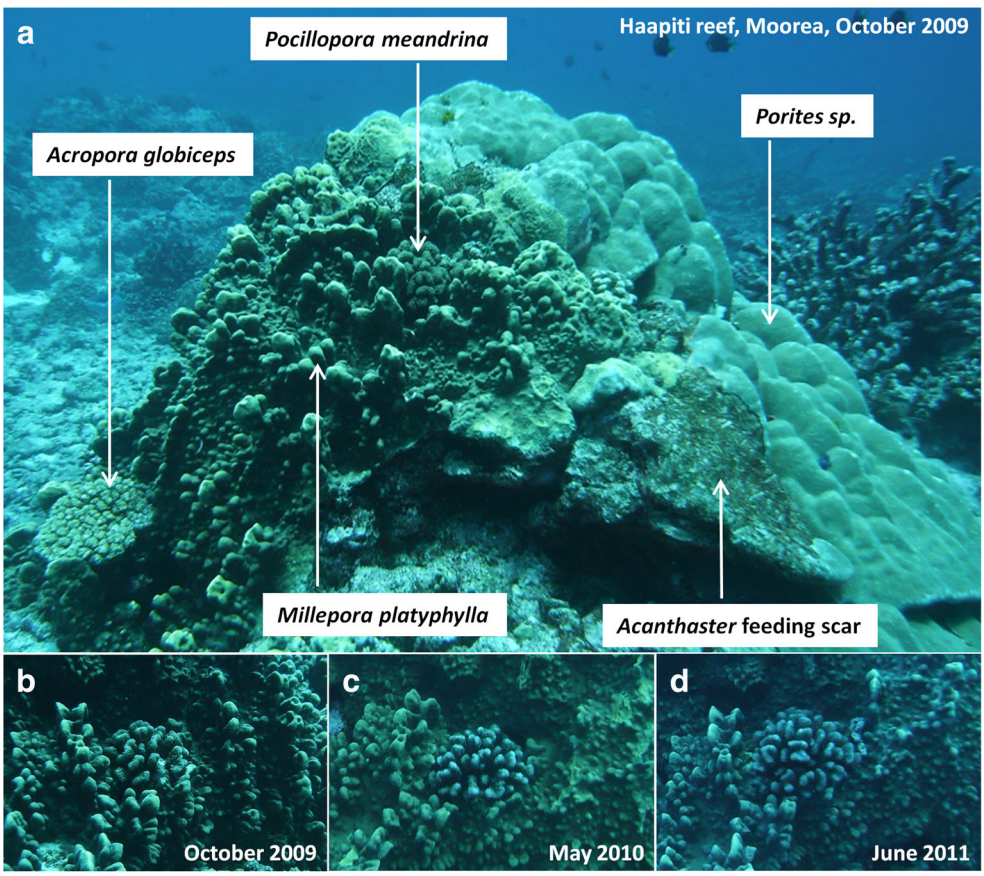

Fig. 2 Scleractinian corals of *Pocillopora* (**a**–**d**) and *Acropora* (**a**) that have escaped predation by *Acanthaster* adjacent to large colonies of *Millepora* on reefs otherwise denuded of their populations. **a** *Millepora* coral overgrowing a massive *Porites* coral, a less preferred scleractinian prey. **b**–**d** The same *Pocillopora* colony depicted through time, showing the durability of the associational refuge with *Millepora* throughout the outbreak

globally. This event affected Moorea from 2003 to 2010, as swarms of starfish (>150,000 ind. km^{-2}) extirpated scleractinian communities from vast portions of reefs, sometimes leaving less than 1 % coral cover behind, but without preying upon a calcifying hydrozoan belonging to *Millepora*, a genus of so-called fire corals (Kayal et al. 2012).

Our observations were performed between 2008 and 2011 during numerous scuba dives dedicated to the study of coral community dynamics on multiple reefs around Moorea. Cases of scleractinian interactions with *Millepora* are common on these reefs, where *Millepora* is relatively abundant at depths of 0–20 m, although the benefits of the association with *Millepora* in the face of predation by *Acanthaster* became particularly striking on reef locations undergoing intense coral extirpation (Kayal et al. 2012). All corals were identified in situ at least to genus, and when possible to species level, based on morphological characteristics as described in Veron (2000) and Razak and Hoeksema (2003).

Results and discussion

As swarms of *Acanthaster* were decimating coral communities around Moorea (Kayal et al. 2012), large colonies of *Millepora platyphylla* were observed to form refuges where enclosed scleractinians escaped predation by the starfish, even on reef locations where their populations were otherwise eradicated from the reefscape (Fig. 1). Such cases were encountered occasionally throughout the outbreak, approximately one observation per scuba dive on reef locations where coral populations had been decimated. The bio-sanctuaries provided to scleractinians by *Millepora* were long-lasting and hosted adult coral refugees from various preferred prey taxa of *Acanthaster* such as *Acropora* and *Pocillopora* (Fig. 2).

This is not the first time that species avoided by *Acanthaster* have been observed to form barriers to the propagation of the starfish (Glynn 1976). The *Acanthaster*-free sanctuaries provided by large *Millepora* colonies are newly recognized forms of associational refuges in corals based on avoidance of predators within large patches of unpalatable prey species (i.e. associational avoidance sensu Milchunas and Noy-Meir 2002). These refuges differ from other indirect positive interactions recently identified among competing corals when exposed to *Acanthaster*, which involve physical impedance of the predator through structural barriers, selection impedance through prey dilution, or defensive impedance through shared benefits of guardian symbionts (Kayal et al. 2011; McKeon and Moore 2014).

In theory, associational refuges take form among competing species when exposed to intense stress if the benefits of the indirect positive interaction between the two species are greater than the direct antagonistic effects (Milchunas and Noy-Meir 2002; Kayal et al. 2011). This was indeed the case in our observations, as the benefits of the refuges provided by *Millepora* became apparent for *Acropora* and *Pocillopora*, preferred prey species of *Acanthaster*, after their populations were devastated. On the other hand, the presence of *Millepora* was not seen to benefit colonies of massive *Porites*, which is a less preferred prey of the starfish that was undergoing lower predation pressure during the outbreak, and is a weak competitor among corals more susceptible to direct overgrowth by *Millepora* (Connell et al. 2004; Kayal et al. 2011; Fig. 2).

Despite the high cost to scleractinians living in the proximity of strong competitors like *Millepora* corals (Lewis 2006; Dubé et al. 2015), our observations suggest that large *Millepora* colonies can constitute survival oases for coral taxa susceptible to *Acanthaster*, and can promote persistence of their populations through outbreak events. Such surviving portions of coral populations are thought to play a possible role in the subsequent recovery from disturbances. This is particularly the case for taxa with life strategies vulnerable to environmental instability, including several *Acropora* species, which in French Polynesia undergo recurrent mass mortality events and show limited capacity for recolonization of habitats after extirpation (Kayal et al. 2015).

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