

Helioseris cucullata as a host coral at St. Eustatius, Dutch Caribbean

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Abstract In order to demonstrate how scleractinian corals contribute to marine biodiversity by their host function, information on associated fauna was gathered during a biological survey at St. Eustatius, eastern Caribbean. This knowledge is especially urgent for a host coral such as *Helioseris cucullata* (Agariciidae), which has undergone strong declines in abundance at various Caribbean localities and has a poor record of associated fauna. New records of *H. cucullata* as host are presented for the coral gall crab *Opecarcinus hypostegus* (Cryptochiridae), the Christmas tree worm *Spirobranchus giganteus* (Serpulidae) and an unidentified serpulid tube worm of the genus *Vermiliopsis*. A second association record is reported for the coral barnacle *Megatrema madreporarum* (Pyrgomatidae). Coral-associated copepods were not found on *H. cucullata* despite a search for these animals. The new records were compared with previous records of other host coral species that showed elements of the same associated

fauna. The present findings indicate that new discoveries concerning Caribbean coral reef biodiversity can still be made during field expeditions by targeting the assemblages of associated fauna of specific benthic host species.

Keywords Associated fauna · Copepod · Coral barnacle · Coral reefs · EDGE species · Gall crab · Serpulid

Introduction

Helioseris cucullata (Ellis and Solander, 1786) (Scleractinia: Agariciidae) is a foliaceous reef coral with a Caribbean distribution. It represents a monospecific clade that is separate from the predominantly Indo-Pacific genus *Leptoseris*, with which it was previously classified (Kitahara et al. 2012). Its calices are arranged in between concentric, discontinuous, lopsided ridges, giving its upper surface a wave-like appearance, for which it has been nicknamed Sunray lettuce coral (Humann and DeLoach 2013).

Live specimens have been recorded from lower reef slopes, including the mesophotic down to 99 m depth (Bak 1975; Kahng et al. 2010; Bongaerts et al. 2013; Jaap 2015; Hoeksema and Van Moorsel 2016). Dead fragments of recently deceased colonies have been dredged from > 150 m depth (Santodomingo et al. 2007). At some localities, declines in its abundance have been recorded, especially reduced densities of its recruits over time, which eventually affect whole populations (Hughes and Tanner 2000; Vermeij et al. 2011; Miller et al. 2016). This is consistent with provenance data available from *H. cucullata* specimens in the coral collection of Naturalis Biodiversity Center (Leiden, The Netherlands). Seven *H. cucullata* corals in this collection were sampled in the 1970s from lower reef slopes (12–30 m depth) at three localities in Curaçao, where the species has become rare or

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absent since then (Hoeksema pers. observ.). These findings are corroborated by observations at other localities on the same island by Vermeij et al. (2011), who linked a drastic decrease in the density of juvenile *H. cucullata* to a decline in reef health. Earlier assessments by Aronson et al. (2008), who stated that no large declines have been observed and that the conservation status of *H. cucullata* in the IUCN Red List of Threatened Species should be considered of “least concern”, are therefore in need of a reevaluation. In view of the recently recognized phylogenetic position of *H. cucullata* (Huang 2012; Kitahara et al. 2012, 2016), such a reconsideration may also result in a higher conservation priority based on its EDGE score (Evolutionarily Distinct and Globally Endangered; see Curnick et al. 2015).

Corals not only contribute to reef biodiversity by themselves, but also serve as host for assemblages of associated fauna (Scott 1987; Stella et al. 2011) that could contain host-specific species (Hoeksema et al. 2012). Hence, the protection of particular corals is also important for the conservation of entire reef faunal assemblages (Huang et al. 2016). Knowledge of coral associates is also relevant, since most of them are filter-feeding heterotrophs. Consequently, their abundance on reefs may also be indicative of environmental stress caused by eutrophication and sedimentation (Risk et al. 2001; Scaps and Denis 2008; Samimi Namin et al. 2010).

Recent studies in the Indo-Pacific targeting scleractinian species for associated fauna have resulted in new host records for small or hidden species of, for example, parasitic snails (Gittenberger and Gittenberger 2011; Gittenberger and Hoeksema 2013), benthic ctenophores (Hoeksema et al. 2013; Alamaru et al. 2016), copepods (Ivanenko et al. 2014), hydroids (Montano et al. 2014, 2015a, b), cryptobenthic fish (Bos 2012; Bos and Hoeksema 2015), and commensal shrimps (Fransen and Rauch 2013; Đuriš and Lin 2016). New host records were also obtained during recent studies of Scleractinia-associated fauna in the Caribbean. They concern, for instance, gall crabs (Van der Meij 2014), serpulids (Hoeksema and Ten Hove 2016), commensal shrimps (Brinkmann and Fransen 2016), hydroids (Montano et al. 2016), and corallivorous snails (Potkamp 2016).

Probably due to its relatively deep distribution range compared to many other reef corals (>12 m depth) and its rarity, only two cases appear to be available concerning *H. cucullata* as a host coral (see Stella et al. 2011). One mentions a single *H. cucullata* coral as host of a corallivorous snail, *Coralliophila galea* (Dillwyn, 1823), erroneously referred to as *C. abbreviata* Lamarck, 1816 (Miller 1981). The other one mentions several *H. cucullata* corals showing infestations by coral barnacles (Scott 1987). Recent studies at Curaçao, in which scleractinians were systematically examined for associated coral gall crabs and serpulid worms, also failed to discover *H. cucullata* specimens as host corals (Van der Meij 2014; Hoeksema and Ten Hove 2016). Therefore, for the

present study it was hypothesized that field surveys targeting coral species with a poor reputation as host coral, such as in this case *H. cucullata* (Scott 1987), would result in new discoveries of associations. During a recent marine biodiversity survey at St. Eustatius (eastern Caribbean; Hoeksema 2016), *H. cucullata* appeared to be relatively common (García-Hernández et al. 2016; Hoeksema and Van Moorsel 2016). This offered an opportunity to study its associated fauna, the topic of the present report.

Material and methods

During the marine biodiversity survey of St. Eustatius, in June 2015, stony corals were inspected for the presence of associated fauna by use of the roving diver technique (Hoeksema and Van Moorsel 2016). St. Eustatius is located in the eastern Caribbean, where it has a wave-exposed coastline at its eastward Atlantic side and a sheltered coast at the western, Caribbean shoreline (Hoeksema 2016). The maximum depth for the observations was 30 m due to SCUBA safety regulations. Among a total of 39 dives of approximately 60 min, 36 dives exceeded 12 m, covering the preferred depth range of *H. cucullata*. Clearly visible associated macrofauna was photographed, sampled, and stored in 96 % ethanol for further examination. In a survey of coral-associated copepods, in as many coral species as possible, four *Helioseris* colonies were examined for the presence of associated copepods (Ivanenko 2016). The corals were collected and isolated in plastic bags underwater; in the laboratory, ethanol was added to the bags (adjusting solution 10%), and the hosts were kept in the solution for 20–30 min; then the symbionts were shaken and the residue with anaesthetized copepods was passed through a fine sieve (mesh size 60 µm). The corals were also examined for presence of copepods living in galls or polyps. The dry coral collection of Naturalis Biodiversity Center was inspected for additional associations involving *H. cucullata*. Collection numbers are coded “RMNH Coel.” for specimens in the collection of the former Rijksmuseum van Natuurlijke Historie and “ZMA Coel.” for the former Zoological Museum, University of Amsterdam.

Results and discussion

Helioseris cucullata was observed during 14 of 36 dives (40%) in a depth range of 12–30 m. All specimens were found at the sheltered Caribbean side of St. Eustatius, where most dive sites were located (Hoeksema and Van Moorsel 2016). On average, two to three specimens (maximum five) were observed on dives where the species was present. Three new association

Table 1 Old and new records of West Atlantic coral species, among them *Helioseris cucullata*, recorded as host of *Spirobranchus giganteus*, *Vermiliopsis* sp., *Opecarcinus hypostegus*, *Megatrema madreporarum*, and Copepoda

	<i>S. giganteus</i>	<i>Vermiliopsis</i>	<i>O. hypostegus</i>	<i>M. madreporarum</i>	Copepoda
Acroporidae					
<i>Acropora palmata</i> (Lamarck, 1816)	a, f	-	-	-	h, j
Agariciidae					
<i>Agaricia agaricites</i> (Linnaeus, 1758)	a	-	c	d, f, g	n
<i>Agaricia fragilis</i> Dana, 1848	-	-	c	g	n
<i>Agaricia grahamae</i> Wells, 1973	-	-	c	f	-
<i>Agaricia humilis</i> Verrill, 1901	a	-	c	-	-
<i>Agaricia lamarcki</i> Milne Edwards and Haime, 1851	a	-	c	f, g	n
<i>Helioseris cucullata</i> (Ellis and Solander, 1786)	+	+	+	f	-
Astrocoeniidae					
<i>Stephanocoenia intersepta</i> (Lamarck, 1816)	a	b	-	f	n
Dendrophylliidae					
<i>Rhizopsammia goesi</i> (Lindström, 1877)	a	-	-	-	-
<i>Tubastraea coccinea</i> Lesson, 1829	a	a	-	-	n
Meandrinidae					
<i>Dendrogyra cylindrus</i> Ehrenberg, 1834	a	-	-	-	h, n
<i>Dichocoenia stokesii</i> Milne Edwards and Haime, 1848	a	-	-	f	h, n
<i>Eusmilia fastigiata</i> (Pallas, 1766)	a	-	-	-	h, n
<i>Meandrina danae</i> (Milne Edwards and Haime, 1848)	-	-	-	-	n
<i>Meandrina meandrites</i> (Linnaeus, 1758)	a	-	-	-	h, j, l, n
Merulinidae					
<i>Orbicella annularis</i> (Ellis and Solander, 1786)	a	-	-	-	h, k, l
<i>Orbicella faveolata</i> (Ellis and Solander, 1786)	a	-	-	-	n
<i>Orbicella franksi</i> (Gregory, 1895)	a	-	-	-	n
Montastraeidae					
<i>Montastraea cavernosa</i> (Linnaeus, 1767)	a	-	-	-	h, i, j, l, n
Mussidae					
<i>Colpophyllia natans</i> (Houttuyn, 1772)	a	-	-	-	h, j, k,
<i>Favia fragum</i> (Esper, 1795)	-	-	-	-	k
<i>Isophyllia rigida</i> (Dana, 1846)	-	-	-	-	n
<i>Isophyllia sinuosa</i> (Ellis and Solander, 1786)	-	-	-	-	n
<i>Manicina areolata</i> (Linnaeus, 1758)	-	-	-	-	h, k, n
<i>Mycetophyllia aliciae</i> Wells, 1973	-	-	-	-	n
<i>Mycetophyllia ferox</i> Wells, 1973	-	-	-	f	-
<i>Mycetophyllia lamarckiana</i> Wells, 1973	-	-	-	-	j, m
<i>Mussa angulosa</i> (Pallas, 1766)	-	-	-	-	n
<i>Mussismilia hispida</i> (Verrill, 1901)	-	-	? c	-	-
<i>Diploria labyrinthiformis</i> (Linnaeus, 1758)	a	-	-	-	h
<i>Pseudodiploria clivosa</i> (Ellis and Solander, 1786)	-	-	-	-	h, j, k, n
<i>Pseudodiploria strigosa</i> (Dana, 1846)	a	-	-	-	h, j, k, n
Oculinidae					
<i>Oculina valenciennesi</i> Milne Edwards and Haime, 1850	a	-	-	-	-
Pocilloporidae					
<i>Madracis auretenra</i> Locke, Weil & Coates, 2007	a	-	-	f	n
<i>Madracis decactis</i> (Lyman, 1859)	a	-	-	e, f	-
<i>Madracis formosa</i> Wells, 1973	a	-	-	-	-
<i>Madracis pharensis</i> (Heller, 1868)	a	-	-	-	-

Table 1 (continued)

	<i>S. giganteus</i>	<i>Vermiliopsis</i>	<i>O. hypostegus</i>	<i>M. madreporarum</i>	Copepoda
Poritidae					
<i>Porites astreoides</i> Lamarck, 1816	a	-	-	-	n
<i>Porites branneri</i> Rathbun, 1887	a	-	-	-	-
<i>Porites divaricata</i> Le Sueur, 1820	-	-	-	-	n
<i>Porites furcata</i> Lamarck, 1816	a	-	-	-	n
<i>Porites porites</i> (Pallas, 1766)	a	-	-	-	-
Siderastreaeidae					
<i>Siderastrea siderea</i> (Ellis and Solander, 1768)	a	-	? c	-	n
<i>Siderastrea stellata</i> (Verrill, 1868)	-	-	? c	-	-
Scleractinia incertae sedis					
<i>Solenastrea bournoni</i> Milne Edwards and Haime, 1849	-	-	-	-	n

New host records are marked by +. Absent records (presumed) by -. Previous host records are from (a) Hoeksema and Ten Hove (2016); (b) Martin and Britayev (1998); (c, ? c = doubtful record) Van der Meij (2014); (d) Ross and Newman (1973); (e) Bacon et al. (1984); (f) Scott (1987); (g) Young (1988); (h) Stock (1975a); (i) Stock (1975b); (j) Herriott and Immermann (1979); (k) Stock (1987); (l) Stock (1989); (m) Varela et al. (2005); (n) Ivanenko (2016)

records with *H. cucullata* were discovered (Table 1): the serpulids *Spirobranchus giganteus* (Pallas, 1766) ($n = 1$) and *Vermiliopsis* sp. ($n = 1$) (Fig. 1), and the cryptochirid *Opecarcinus hypostegus* (Shaw and Hopkins, 1977) ($n = 1$). A second association record (first by Scott 1987) is reported for the coral barnacle *Megatrema madreporarum* (Bosc, 1812), in this case with up to ~20 specimens per host (Fig. 2). Although 26 reef coral species were observed hosting copepods (Table 1; Ivanenko 2016) they were not found in *H. cucullata*. One *H. cucullata* colony has been observed in association with a sponge of the species *Agelas conifer* (Schmidt, 1870), showing the same kind of interactive behaviour as *Agaricia* corals, viz. overgrowing the sponge (García-Hernández et al. 2016). Scleractinia-associated hydroids were discovered for the first time in the Atlantic during the St. Eustatius expedition in 2015 (Montano et al. 2016), but not on *H. cucullata*. They could have been overlooked due to their small sizes (~1 mm; see, for example, Montano et al. 2015a, 2016).

Only a few new associations were recorded. Although *Spirobranchus giganteus* appears not to have been recorded from St. Eustatius before (Ten Hove 1970), during the 2015 survey it was common on various host coral species. Only a single specimen was found in association with *H. cucullata* (Fig. 1a, b), representing the 29th host record (Table 1). This is consistent with the finding that this serpulid is a common host generalist (Hunte et al. 1990; Hoeksema and Ten Hove 2016). Earlier, this association was probably not reported because this host is usually less common than other corals (e.g., Scott 1987) and virtually absent in shallow waters (<10 m depth). Other new host discoveries for *Spirobranchus* were also made by targeting various potential host species (Hoeksema and Ten Hove 2014, 2016; Hoeksema et al. 2015; Van der Schoot et al. 2016).

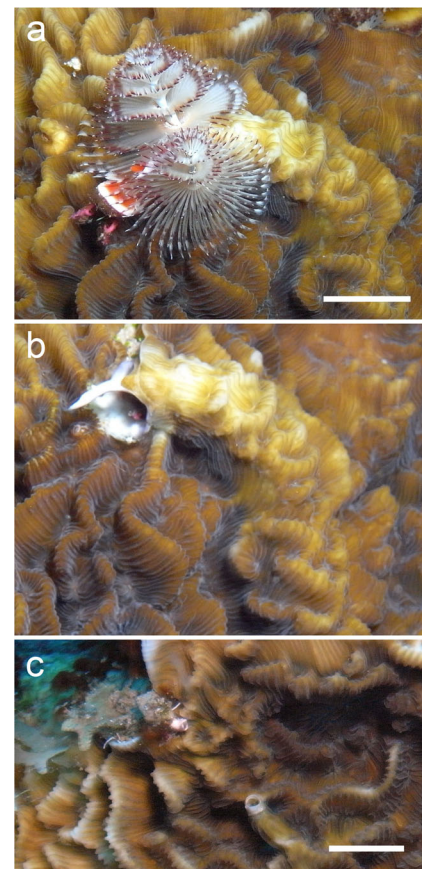
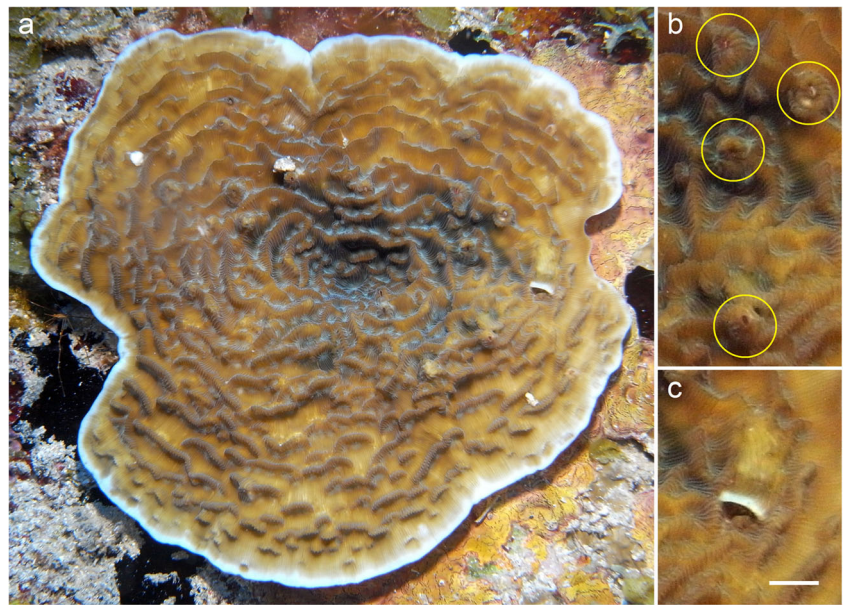


Fig. 1 *Helioseris cucullata* host corals with serpulid worms at St. Eustatius. **a** Extended *Spirobranchus giganteus* worm showing twin spiral branchiae and pink antler-shaped opercular spines. **b** Same worm contracted, showing the coral-embedded tube and a large spine at its opening. **c** Two tubes of *Vermiliopsis* sp., one growing from the lower side with opening at the corallum margin and one embedded in the coral with opening in the centre. Scale bars: 0.5 cm

Fig. 2 *Helioseris cucullata* host coral with associated crustacean fauna at St. Eustatius. **a** Entire coral. **b** Close-up showing barnacles, *Megatrema madreporarum*. **c** Close-up of dwelling occupied by a gall crab, *Opecarcinus hypostegus*. Scale bar (for **b** and **c**): 0.5 cm



One specimen of *H. cucullata* showed an association with two individuals of another serpulid, an unidentified *Vermiliopsis* sp. (Fig. 1c). The radioles were retracted inside the tubes, but the genus was identified based on its light-brown chitinous (horn-like) operculum cap (Ten Hove and Kupriyanova 2009). One species, *Vermiliopsis annulata* (Schmarda, 1861), is common in the Caribbean and was also found during the St. Eustatius expedition, but not always associated with corals (e.g., Ten Hove and San Martín 1995; Bastida-Zavala 2012; Hepburn et al. 2015). Observations of *Vermiliopsis* spp. in corals are rare (Table 1), and in literature reviews of coral-associated polychaetes they are usually not mentioned (Stella et al. 2011; Molodtsova et al. 2016). So far it only appeared to have been reported as an associate of *Stephanocoenia intersepta* (Martin and Britayev 1998; Humann et al. 2013) and the invasive *Tubastraea coccinea* (Lesson, 1829) (Hoeksema and Ten Hove 2016). These serpulids prefer downward-facing substrates (Hepburn et al. 2015), and are therefore most likely found at the undersurface of corals (e.g., Hoeksema and Ten Hove 2016). One individual in the present study was primarily attached to the lower side of the coral margin, while the other penetrated the coral's upper surface (Fig. 1c). In *H. cucullata* no specimens were observed of the Caribbean coral-dwelling serpulid *Pseudovermilia madracicola* Ten Hove, 1989, so far only recorded from *Madracis decactis* and *Madracis pharensis* (Ten Hove 1989). During the survey at St. Eustatius, this serpulid with red radioles was observed in specimens of *M. pharensis* and *Madracis senaria* Wells, 1973.

Coral gall crabs are considered part of the reef's cryptofauna because they are small and reside in dwellings on the coral surface. They are easily overlooked but may appear to be abundant when received special focus in field surveys (Hoeksema and Van

der Meij 2013; Van der Meij and Hoeksema 2013). At St. Eustatius, one non-ovigerous *Opecarcinus hypostegus* female was found in *H. cucullata* at 30 m depth (Fig. 2a, c). Previously, this crab was reported from eight host coral species, but three of these records are doubtful (Table 1). New records show that *O. hypostegus* probably only occurs in species belonging to the coral family Agariciidae. Earlier records from the Siderastreidae should probably be attributed to the recently described cryptochirid species *Kroppcarcinus siderastreicola* Badaro, Castro, and Johnson, 2012 (Van der Meij 2014; Van der Meij et al. 2015a). Again, the relatively low abundance of the host at other localities may have prevented earlier discoveries of this association (Van der Meij 2014). In *Agaricia* hosts, this crab appears to be most abundant at lower reef slopes (Van Tienderen and Van der Meij 2016), and occurs even at 60 m depth (Van der Meij et al. 2015a). The present gall crab observation is consistent with our hypothesis that a specific search for associated fauna in potential host corals may result in new association records (see also Van der Meij 2014, 2015a, 2015b; Van der Meij et al. 2015b).

Coral-inhabiting barnacles are common on reefs, and therefore the second record of an association between *Megatrema madreporarum* and *H. cucullata*, after Scott's (1987), is not surprising (Fig. 2b), considering that few studies on these barnacles have been performed in the Caribbean. Six *H. cucullata* corals in the coral collection of Naturalis Biodiversity Center also contain such barnacles. Out of eight colonies collected at Curaçao in 1974 and 1977, four hosted barnacles: RMNH Coel. 8570, 13783 — two specimens, ZMA Coel. 7522. Two more hosts were collected in 1972 close to St. Eustatius: at Saba (RMNH Coel. 8569) and at Saba Bank (RMNH Coel. 8573). Apparently, these *H. cucullata* specimens were overlooked in the collection,

since they were not recorded in the expedition report (Van der Land 1977). These results confirm the importance of reference collections in baseline studies (Hoeksema et al. 2011).

The taxonomy of *Megatrema madreporarum* is described in detail by Ross and Newman (1973). They present a clear illustration of several specimens (as *Boscia*) in an *Agaricia* coral from Key West, Florida. In total, *M. madreporarum* has been reported from ten host species, among them *H. cucullata* and four *Agaricia* spp. (Table 1). An extensive overview of Caribbean coral barnacles and their hosts is not available yet (Table 1; Ross and Newman 2002). Recent studies have shed more light on the phylogenetic relations of coral-dwelling barnacles, but these included only three Atlantic species and not *Megatrema* (Malay and Michonneau 2014; Simon-Blecher et al. 2016).

No associated copepods were found in *H. cucullata*. Also, no previous records are known for this coral (Cheng et al. 2016; Walter and Boxshall 2016), whereas 26 other scleractinians in the present survey appeared to serve as host for copepods out of a total of 32 host corals for the whole Caribbean (Table 1). Three of these scleractinians (*Agaricia* spp.) belong to the same family (Agariciidae) as *Helioseris*. The 21 coral-dwelling copepod species consisted of ten endosymbionts (Poecilostomatoida: Corallovexiidae) (Stock 1975a; Butter 1979; Herriott and Immermann 1979) and 11 ectosymbionts (Siphonostomatoida: Asterocheridae) (Stock 1975b, 1987, 1989; Varela et al. 2005; Kim 2010).

The present study shows that surveys targeting specific coral species can result in new association records, in this case involving serpulid worms and a coral gall crab as associates of *H. cucullata*. Due to the approach followed in the present study, by dealing specifically with the associated fauna of a single host coral species, *H. cucullata* appears to be richer in associates than many other Caribbean coral species (Table 1). This probably reflects the additional research effort executed in this study.

Little is known about differences in possible biological defense mechanisms among coral species. Such mechanisms might explain why some corals are more hospitable hosts than others, or behave differently (adaptive, aggressive, evasive, submissive, or neutrally tolerant) when they come in contact with other organisms (Chadwick and Morrow 2011; Hoeksema and De Voogd 2012; Hoeksema et al. 2014; Elliott et al. 2016; García-Hernández et al. 2016; Hammerman and García-Hernández 2016). Other associations may simply occur at greater depths and may require other methods than use of SCUBA for their discovery or for examination of their lower depth ranges (e.g., Van der Meij et al. 2015a). Many interspecific associations may remain undiscovered, particularly when hosts are increasingly threatened with extinction (see Carpenter et al. 2008; Huang 2012; Curnick et al. 2015). Attention to the number of coral associates per host coral (Scott 1987; Hoeksema et al. 2012) may therefore offer valuable information in studies of coral-reef conservation status (Stella et al. 2011).

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