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ORIGINAL ARTICLE

Mushroom corals as newly recorded hosts of the hydrozoan symbiont *Zanclea* sp.

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Abstract

Mushroom corals (Anthozoa: Scleractinia: Fungiidae) have been well documented as hosts of a rich associated fauna, but no records involving the symbiotic hydrozoan genus *Zanclea* (Hydrozoa: Capitata: Zancleidae) are known. These small (~1 mm long), coral-associated hydroids have only been reported from associations involving 23 non-fungiid scleractinian host species in the Indo-Pacific. Since both groups, Fungiidae and coral-dwelling *Zanclea* hydroids, are known to occur on Indo-Pacific coral reefs, it was unclear why no mushroom coral hosts were known. Therefore, a survey in the Maldives was performed aiming at the discovery of *Zanclea*–Fungiidae associations. Subsequently, 10 new host species were discovered and the number of recorded coral host genera increased from 17 to 24, taking recent taxonomic revisions into account. These findings indicate that the coral-associated biodiversity is still insufficiently explored.

Key words: *Fungiidae, host specificity, Hydrozoa, Maldives, Scleractinia, symbiosis*

Introduction

Scleractinian reef corals are traditionally known to act as hosts for many kinds of associated organisms such as crustaceans, fishes, molluscs and polychaetes (Patton 1994; Stella et al. 2011; Bos 2012; Hoeksema et al. 2012; Bos & Hoeksema 2015). Scleractinians were also reported to host colonial hydrozoans of the genus *Zanclea* Gegenbaur, 1857 (Hydrozoa, Zancleidae) in polyp stage (Millard & Bouillon 1974; Millard 1975; Boero et al. 2000), but their host species remained unspecified for many years and more specific research on the *Zanclea*–Scleractinia symbiosis only started recently (Pantos & Bythell 2010; Hirose & Hirose 2011; Fontana et al. 2012; Gravier-Bonnet & Bourmaud 2012; Montano et al. 2013, 2014, 2015). Otherwise, *Zanclea* polyps are known to live in association with other sessile invertebrates, predominantly through specific relationships with bryozoans, bivalves or octocorals, although host generalist *Zanclea* species have also been reported (Gravili et al 1996; Boero et al. 2000; Puce et al. 2002, 2007, 2008a, 2008b). *Zanclea* species are not only known from their polyp stage, since polyps attached to corals and other invertebrates have been observed to release medusae that can move away from their host (Boero et al. 2000; Hirose & Hirose 2011) (Figure 2h).

So far, four *Zanclea* species have been reported to live in symbiosis with scleractinians, all of which occur in the Indo-Pacific, but none in the Atlantic, namely *Zanclea gilii* Boero, Bouillon & Graviliet, 2000, *Z. margarita* Pantos & Bythell, 2010, *Z. sango* Hirose & Hirose, 2011, and *Z. gallii* Montano, Maggioni & Puce, 2015. The first identified host coral was an *Acropora* species (Acroporidae) (Pantos & Bythell 2010). Various scleractinian host taxa have been added since, but mushroom corals (Fungiidae)

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have not been recorded. Mushroom corals are known to occur exclusively in the Indo-Pacific (Hoeksema 1989), except for one species that was introduced in Jamaica (Bush et al. 2004). Most fungiids are free-living and monostomatous (with a single mouth) as full-grown corals, but other species are attached and monostomatous, free-living and polystomatous (with more than one mouth), or attached and polystomatous (Gittenberger et al. 2011; Benzoni et al. 2012).

The role of mushroom corals as a habitat for associated fauna has been the subject of a review, but hydroid symbionts have not been included (Hoeksema et al. 2012). Due to their small size, with lengths of ~1 mm (Montano et al. 2013), *Zanclea* polyps are hardly noticeable, whereas many mushroom coral species are iconic because of their large size as free-living corals of up to nearly 1 m in diameter (Hoeksema 1991). To examine whether a lack of observation effort could be the cause of any unknown mushroom coral hosts, assuming that fungiids were not sufficiently searched for the presence of *Zanclea* in previous studies, a systematic survey of Fungiidae for the presence of *Zanclea* associates was undertaken. Finally, in the light of recent taxonomic revisions of various coral families, the new records have been added to an updated overview of previously recorded *Zanclea*–Scleractinia associations.

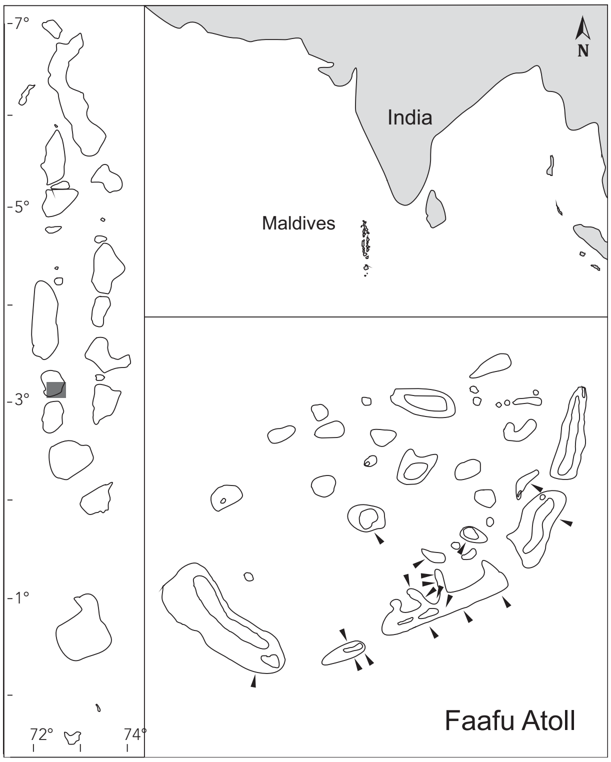

Figure 1. Maps showing the Republic of Maldives (Indian Ocean), the square indicating the study area, an overview of its position in relation to India and the survey localities inside and outside Faafu Atoll (arrowheads).

Materials and methods

The study was conducted in the waters of Faafu Atoll, Republic of Maldives in May 2014. We explored 18 localities, chosen randomly among accessible sites on outer and inner coral reefs (Figure 1). The presence of *Zanclea* in fungiids was recorded qualitatively (presence only) 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 (15–30 m) and moving to shallower water from there (Hoeksema & Koh 2009). For documentary purposes underwater photographs of *Zanclea*-fungiid associations were taken using a Canon G11 camera in a Canon WP-DC 34 underwater housing and a Sea & Sea 2G camera. Free-living mushroom corals and fragments of attached fungiids colonized by *Zanclea* were transported to an outdoor tank at the MaRHE Center of Magoodhoo Island. In the laboratory, colonized corals were placed in a bowl filled with seawater under a stereo microscope, from where the hydroid polyps were carefully collected from the host using a syringe needle. They were immediately fixed and preserved in 4% formalin for future taxonomic identification. Microphotographs (×32) of hydroids protruding from the coral skeletons were taken using a Leica EZ4 D stereo microscope equipped with a Canon G11 camera. All hydroids were identified to genus level (according to Bouillon et al. 2006), while all fungiid host corals were identified *in situ* at species level following the taxonomic revision by Hoeksema (1989) and more recent species descriptions (Hoeksema 1993; Veron 2000).

The new host records have been added to previous ones (Table I) following revised taxonomic classifications: Acroporidae (Wallace et al. 2012), Fungiidae (Gittenberger et al. 2011; Benzoni et al. 2012), Lobophylliidae (Budd et al. 2012; Arrigoni et al. 2014), Merulinidae (Budd et al. 2012; Huang et al. 2014a, 2014b), Poritidae (Kitano et al. 2014), and Psammocoridae (Benzoni et al. 2007, 2010).

Results

Twenty-two species of mushroom corals were found during the survey, with nearly 50% of them colonized by *Zanclea*. Ten species and seven genera of Fungiidae were newly discovered host taxa for *Zanclea* (Figure 2, Table I). These 10 fungiids together do not form a monophyletic lineage within the Fungiidae (Gittenberger et al. 2011; Benzoni

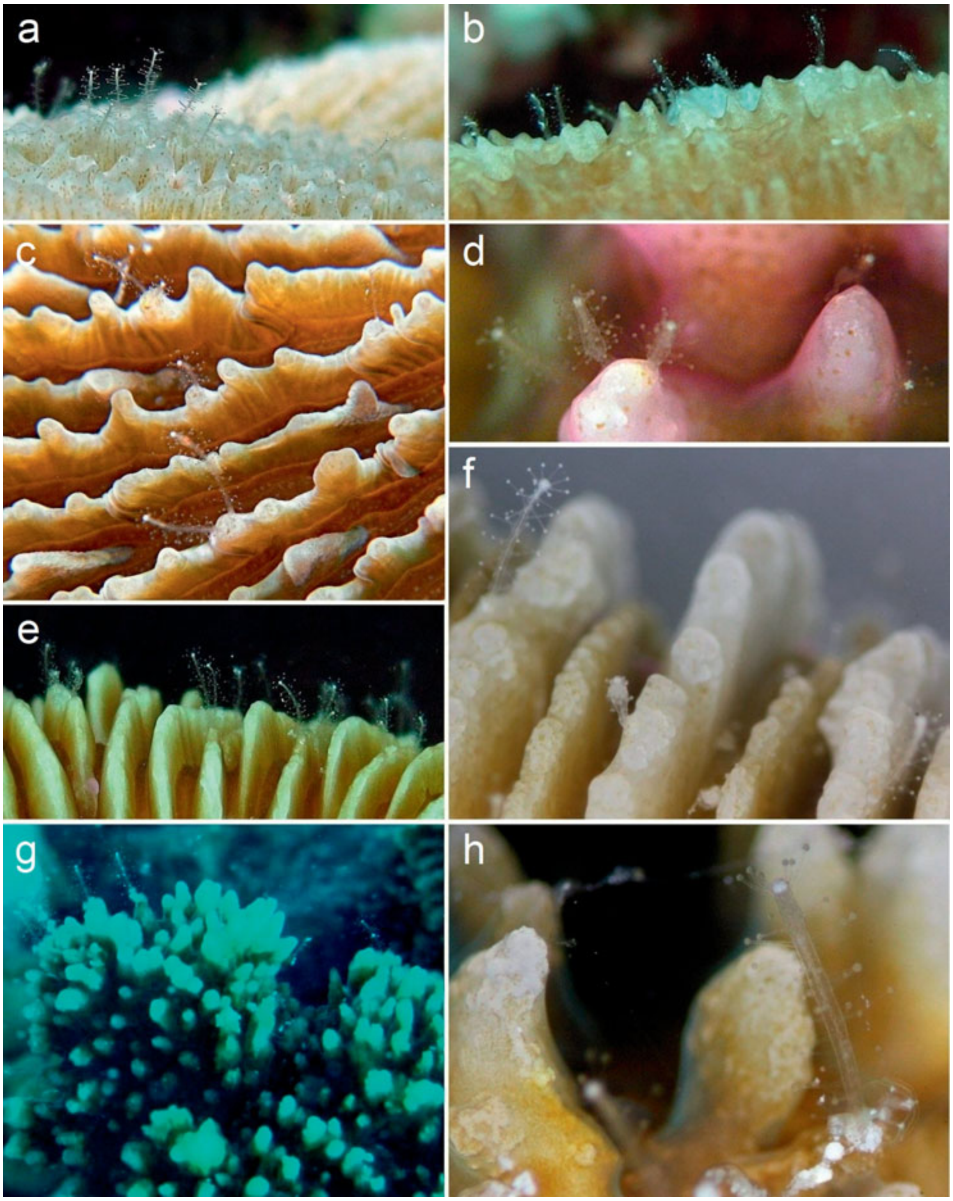

Figure 2. The position of *Zanclea* polyps on some newly recorded hosts (Scleractinia: Fungiidae), one with a medusa at its base (h). (a) *Danafungia horrida*, (b) *Lithophyllon repanda*, (c) *Danafungia scruposa*, (d) *Halomitra pileus*, (e,f) *Pleuractis paumotensis*, (g,h) *Podabacia lankaensis*. Length of hydroid colony ≈ 1 mm.

et al. 2012). Therefore, overall they do not show distinctly closer phylogenetic relationships with each other than with species without *Zanclea*, except for two *Danafungia* species and three *Pleuractis* species (Table I). With regard to life history strategy and growth form (compare Hoeksema 1989; Gittenberger et al. 2011), *Zanclea*-hosting mushroom corals are either the free-living and monostomatous *Danafungia horrida* (Dana, 1846), *D. scruposa* (Kluzinger, 1879), *Fungia fungites* (Linnaeus, 1758), *Lithophyllon repanda* (Dana, 1846), *Lobactis scutaria* (Lamarck, 1801), *Pleuractis granulosa* (Kluzinger, 1879), *P. moluccensis* (Van der Horst, 1919), and *P. paumotensis* (Stutchbury, 1833), the free-living and polystomatous *Halomitra pileus* (Linnaeus, 1758), or the attached and polystomatous *Podabacia lankaensis* Veron, 2000.

It is unclear how the hydroids settle on their hosts, how both partners physically interact and the nature of their relationship. Observations on the single hydroid polyps reveal the presence of a long hydrorhiza covered by a perisarc that grows at the interface between the soft tissues and the skeleton of the fungiid hosts, like in other scleractinians (Montano et al. 2015). The spatial distribution of the hydroids on the coral surface appears to be host-dependent (Figure 2). *Zanclea* hydroids were commonly observed on the septal edges of fungiids, but also randomly on the granulated septal sides and on the

Table I. Scleractinians hosting *Zanclea* associations observed at various localities, including new records.

Host coral taxon	Locality	Reference
Acroporidae		
Acropora aspera (Dana, 1846)	Eastern Australia (GBR)	3
Acropora divaricata (Dana, 1846)	Taiwan	3
Acropora gemmifera (Brook, 1892)	Eastern Australia (GBR), Taiwan	3
Acropora granulosa (Milne Edwards, 1860)	Eastern Australia (GBR)	3
Acropora humilis (Dana, 1846)	Eastern Australia (GBR), Taiwan	3
Acropora hyacinthus (Dana, 1846)	Taiwan	3
Acropora loripes (Brook, 1892)	Eastern Australia (GBR)	3
Acropora millepora (Ehrenberg, 1834)	Eastern Australia (GBR)	3
Acropora muricata (Linnaeus, 1758)	Eastern Australia (GBR), Taiwan, Maldives	1, 3, 4, 6
Acropora pulchra (Brook, 1891)	Eastern Australia (GBR), Taiwan	3
Acropora samoensis (Brook, 1891)	Eastern Australia (GBR)	3
Acropora spathulata (Brook, 1891)	Eastern Australia (GBR)	3
Acropora speciosa (Quelch, 1886)	Eastern Australia (GBR)	3
Acropora valida (Dana, 1846)	Taiwan	3
Acropora spp.	Eastern Australia (GBR), Taiwan, Egypt (Red Sea)	3, 5
Anacropora spp.	Indonesia, Taiwan	3
Astreopora spp.	Taiwan	3
Isopora palifera (Lamarck, 1816)	Taiwan	3
Montipora spp.	Taiwan, Maldives, Egypt (Red Sea)	3, 4, 5
Agariciidae		
Leptoseris sp.	Maldives	6
Pavona divaricata Lamarck, 1816	Southern Japan	2
Pavona varians Verrill, 1864	Maldives	6
Pavona venosa (Ehrenberg, 1834)	Southern Japan	2
Pavona spp.	Maldives, Egypt (Red Sea)	4, 5
Fungiidae		
Danafungia horrida (Dana, 1846)	Maldives	Present study
Danafungia scruposa (Klunzinger, 1879)	Maldives	Present study
Fungia fungites (Linnaeus, 1758)	Maldives	Present study
Halomitra pileus (Linnaeus, 1758)	Maldives	Present study
Lithophyllon repanda (Dana, 1846)	Maldives	Present study
Lobactis scutaria (Lamarck, 1801)	Maldives	Present study
Pleuractis granulosa (Klunzinger, 1879)	Maldives	Present study
Pleuractis moluccensis (Van der Horst, 1919)	Maldives	Present study
Pleuractis paumotensis (Stutchbury, 1833)	Maldives	Present study
Podabacia lankaensis Veron, 2000	Maldives	Present study
Lobophylliidae		
Symphyllia sp.	Maldives	4
Merulinidae		
Cyphastrea sp.	Egypt (Red Sea)	5
Dipsastraea favus (Forskål, 1775)	Maldives	4
Dipsastraea sp.	Egypt (Red Sea)	5
Echinopora sp.	Egypt (Red Sea)	5
Favites halicora (Ehrenberg, 1834)	Maldives	4
Favites sp.	Egypt (Red Sea)	5
Goniastrea sp.	Egypt (Red Sea)	5
Platygyra sp.	Egypt (Red Sea)	5
Psammocoridae		
Psammocora contigua (Esper, 1794)	Southern Japan	2
Psammocora sp.	Egypt (Red Sea)	5
Poritidae		
Porites cylindrica Dana, 1846	Maldives	4
Scleractinia incertae sedis		
Leptastrea purpurea (Dana, 1846)	Maldives	4
Leptastrea sp.	Maldives	6

References: 1, Pantos & Bythell (2010); 2, Hirose & Hirose (2011); 3, Fontana et al. (2012); 4, Montano et al. (2013); 5, Montano et al. (2014); 6, Montano et al. (2015).

fulturae, i.e. skeleton structures in between the septa (see Hoeksema 1989 for terminology of fungiid skeletons). In *L. repanda* and *P. paumotensis*, *Zanclea* hydroids were also found at the septal base. The highest densities of *Zanclea* polyps (> 10 hydroids/cm^2) were observed on the tips of the septal dentations of two polystomatous fungiid species, *P. lankaensis* and *H. pileus*.

Twelve mushroom coral species at the Maldives that were not observed with any *Zanclea* are either free-living and monostomatous (*Cycloseris costulata* (Ortmann, 1889), *C. tenuis* (Dana, 1846), *C. vaughani* (Boschma, 1923), *Lithophyllon concinna* (Verrill, 1864), *Pleuractis seychellensis* Hoeksema, 1993), free-living and polystomatous (*Ctenactis crassa* (Dana, 1846), *Herpolitha limax* (Esper, 1797), *Polyphyllia talpina* (Lamarck, 1801), *Sandalolitha dentata* Quelch, 1884), or attached and polystomatous (*Cycloseris explanulata* (Van der Horst, 1922), *C. wellsi* (Veron & Pichon, 1980)).

With 10 host species, the Fungiidae as a scleractinian family is only second to the Acroporidae, with 13 species harbouring *Zanclea* associates (Table I). The addition of the *Zanclea*-hosting mushroom coral species to those of previously recorded scleractinian hosts (after application of recent taxonomic revisions) resulted in a total of 33 coral species and 24 genera (Table 1). This addition constitutes 30% of the total number. All of the previously recorded hosts are attached scleractinians with polystomatous or colonial growth forms.

Discussion

This large addition (30% of the total) to the list of known host coral records for hydroids belonging to the genus *Zanclea* indicates that observation effort is essential for the discovery of these tiny symbionts. *Zanclea* surveys have so far only been performed in a limited number of Indo-Pacific localities, with the Maldives having the highest host record (Montano et al. 2014) (Table I). It is likely that additional scleractinian host species (including Fungiidae) will be found in areas that are richer in coral species, such as the Coral Triangle (Hoeksema 2007) and the South China Sea (Huang et al. 2015). The total number of mushroom coral species recorded during the present survey (n = 22) is only half of the maximum number encountered (n = 44) off north-eastern Borneo (Waheed & Hoeksema 2013).

Recent studies show that the associated fauna of fungiids can be rich, involving shrimps (Hoeksema & Fransen 2011), fishes (Bos 2012; Bos & Hoeksema 2015), acoelomorph flatworms (Hoeksema & Farenzena 2012), gall crabs (Van der Meij & Hoeksema 2013), benthic ctenophores (Hoeksema et al. 2013), parasitic snails (Gittenberger & Hoeksema 2013), serpulid polychaetes (Hoeksema & Ten Hove 2014) and various other animals (Hoeksema et al. 2012). Several of these associations are host-specific at the family, genus or species level, especially if they live inside or attached to the surface of the host coral (Gittenberger & Gittenberger 2005, 2011; Owada & Hoeksema 2011; Hoeksema et al. 2012). The recent additions to the known associated fauna of the Fungiidae illustrate that a focused search effort is a critical factor.

Because the hydrozoans on mushroom corals could not be identified at species level, their degree of host specificity is unclear. A molecular study involving *Acropora* corals suggests a genus-specific association between *Zanclea* hydroids and their coral hosts (Fontana et al. 2012). More molecular research is needed to investigate the number of *Zanclea* species and the specificity of their host relationships.

It is unclear why some mushroom coral species have *Zanclea* symbionts and others have not. The presence of a medusa life stage (see e.g. Figure 2h) may enhance the large-scale dispersal of this genus. The planulae are supposedly attracted by substrates, such as scleractinian corals, including Fungiidae, and this behaviour may result in clusters of *Zanclea* colonies. Nevertheless, whether morphological, chemical or ecological features of the involved species have led to the evolution of this kind of association still needs to be elucidated. Depth range may be a regulating factor in host species preference, since these hydrozoans have predominantly been found in shallow water, but this may reflect a sampling bias, because they have also been recorded at 38 m depth (Montano et al. 2014). Host coral size could also be a regulating factor in host preference, since free-living corals of the genus *Cycloseris* were abundant during the present survey, but none of them exhibited *Zanclea* symbionts. Such *Cycloseris* corals are usually smaller than those of other fungiid species and offer little settling space for symbionts (Hoeksema et al. 2012; Hoeksema 2014). The nature of the *Zanclea*-coral association is unclear. Since *Zanclea* polyps do not appear to cause any visible harm to the corals, they may not be parasites, unlike other species of epibionts, such as acoel flatworms, that are capable of killing their host (Hoeksema & Farenzena 2012).

Nine out of 10 fungiid species acting as hosts for *Zanclea* are free-living. This is not an obvious result, since free-living mushroom corals could be a hostile environment for *Zanclea* symbionts. Their mobility enables fungiids to colonize sandy substrates over a wide depth range (Hoeksema 2012), where they need to free themselves from sediments after burial

(Bongaerts et al. 2012). They can also become turned upside-down by accident (Hoeksema 1988; Chadwick-Furman & Loya 1992; Gittenberger & Hoeksema 2013) and any *Zanclea* on their oral surface would risk becoming crushed under the coral's weight. However, many hydroids are known to regress under stress conditions and to return to an active state when conditions improve again (Gili & Hughes 1995). Therefore, future research should not only focus on additional host coral species, especially in the Atlantic, where no coral-dwelling *Zanclea* have so far been found, but also on the ecology and life history strategies of coral-associated *Zanclea*.

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