



Article

# Morphological Modifications and Injuries of Corals Caused by Symbiotic Feather Duster Worms (Sabellidae) in the Caribbean

Bert W. Hoeksema <sup>1,2,3,\*</sup>, Rosalie F. Timmerman <sup>1,2</sup>, Roselle Spaargaren <sup>1,2</sup>, Annabel Smith-Moorhouse <sup>1,2</sup>, Roel J. van der Schoot <sup>1,2</sup>, Sean J. Langdon-Down <sup>1,2</sup> and Charlotte E. Harper <sup>1,2</sup>

- Taxonomy, Systematics and Geodiversity Group, Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands; r.f.timmerman@student.rug.nl (R.F.T.); r.spaargaren@student.rug.nl (R.S.); a.smith-moorhouse@student.rug.nl (A.S.-M.); roel.vanderschoot@naturalis.nl (R.J.v.d.S.); s.langdon-down@student.rug.nl (S.J.L.-D.); c.harper@student.rug.nl (C.E.H.)
- Groningen Institute for Evolutionary Life Sciences, University of Groningen, P.O. Box 11103, 9700 CC Groningen, The Netherlands
- <sup>3</sup> Institute of Biology Leiden, Leiden University, P.O. Box 9505, 2300 RA Leiden, The Netherlands
- \* Correspondence: bert.hoeksema@naturalis.nl

**Abstract:** Some coral-associated invertebrates are known for the negative impact they have on the health of their hosts. During biodiversity surveys on the coral reefs of Curaçao and a study of photo archives of Curaçao, Bonaire, and St. Eustatius, the Caribbean split-crown feather duster worm *Anamobaea* sp. (Sabellidae) was discovered as an associate of 27 stony coral species (Scleractinia spp. and *Millepora* spp.). The worm was also found in association with an encrusting octocoral (*Erythropodium caribaeorum*), a colonial tunicate (*Trididemnum solidum*), various sponge species, and thallose algae (mainly *Lobophora* sp.), each hypothesized to be secondary hosts. The worms were also common on dead coral. Sabellids of the genera *Bispira* and *Sabellastarte* were all found on dead coral. Some of them appeared to have settled next to live corals or on patches of dead coral skeleton surrounded by living coral tissue, forming pseudo-associations. Associated *Anamobaea* worms can cause distinct injuries in most host coral species and morphological deformities in a few of them. Since *Anamobaea* worms can form high densities, they have the potential to become a pest species on Caribbean coral reefs when environmental conditions become more favorable for them.

**Keywords:** *Anamobaea*; *Bispira*; coral damage; host generalist; Polychaeta; pseudo-association; *Sabellastarte* 



Citation: Hoeksema, B.W.; Timmerman, R.F.; Spaargaren, R.; Smith-Moorhouse, A.; van der Schoot, R.J.; Langdon-Down, S.J.; Harper, C.E. Morphological Modifications and Injuries of Corals Caused by Symbiotic Feather Duster Worms (Sabellidae) in the Caribbean. *Diversity* 2022, 14, 332. https:// doi.org/10.3390/d14050332

Academic Editor: Cinzia Corinaldesi

Received: 27 March 2022 Accepted: 21 April 2022 Published: 25 April 2022

**Publisher's Note:** MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https://creativecommons.org/licenses/by/4.0/).

### 1. Introduction

As foundation species, reef corals provide a habitat to a large diversity of marine invertebrates, which represent a variety of phyla [1–4]. A large proportion of these invertebrate taxa use these corals as living hosts, whereas others only need dead coral as a rocky substrate for settlement and growth. The first category mostly contains species that live in strict symbiotic relations with their host corals (be it commensalistic, mutualistic, or parasitic) and are generally known as coral-associated fauna [5,6]. Due to their vulnerability to disturbance, their presence is supposed to be indicative of reef health [7,8]. These relations may vary because, in some studies, coral-associated species are reported as beneficial to their host by offering protection against predators and diseases [9–13] or cleaning services [14]. In other hosts, associated species are shown to be harmful by causing coral injuries or by obstructing the host's growth [15–20].

It is not precisely known if some reef-dwelling invertebrates, such as feather duster worms (fan worms) of the family Sabellidae, live in symbiosis with corals. Sabellida are tube-forming, solitary, or colonial sedentary polychaetes occurring in benthic environments. The protective tube is usually flexible and predominantly buried in sediment or attached to

Diversity 2022, 14, 332 2 of 19

a hard substrate [21]. The animals have two sets of colorful radiolar tentacles (radioles), which normally extend from their tube and are used for feeding and respiration [22–24].

Although various sabellid species have been reported to live in coral reefs or more specifically on dead coral [25–32], they have received little or no attention in the literature about coral-associated fauna [8,33-45] and symbiotic polychaetes [46-48], in contrast with serpulid worms. Only a few publications mention the identity of sabellid worms and their host coral species, such as the sabellids Amphicorina schlenzae Nogueira & Amaral, 2000 and Pseudobranchiomma minima Nogueira & Knight-Jones, 2002 in living colonies of the Brazilian endemic scleractinian Mussimilia hispida (Verrill, 1901) [49,50]. Furthermore, there are records from Indonesia of Perkinsiana anodina Capa, 2007 in an encrusting mushroom coral Cycloseris explanulata (van der Horst, 1922), misidentified as C. wellsi (Veron & Pichon, 1980) [51,52], and Notaulax montiporicola Tovar-Hernández & ten Hove, 2020, associated with the foliaceous coral Montipora nodosa (Dana, 1846) [24,32,51]. Finally, the fan worm Notaulax yamasui Nishi et al., 2017 was recorded from dead and living Porites sp. in Okinawa Island, southern Japan [53]. None of these association records are from the Caribbean. However, there is a published photograph of a colonial feather duster worm Bispira brunnea (Treadwell, 1917) on top of a coral wound of an unidentified scleractinian in the Mexican Caribbean [54].

During a recent biodiversity survey of coral reefs of Curaçao (southern Caribbean), associations of split-crown feather duster worms (*Anamobaea* sp.) [22,27,29] with corals were observed to be abundant. Because these associations were not reported before and the presence of these worms appeared to cause aberrant growth forms and injuries in host corals, we investigated which host coral species were affected. The present report serves to create awareness of these associations and of the potential damage the worms may cause to Caribbean coral reefs. Several sabellids of the genera *Bispira* Krøyer, 1856 and *Sabellastarte* Krøyer, 1856 [22,27,29] were found in close proximity to corals, but appeared to have settled next to their hosts or on patches of dead coral skeleton surrounded by living coral tissue.

## 2. Materials and Methods

The surveys took place during October–December 2021 and April 2022 along the leeward side of the island of Curaçao at depths down to 20 m. To investigate the preferred habitats of symbiotic feather duster worms, all observed host coral species were recorded and photographed, as well as other host species that were encountered. Because coral-dwelling feather duster worms were not recorded before in the Caribbean, coral photographs taken by the first author during earlier surveys were also checked for the presence of symbiotic feather duster worms: Curaçao (in 2017, 2015, and 2014), Bonaire (in 2019), and St. Eustatius (in 2015). Curaçao and Bonaire are located in the Southern Caribbean, and St. Eustatius is in the Eastern Caribbean (Figure 1). All association records were listed per island and year (Table 1).

#### 3. Results

Twenty-seven host-coral species, consisting of 25 scleractinians (Anthozoa) and two milleporids (Hydrozoa), were recorded for the coral-associated feather duster worm, divided over 10 families and 16 genera (Table 1; Figures 2–7). In addition, the species was found in association with the encrusting octocoral *Erythropodium caribaeorum* (Figure 8A,B), the colonial tunicate *Trididemnum solidum* (Figure 8C,D), phaeophyceaen algae, in particular *Lobophora* sp. (Figure 8E,F), and various sponge species (Figure 9). The records were from the southern Caribbean islands of Bonaire and Curação and the Eastern Caribbean island of St. Eustatius (Table 1).

Diversity 2022, 14, 332 3 of 19



**Figure 1.** Map of the eastern part of the Caribbean showing the position of Curaçao, Bonaire, and St. Eustatius, where the presence of coral-associated feather duster worms was investigated.

The symbiotic worms, identified as split-crown feather duster worms of the genus *Anamobaea* Krøyer, 1856 [22,27,29], showed some variation in coloration, ranging from white to dark red and various combination patterns of these colors (Figures 2, 3 and 9A). Two species from the Caribbean have been described, which can be distinguished by two morphological characters [27,29,32] that are not clearly visible in the photographs: *Anamobaea phyllisae* Tovar-Hernández & Salazar-Vallejo, 2006 has two dorsal kidney-shaped shields over the anterior margin of the base of its crown and smooth flanges (without papillae) and *Anamobaea orstedi* Krøyer, 1856 does not have such shields, and its flanges are wrinkled (with papillae). The former species has so far only been reported from the type locality in the British Virgin Islands, whereas the latter has a wider geographic range [29,32]. Because we are not sure about the identity of the associated worms, we refer to them as *Anamobaea* sp.

Most observed worms were withdrawn in their tubes; only a few of them were observed with extended radioles protruding from the tube (Figures 2 and 3). Some extended worms appeared to be shy and quickly retracted into the tube when their pictures were taken (Figure 3). On some occasions, the worms showed high densities, either inside a living host (Figures 2A,B,D, 4E and 6A) or on dead coral (Figure 3C,D).

Some host coral species showed peak-shaped deformities around the worm tubes (Figure 4). In the foliaceous coral *Agaricia lamarcki*, the deformity resembles a sleeve that continues to grow upward and in thickness around the worm's tube, allowing the top to remain free (Figure 4A,B). Peak-shaped deformities in various sizes were most abundantly found in *Pseudodiploria strigosa* (Figure 4C–E) and less commonly in *Orbicella annularis* and *O. franksi* (Figure 4F,G). When the largest peak found in *P. strigosa* (Figure 4C) was removed, the worm tube appeared to be at least 8 cm long and deeply embedded inside the remaining part of the host coral (Figure 5).

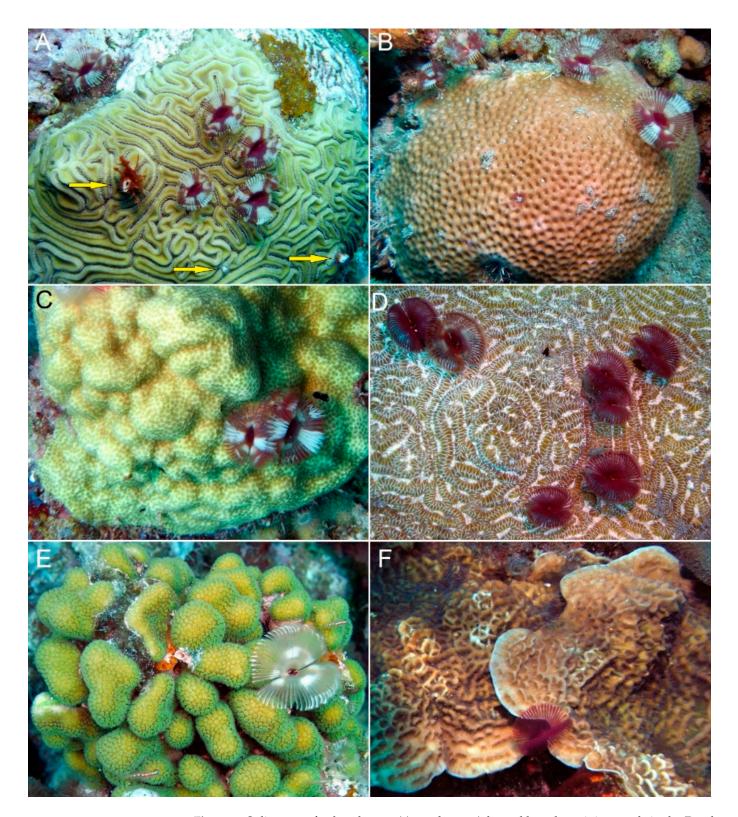
Coral injuries were abundant around worm tubes in various coral species (Figures 6 and 7). The wounds, visible as dead lesions, were either at the periphery of live coral tissue (Figure 6A,B) or more toward the middle and surrounded by live coral tissue (Figures 6C,D and 7). Some dead patches were used as substrates by algae and sponges (Figures 6 and 7). In some coral species, the live tissue around the gash showed a discoloration, suggesting that it was spreading from the wound centered around the worm (Figure 7C,D,F).

Diversity 2022, 14, 332 4 of 19

**Table 1.** Records of stony corals and other sessile invertebrates as host species (by family) for sabellid worms (*Anamobaea* sp.) based on photographs taken at Curaçao (a: 2021 and 2022; b: 2017; c: 2015; and d: 2014), Bonaire (e: 2019), and St. Eustatius (f: 2015).

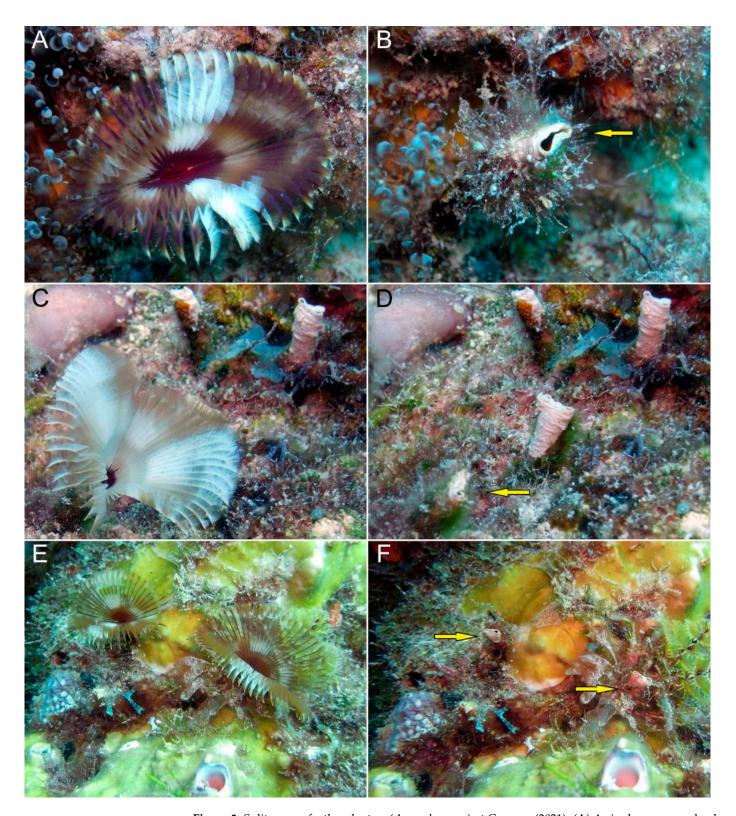
Host Species	Curaçao	Bonaire	St. Eustatius
Cnidaria: Anthozoa: Scleractinia			
Agariciidae			
Agaricia agaricites (Linnaeus, 1758)	a	e	-
Agaricia fragilis Dana, 1846	a	-	f
Agaricia humilis (Verrill, 1901)	a	-	-
Agaricia lamarcki Milne Edwards & Haime, 1851	a,b,d	-	f
Helioseris cucullata (Ellis and Solander, 1786)	a	-	f
Astrocoeniidae			
Stephanocoenia intersepta (Esper, 1795)	a,b	-	f
Faviidae: Faviinae			
Colpophyllia natans (Houttuyn, 1772)	a,b	-	-
Diploria labyrinthiformis (Linnaeus, 1758)	a	-	f
Pseudodiploria strigosa (Dana, 1846)	a,d	_	-
Faviidae: Mussiinae			
Mycetophyllia aliciae Wells, 1973	-	_	f
Meandrinidae			
Eusmilia fastigiata (Pallas, 1766)	b	-	-
Meandrina jacksoni Weil & Pinzón, 2011	_	_	f
<i>Meandrina meandrites</i> (Linnaeus, 1758)	a,c	e	f
Merulinidae	u/c	C	•
Dendrogyra cylindrus (Ehrenberg, 1834)	a	_	-
Orbicella annularis (Ellis & Solander, 1786)	a	_	f
Orbicella faveolata (Ellis & Solander, 1766)	a	-	1
Orbicella franksi (Gregory, 1895)		e	f
Montastraeidae	a,b,d	e	1
	a b		
Montastraea cavernosa (Linnaeus, 1767)	a,b	-	-
Pocilloporidae	- 1-		
Madracis auretenra Locke, Weil & Coates, 2007	a,b	-	-
Madracis decactis (Lyman, 1859)	a	-	-
Madracis pharensis (Heller, 1868)	a,b	e	f
Madracis senaria Wells, 1973	a,b	e	-
Poritidae			
Porites astreoides Lamarck, 1816	a,d	e	f
Porites porites (Pallas, 1766)	-	-	f
Rhizangiidae			
Siderastrea siderea (Ellis & Solander, 1768)	a,b	=	f
Cnidaria: Hydrozoa			
Milleporidae			
Millepora alcicornis Linnaeus, 1758	a	e	-
Millepora complanata Lamarck, 1816	a	-	-
Cnidaria: Anthozoa: Alcyonacea			
Anthothelidae			
Erythropodium caribaeorum	_		
(Duchassaing & Michelotti, 1860)	a	-	-
Chordata: Tunicata: Ascidiacea			
Didemnidae			
Trididemnum solidum (Van Name, 1902)	a,b	_	-
Porifera spp.	a	_	-
I UIII EI a SDD.			

Diversity **2022**, 14, 332 5 of 19



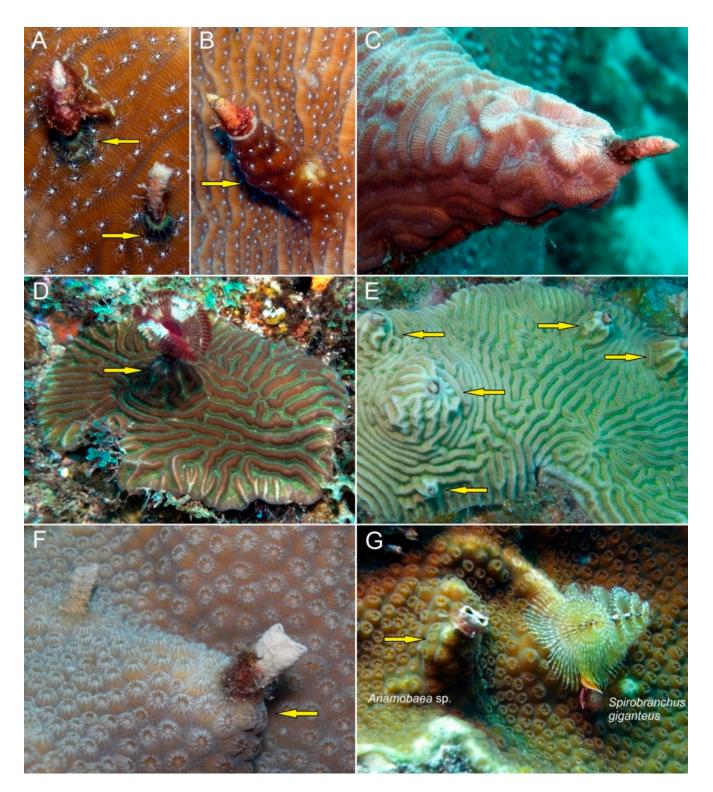
**Figure 2.** Split-crown feather dusters (*Anamobaea* sp.) hosted by scleractinian corals in the Dutch Caribbean. (**A**) *Diploria labyrinthiformis* at St. Eustatius (2015) hosting five extended worms (one next to the coral colony) and three contracted ones (arrows). (**B**) *Siderastrea siderea* at St. Eustatius (2015) with four extended worms (two next to the coral colony). (**C**) *Porites astreoides* at St. Eustatius (2015) showing two extended worms. (**D**) *Meandrina jacksoni* at St. Eustatius (2015) hosting seven extended worms. (**E**) *Madracis decactis* at Bonaire (2019) with two extended worms. (**F**) *Helioseris cucullata* at St. Eustatius (2015) with one extended worm.

Diversity **2022**, 14, 332 6 of 19



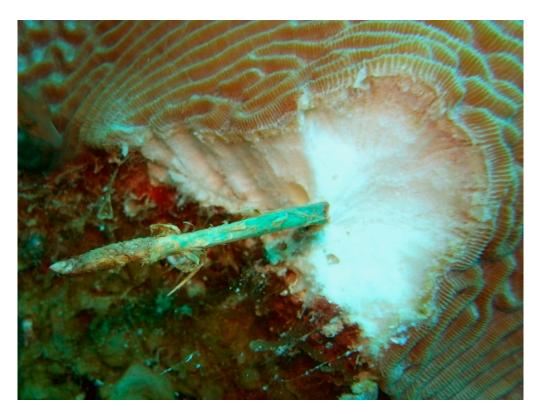
**Figure 3.** Split-crown feather dusters (*Anamobaea* sp.) at Curaçao (2021). (**A**) A single worm on dead coral in the extended condition, showing its radioles. (**B**) The same worm withdrawn inside its tube, overgrown by filamentous algae. (**C**) Four worms on dead coral, one extended. (**D**) The same worms, all withdrawn. (**E**) Two extended worms in association with a *Millepora alcicornis* coral. (**F**) Both worms retracted. Arrows indicate worms that had just retracted. The maximum width of the worm tubes is ca. 5 mm.

Diversity **2022**, 14, 332 7 of 19



**Figure 4.** Coral deformations caused by the presence of split-crown feather dusters (*Anamobaea* sp.) in various host coral species. (**A**,**B**) The host coral *Agaricia lamarcki* at Curaçao (2021) with two peaks in their initial phase (**A**: arrows) and a large peak (**B**: arrow). (**C**) Close-up of the coral *Pseudodiploria strigosa* at Curaçao (2021) showing a large peak. (**D**,**E**) Corals of *P. strigosa* at St. Eustatius (2015), one showing a peak with an extended worm inside (**D**: arrow) and another one with five worm peaks (**E**: arrows). (**F**) *Orbicella annularis* at Curaçao (2021) with one worm peak (arrow). (**G**) *Orbicella franksi* at St. Eustatius (2015) with a small worm peak (arrow), next to a serpulid Christmas tree worm (*S. giganteus*). The maximum width of each sabellid tube is ca. 5 mm.

Diversity 2022, 14, 332 8 of 19



**Figure 5.** Tube of a split-crown feather duster (*Anamobaea* sp.) after removal of the peak-shaped deformation in a *Pseudodiploria strigosa* coral (see Figure 4C). The visible part of the tube is 8 cm long.

Feather duster worms of two other species were not observed inside living corals but in dead skeleton directly next to a living coral or in a patch of dead coral surrounded by healthy coral tissue. They are the magnificent feather duster Sabellastarte magnifica (Shaw, 1800) (Figure 10) and the social feather duster Bispira brunnea (Treadwell, 1917) (Figure 11). Sabellastarte magnifica was found in or next to live coral colonies of the corals Diploria labyrinthiformis, Madracis auretenra, Meandrina meandrites, Millepora alcicornis, Orbicella annularis, Pseudodiploria strigosa, and Stephanocoenia intersepta. Their tubes reached diameters of nearly 2 cm and could therefore be distinguished from the tubes of Anamobaea sp., which reached up to 0.5 cm in width. Bispira brunnea was only found on dead patches of Montastraea cavernosa and Orbicella annularis (Figure 11). A published photograph from the Mexican Caribbean shows *B. brunnea* in a coral injury on top of a colony of *Siderastrea* siderea [54]. This worm species can be distinguished from the other two because it occurs as colonies instead of single individuals and because its tubes and radioles are much smaller than those of the others. Because all Bispira and Sabellastarte worms appeared to live on dead coral skeleton, near live coral, or at a distance, it is unclear whether they were symbionts or part of pseudo-associations.

#### 4. Discussion

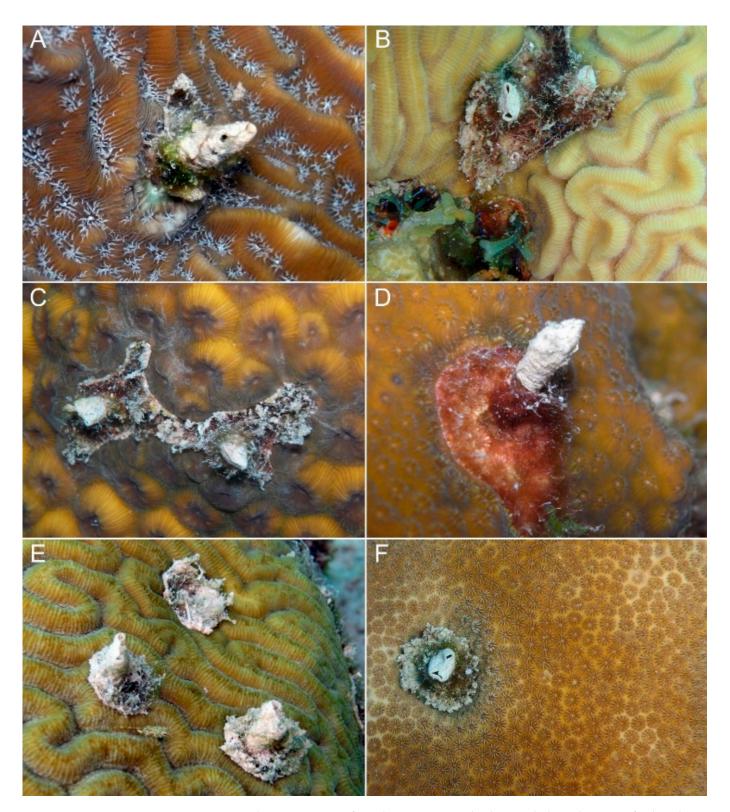
This report presents, for the first time, extensive evidence for the association of feather duster worms with corals, other sessile invertebrates, and algae in the Caribbean. This discovery is remarkable because of the strikingly large wounds and deformities inflicted by them on their host corals. Photographs of the worms indicate that these associations have been present at least since 2014 on the coral reefs of Curaçao (Southern Caribbean) and since 2015 at St. Eustatius (Eastern Caribbean). Prior to that, they may have remained unnoticed because of the worm's withdrawal behavior, because it was perhaps less abundant in the past, or because scientists studying the worms did not pay much attention to the hosts.

Diversity **2022**, 14, 332 9 of 19



**Figure 6.** Overview (**A**) and close-up images (**B**–**F**) of coral damage caused by split-crown feather dusters (*Anamobaea* sp.) on a large *Colpophyllia natans* colony at Curaçao (2021). The images show various developmental stages of coral injuries (dead skeleton covered by turf algae) forming coves at the coral margin (**A**,**B**) and circular patches over the colony surface (**C**–**F**). The maximum width of each tube is ca. 5 mm.

Diversity **2022**, 14, 332



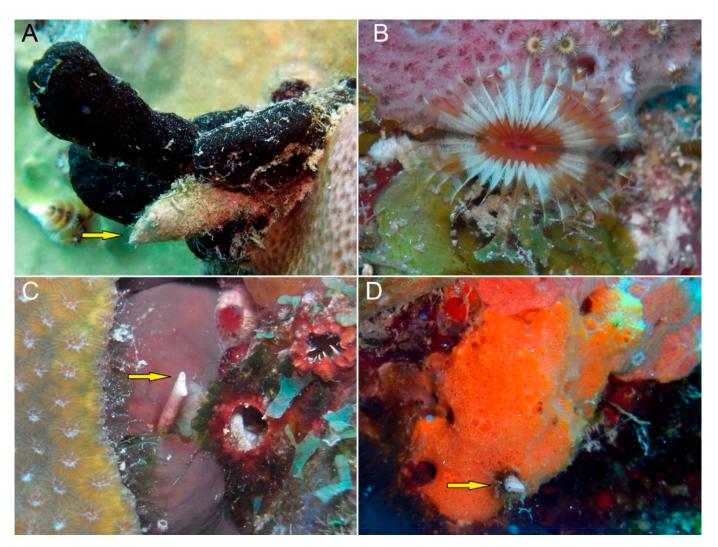
**Figure 7.** Close-up images of coral injuries around tubes made by split-crown feather dusters (*Anamobaea* sp.) shown in retracted condition at Curaçao (2021). The coral injuries are observed in various host species, such as (**A**) *Agaricia lamarcki*, (**B**) *Diploria labyrinthiformis*, (**C**) *Montastraea cavernosa*, (**D**) *Orbicella annularis*, (**E**) *Pseudodiploria strigosa*, and (**F**) *Stephanocoenia intersepta*. In some species, the live tissue around the wound shows a discoloration (**C**,**D**,**F**). The maximum width of each tube is ca. 5 mm.

Diversity **2022**, 14, 332



**Figure 8.** Split-crown feather dusters (*Anamobaea* sp.) hosted by noncoral invertebrates and algae that have overgrown corals: (**A,B**) The encrusting soft coral *Erythropodium caribaeorum* acting as a host on dead coral at Curaçao (2021), with tentacles extended (**A**) and retracted (**B**). (**C,D**) The encrusting colonial ascidian *Trididemnum solidum* at Curaçao overgrowing scleractinian host corals and worm tubes (except for the tube opening): on a scleractinian coral *Eusmilia fastigiata* in 2017 (**C**) and on dead coral in 2021 (**D**). (**E,F**) The phaeophyceaen alga *Lobophora* sp. at Curaçao (2021). Arrows indicate worm tubes. The maximum width of each tube is ca. 5 mm.

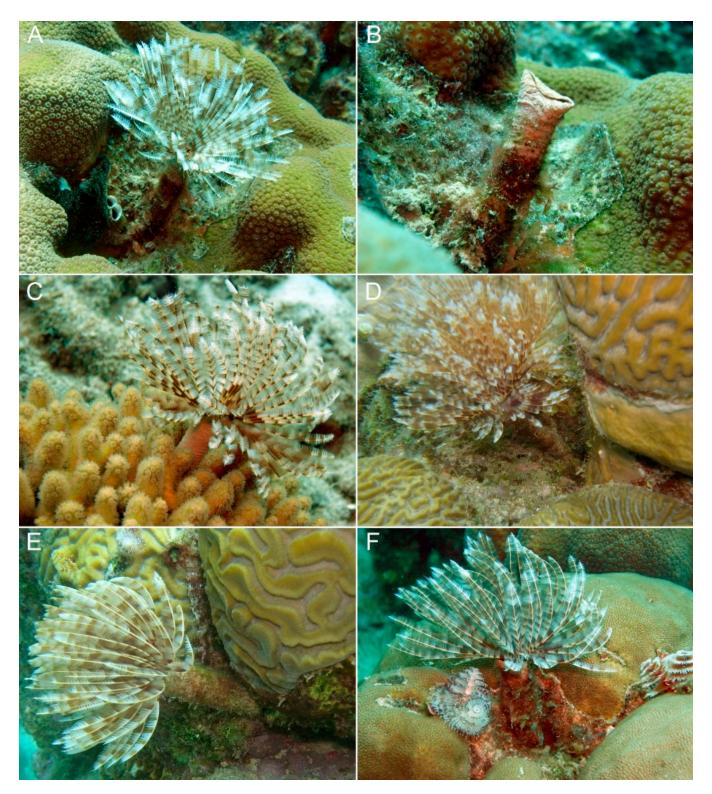
Diversity 2022, 14, 332 12 of 19



**Figure 9.** Split-crown feather dusters (*Anamobaea* sp.) at Curaçao (2021 and 2022) hosted by sponges that probably act as secondary hosts: (**A**) An unidentified black sponge partly overgrowing a worm tube and its host coral, *Siderastrea siderea*. (**B**) A zoantharian-infested sponge, *Niphates* sp., with an expanded worm. (**C**) A dark-red sponge, *Plakortis* sp., with a worm tube (arrow) next to the original host coral, *Orbicella franksi*. (**D**) An orange-red sponge, *Scopalina ruetzleri* (Wiedenmayer, 1977) with one worm tube (arrow). The maximum width of each tube is ca. 5 mm.

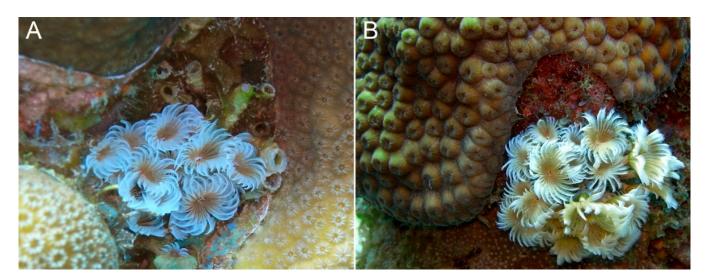
Coral deformities around sabellid worms embedded in the host's skeleton appear to be limited to a few scleractinian species of which *Pseudodiploria strigosa* appears to be the most common. Because coral-dwelling sabellids have been observed deep inside the coral skeleton, and the life span of sabellids may be over 10 years [55], these deformations have taken several years to develop. Morphological anomalies are not exceptional among corals inhabited by associated fauna. For example, the sabellid *Perkinsiana anodina* lives in short tube-shaped protuberances on the surface of an encrusting mushroom coral, which are part of the host's coral skeleton [32,51]. Coral gall crabs have received much attention because of the crescent-, canopy, slit-, and basket-shaped pits inside various coral species [44,56–59]. Coral cysts and pits made by other crabs and by shrimps in stony corals have also been described [60,61], which should not be confused with gall-shaped excavations made by shrimps [62,63], bivalves [64–67], and gastropods [34,68]. Copepods are also known to induce the forming of dwellings in corals, either as galls [69,70] or as tubular outgrowths [71,72]. Ascothoracidan crustaceans of the genus *Petrarca* Fowler, 1889 are known to form conspicuous galls in shallow-water and deep-sea corals [73–75].

Diversity **2022**, 14, 332



**Figure 10.** Magnificent feather dusters (*Sabellastarte magnifica*) at Curaçao (2022) in close proximity to corals. (**A**) An extended worm on a dead coral patch of *Orbicella annularis*. (**B**) Same individual retracted inside its tube. (**C**) A worm in a colony of *Madracis auretenra* surrounded by healthy branch tips but attached to their dead base. (**D**) A worm surrounded by colonies of *Millepora alcicornis* and *Pseudodiploria strigosa*. (**E**) A worm underneath a colony of *Diploria labyrinthiformis*. (**F**) A worm on a dead patch of *Orbicella annularis* surrounded by healthy coral tissue. The width of each worm tube is ca. 2 cm.

Diversity 2022, 14, 332 14 of 19



**Figure 11.** Social feather dusters (*Sabellastarte magnifa*) at Curação (2022) in close proximity to live coral. (**A**) A worm colony on a dead patch of *Orbicella annularis*. (**B**) Another worm colony on dead coral underneath a *Montastraea cavernosa*.

Tube-dwelling gammarid amphipods and chaetopterid polychaete worms have been reported to induce the forming of densely distributed finger-like structures in Montipora corals [76,77]. Coral barnacles usually become embedded in the coral skeleton and become partly overgrown by coral tissue [44,60]. Some alterations in the coral skeleton morphology are microscopic and hardly visible, such as those caused by coral-dwelling hydroids of the genus Zanclea [78–80]. In contrast, vermetid snails that live inside branching Stylophora and massive *Porites* corals are known to modify the host's morphology on a larger scale by flattening its surface relief, which is attributed to growth inhibition caused by the snail's toxic mucus webs [81–83]. In contrast, large growth alterations in massive, branching, and encrusting corals consisting of deep fissures can be formed by Pedum scallops embedded in corals [34,66,67]. Some aggressive coral-dwelling sponges are not considered long-term associated fauna because they usually tend to overgrow and kill their hosts, but in some foliose corals, they evoke a morphological response, which is visible as the growth of flap-like protrusions that overlap the approaching sponges [84]. A modified morphology is also seen in other foliose corals that overgrow sponges as if the coral shape is molded by that of the sponge [85]. All these examples indicate that some corals may adapt their shape to resist the presence of potentially harmful associated fauna or competitors for space.

Coral injuries caused by feather duster worms have not been reported before. These appear to be much larger than those caused by coral-dwelling *Spirobranchus* worms [18,19,86]. On the other hand, large densities of serpulid worms overgrowing live coral may eventually cause partial coral mortality [87]. Many feather duster worms in the present study were found on dead coral (Figure 3A,B), and some of them formed clusters (Figure 3C,D). In some cases, the worm-infested dead-coral area was next to live coral, suggesting that the worms contributed to partial coral mortality (Figures 3E,F and 5A). A few patches of dead coral were surrounded by discolored live-coral tissue (Figure 6C,D,F). This may represent a reaction to stress as seen in some massive *Porites* corals in which polyps in contact with algae or epifauna show pink or purple pigmentation [18,66,88–90]. The difference is that there may not be extra pigmentation in the examples of the present study.

Some split-crown feather dusters at Curaçao were not hosted by stony corals but by other invertebrates. These invertebrates may have either colonized dead coral or overgrown living corals and became secondary hosts when the worms were able to resist becoming overgrown as well. The last scenario has been shown by serpulid Christmas tree worms of the genus *Spirobranchus*. The encrusting octocoral *Erythropodium caribaeorum* is recognized as an aggressive competitor for space in the Caribbean [91], which is able to overgrow corals but apparently not their symbiotic *Spirobranchus* worms [92], similar to some feather

Diversity 2022, 14, 332 15 of 19

duster worms at Curaçao in the present study (Figure 8A,B). Similarly, the colonial tunicate *Trididemnum solidum* is notorious for overgrowing Caribbean corals [93,94], except for their associated *Spirobranchus* [95] and seemingly also individuals of symbiotic *Anamobaea* sp. (Figure 8C,D). Sponges are also able to overgrow corals with the exception of symbiotic *Spirobranchus* [96,97] and apparently also *Anamobaea* sp. (Figure 9). The feather duster worm was also observed in association with algae, in particular the brown algae *Lobophora* sp. (Figure 8E,F). *Lobophora* has increased in abundance over the last decades at Curaçao and is able to overgrow live coral [98,99]. It is likely that it is able to overgrow dead and live coral containing *Anamobaea* sp., but apparently the worm tubes protrude too far to become outcompeted.

The cause of the injurious effect of the feather duster worms is unclear. The size of the wounds suggests that the worms produce toxins, but there is limited information on toxicity as a defense mechanism in Sabellidae [100]. The use of toxins can perhaps prevent worms from becoming overgrown by their hosts, as seen in *Pedum* scallops [66]. The mucus secreted by some sabellid species proves to have antibacterial properties [101–103]. According to a recent review paper on polychaete toxins, no relevant information appears to be available on the negative effect of sabellid mucus on other organisms [104]. In contrast, coral-dwelling worm snails, which occupy the same ecological niche as the feather duster worms of the present study [20], are well known for their venomous mucus and the damage this may inflict on the host corals [105,106].

Unlike *Anamobaea* sp., the relation of *Sabellastarte magnifica* and *Bispira brunnea* to corals is unclear because they were never found in living coral tissue (Figures 10 and 11). A close proximity to live corals shown by these two species may be unusual since they were also commonly found at a distance from live corals. Therefore, it may be more appropriate to use the term "pseudo-association" for this kind of unclear relation. On the other hand, it is also possible that these worms cause damage to corals and are responsible for coral mortality in their proximity.

The present study shows that the Caribbean feather duster worm *Anamobaea* sp. is more common and harmful to corals than previously known. The species has a symbiotic relation with a large range of corals and other invertebrates, which was also unknown before. It is unclear if the species has increased in abundance recently. Because this worm has the potential to become a pest species, future research should focus on its population dynamics, its settling behavior on live corals (as done with larvae of symbiotic barnacles [107,108]), and the cause, growth, and extension of coral wounds around its tubes. The larval settlement behavior of *S. magnifica* and *B. brunnea* also needs to be investigated in order to find out whether these species prefer to live in close proximity to corals or not.

Author Contributions: Conceptualization, B.W.H. and R.J.v.d.S.; methodology, B.W.H., C.E.H., S.J.L.-D., R.J.v.d.S., A.S.-M., R.S., and R.F.T.; validation, B.W.H.; formal analysis, B.W.H.; investigation, B.W.H., C.E.H., S.J.L.-D., R.J.v.d.S., A.S.-M., R.S., and R.F.T.; resources, B.W.H., C.E.H., S.J.L.-D., R.J.v.d.S., A.S.-M., R.S., and R.F.T.; data curation, B.W.H., C.E.H., S.J.L.-D., R.J.v.d.S., A.S.-M., R.S., and R.F.T.; writing—original draft preparation, B.W.H.; writing—review and editing, B.W.H., C.E.H., S.J.L.-D., R.J.v.d.S., A.S.-M., R.S., and R.F.T.; visualization, B.W.H., C.E.H., S.J.L.-D., R.J.v.d.S., A.S.-M., R.S., and R.F.T.; project administration, B.W.H.; funding acquisition, B.W.H., C.E.H., S.J.L.-D., R.J.v.d.S., A.S.-M., R.S., and R.F.T. All authors have read and agreed to the published version of the manuscript.

**Funding:** The field research at Curaçao was funded by the Alida M. Buitendijk Fund, the Jan-Joost ter Pelkwijk Fund, the Holthuis Fund, the Groningen University Fund, and the Dutch Research Council (NWO) Doctoral Grant for Teachers Programme (nr. 023.015.036). Fieldwork at Bonaire was supported by the World Wildlife Fund (WWF) Netherlands. The Treub Maatschappij (Society for the Advancement of Research in the Tropics) funded research at Bonaire and Curaçao.

Institutional Review Board Statement: Not applicable.

**Informed Consent Statement:** Not applicable.

Data Availability Statement: Data sharing not applicable.

Diversity 2022, 14, 332 16 of 19

Acknowledgments: We are grateful to the funding agencies mentioned above. We thank María Ana Tovar-Hernández (Universidad Autónoma de Nuevo León, Mexico) for confirming the identity of the sabellid worms and Jaaziel E. García-Hernández for confirming the identity of the host sponges. We thank the staff of CARMABI (Curaçao) and the Dive Shop for their hospitality and assistance during the fieldwork. BWH is also grateful to Stichting Nationale Parken Bonaire (STINAPA), the Dutch Caribbean Nature Alliance (DCNA) and Dive Friends (Bonaire) for logistic support at Bonaire, the Caribbean Netherlands Science Institute (CNSI), St. Eustatius National Parks Foundation (STENAPA), and Scubaqua Dive Center for facilitating research at St. Eustatius. We want to thank three anonymous reviewers for their constructive comments, which helped us to improve the manuscript.

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

#### References

- 1. Reaka-Kudla, M.L. The global biodiversity of coral reefs: A comparison with rain forests. In *Biodiversity II: Understanding and Protecting Our Natural Resources*; Reaka-Kudla, M.L., Wilson, D.E., Wilson, E.O., Eds.; Joseph Henry/National Academy Press: Washington, DC, USA, 1997; pp. 83–108.
- 2. Knowlton, N.; Brainard, R.E.; Fisher, R.; Moews, M.; Plaisance, L.; Caley, M.J. Coral reef biodiversity. In *Life in the World's Oceans: Diversity, Distribution and Abundance*; McIntyre, A.D., Ed.; Wiley-Blackwell: Chichester, UK, 2010; pp. 65–74.
- 3. Glynn, P.W.; Enochs, I.C. Invertebrates and their roles in coral reef ecosystems. In *Coral Reefs: An Ecosystem in Transition*; Dubinsky, Z., Stambler, N., Eds.; Springer: Dordrecht, The Netherlands, 2011; pp. 273–325. [CrossRef]
- 4. Nelson, H.R.; Kuempel, C.D.; Altieri, A.H. The resilience of reef invertebrate biodiversity to coral mortality. *Ecosphere* **2016**, 7, e01399. [CrossRef]
- 5. Castro, P. Animal symbioses in coral reef communities: A review. Symbiosis 1988, 5, 161–184.
- 6. Montano, S. The extraordinary importance of coral-associated fauna. Diversity 2020, 12, 357. [CrossRef]
- 7. Scaps, P.; Denis, V. Can organisms associated with live scleractinian corals be used as indicators of coral reef status? *Atoll Res. Bull.* **2008**, *566*, 1–18. [CrossRef]
- 8. Stella, J.S.; Pratchett, M.S.; Hutchings, P.A.; Jones, G.P. Coral-associated invertebrates: Diversity, ecology importance and vulnerability to disturbance. *Oceanogr. Mar. Biol. Ann. Rev.* **2011**, *49*, 43–104.
- 9. DeVantier, L.M.; Reichelt, R.E.; Bradbury, R.H. Does *Spirobranchus giganteus* protect host *Porites* from predation by *Acanthaster planci*: Predator pressure as a mechanism of coevolution? *Mar. Ecol. Prog. Ser.* **1986**, *32*, 307–310. [CrossRef]
- 10. Pratchett, M.S. Influence of coral symbionts on feeding preferences of crown-of-thorns starfish *Acanthaster planci* in the western Pacific. *Mar. Ecol. Prog. Ser.* **2001**, *214*, 111–119. [CrossRef]
- 11. Ben-Tzvi, O.; Einbinder, S.; Brokovich, E. A beneficial association between a polychaete worm and a scleractinian coral? *Coral Reefs* **2006**, 25, 98. [CrossRef]
- 12. Rouzé, H.; Lecellier, G.; Mills, S.C.; Planes, S.; Berteaux-Lecellier, V.; Stewart, H. Juvenile *Trapezia* spp. crabs can increase juvenile host coral survival by protection from predation. *Mar. Ecol. Prog. Ser.* **2014**, *515*, 151–159. [CrossRef]
- 13. 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]
- 14. Stewart, H.L.; Holbrook, S.J.; Schmitt, R.J.; Brooks, A.J. Symbiotic crabs maintain coral health by clearing sediments. *Coral Reefs* **2006**, 25, 609–615. [CrossRef]
- 15. Shima, J.S.; Osenberg, C.W.; Stier, A. The vermetid gastropod *Dendropoma maximum* reduces coral growth and survival. *Biol. Lett.* **2010**, *6*, 815–818. [CrossRef] [PubMed]
- 16. Carballo, J.L.; Bautista, E.; Nava, H.; Cruz-Barraza, J.A.; Chávez, J.A. Boring sponges, an increasing threat for coral reefs affected by bleaching events. *Ecol. Evol.* **2013**, *3*, 872–886. [CrossRef] [PubMed]
- 17. De Bakker, D.M.; Webb, A.E.; van den Bogaart, L.A.; van Heuven, S.M.A.C.; Meesters, E.H.; van Duyl, F.C. Quantification of chemical and mechanical bioerosion rates of six Caribbean excavating sponge species found on the coral reefs of Curação. *PLoS ONE* 2018, 13, e0197824. [CrossRef] [PubMed]
- 18. Hoeksema, B.W.; van der Schoot, R.J.; Wels, D.; Scott, C.M.; ten Hove, H.A. Filamentous turf algae on tube worms intensify damage in massive *Porites* corals. *Ecology* **2019**, *100*, e02668. [CrossRef] [PubMed]
- 19. Hoeksema, B.W.; Wels, D.; van der Schoot, R.J.; ten Hove, H.A. Coral injuries caused by *Spirobranchus* opercula with and without epibiotic turf algae at Curaçao. *Mar. Biol.* **2019**, *166*, 60. [CrossRef]
- 20. Hoeksema, B.W.; Harper, C.E.; Langdon-Down, S.J.; van der Schoot, R.J.; Smith-Moorhouse, A.; Spaargaren, R.; Timmerman, R.F. Host range of the coral-associated worm snail *Petaloconchus* sp. (Gastropoda: Vermetidae), a newly discovered cryptogenic pest species in the southern Caribbean. *Diversity* **2022**, *14*, 196. [CrossRef]
- 21. Vinn, O.; Zatoń, M.; Tovar-Hernández, M.A. Tube microstructure and formation in some feather duster worms (Polychaeta, Sabellidae). *Mar. Biol.* **2018**, *165*, 98. [CrossRef]
- 22. Humann, P.; Deloach, N.; Wilk, L. *Reef Creature Identification: Florida, Caribbean, Bahamas*, 3rd ed.; New World Publications: Jacksonville, FL, USA, 2013; 366p.

Diversity 2022, 14, 332 17 of 19

23. Bok, M.J.; Capa, M.; Nilsson, D.E. Here, there and everywhere: The radiolar eyes of fan worms (Annelida, Sabellidae). *Integr. Comp. Biol.* **2016**, *56*, 784–795. [CrossRef]

- 24. Capa, M.; Kupriyanova, E.; Nogueira, J.M.D.M.; Bick, A.; Tovar-Hernández, M.A. Fanworms: Yesterday, today and tomorrow. *Diversity* **2021**, *13*, 130. [CrossRef]
- 25. Capa, M.; López, E. Sabellidae (Annelida: Polychaeta) living in blocks of dead coral in the Coiba National Park, Panamá. *J. Mar. Biol. Assoc. U. K.* **2004**, *84*, 63–72. [CrossRef]
- Tovar-Hernández, M.A.; Knight-Jones, P. Species of Branchiomma (Polychaeta: Sabellidae) from the Caribbean Sea and Pacific coast of Panama. Zootaxa 2006, 1189, 1–37. [CrossRef]
- 27. Tovar-Hernández, M.A.; Salazar-Vallejo, S.I. Sabellids (Polychaeta: Sabellidae) from the Grand Caribbean. *Zool. Stud.* **2006**, 45, 24–66.
- 28. Giangrande, A.; Licciano, M.; Gambi, M.C. A collection of Sabellidae (Polychaeta) from Carrie Bow Cay (Belize, western Caribbean Sea) with the description of two new species. *Zootaxa* **2007**, *1650*, 41–53. [CrossRef]
- 29. Tovar-Hernández, M.A.; Salazar-Silva, P. Catalogue of Sabellidae (Annelida: Polychaeta) from the Grand Caribbean Region. *Zootaxa* **2008**, *1894*, 1–22. [CrossRef]
- 30. Bastida-Zavala, J.R.; Buelna, A.S.R.; De Leon-Gonzalez, J.A.; Camacho-Cruz, K.A.; Carmona, I. New records of sabellids and serpulids (Polychaeta: Sabellidae, Serpulidae) from the Tropical Eastern Pacific. *Zootaxa* **2016**, 4184, 401–457. [CrossRef]
- 31. Dávila-Jiménez, Y.; Tovar-Hernández, M.A.; Simōes, N. The social feather duster worm *Bispira brunnea* (Polychaeta: Sabellidae): Aggregations, morphology and reproduction. *Mar. Biol. Res.* **2017**, *13*, 782–796. [CrossRef]
- 32. Tovar-Hernández, M.A.; García-Garza, M.E.; de León-González, J.A. Sclerozoan and fouling sabellid worms (Annelida: Sabellidae) from Mexico with the establishment of two new species. *Biodivers. Data J.* **2020**, *8*, e57471. [CrossRef]
- 33. Patton, W.K. Animal associates of living reef corals. In *Biology and Geology of Coral Reefs III. Biology* 2; Jones, O.A., Endean, R., Eds.; Academic Press: New York, NY, USA, 1976; pp. 1–37.
- 34. Zann, L.P. Living Together in the Sea; T.F.H. Publications: Neptune, NY, USA, 1980; 416p.
- 35. Scott, P.J.B. Aspects of living coral associates in Jamaica. In Proceedings of the 5th International Coral Reef Congress, Tahiti, French Polynesia, 27 May–1 June 1985; Volume 5, pp. 345–350.
- Scott, P.J.B. Associations between corals and macro-infaunal invertebrates in Jamaica, with a list of Caribbean and Atlantic coral associates. Bull. Mar. Sci. 1987, 40, 271–286.
- 37. Perry, C.T. Macroborers within coral framework at Discovery Bay, north Jamaica: Species distribution and abundance, and effects on coral preservation. *Coral Reefs* 1998, 17, 277–287. [CrossRef]
- 38. Lewis, J.B. Biology and ecology of the hydrocoral Millepora on coral reefs. Adv. Mar. Biol. 2000, 50, 1–55. [CrossRef]
- 39. Nogueira, J.M.M. Fauna living in colonies of *Mussismilia hispida* (Verrill) (Cnidaria: Scleractinia) in four South-eastern Brazil Islands. *Braz. Arch. Biol. Technol.* **2003**, *46*, 421–432. [CrossRef]
- 40. Castro, C.; Monroy, M.; Solano, O.D. Estructura de la comunidad epifaunal asociada a colonias de vida libre del hydrocoral *Millepora alcicornis* Linnaeus, 1758 en Bahía Portete, Caribe Colombiano. *Bol. Investig. Mar. Cost.* **2006**, 35, 195–206.
- 41. Oigman-Pszczol, S.S.; Creed, J.C. Distribution and abundance of fauna on living tissues of two Brazilian hermatypic corals (*Mussismilia hispida* (Verril 1902) and *Siderastrea stellata* Verril, 1868). *Hydrobiologia* **2006**, 563, 143–154. [CrossRef]
- 42. Stella, J.S.; Jones, G.P.; Pratchett, M.S. Variation in the structure of epifaunal invertebrate assemblages among coral hosts. *Coral Reefs* **2010**, 29, 957–973. [CrossRef]
- 43. Hoeksema, B.W.; van der Meij, S.E.T.; Fransen, C.H.J.M. The mushroom coral as a habitat. *J. Mar. Biol. Assoc. UK* **2012**, 92, 647–663. [CrossRef]
- 44. 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]
- 45. Lymperaki, M.M.; Hill, C.E.; Hoeksema, B.W. The effects of wave exposure and host cover on coral-associated fauna of a centuries-old artificial reef in the Caribbean. *Ecol. Eng.* **2022**, *176*, 106536. [CrossRef]
- 46. Martin, D.; Britayev, T.A. Symbiotic polychaetes: Review of known species. Oceanogr. Mar. Biol. Ann. Rev. 1998, 36, 217–340.
- 47. Molodtsova, T.N.; Britayev, T.A.; Martin, D. Cnidarians and their polychaete symbionts. In *The Cnidaria, Past, Present and Future*; Goffredo, S., Dubinsky, Z., Eds.; Springer: Cham, Switzerland, 2016; pp. 387–413. [CrossRef]
- 48. 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*, 371–447. [CrossRef]
- 49. Nogueira, J.M.M.; Knight-Jones, P. A new species of *Pseudobranchiomma* Jones (Polychaeta: Sabellidae) found amongst Brazilian coral, with a redescription of *P. punctata* (Treadwell, 1906) from Hawaii. *J. Nat. Hist.* **2002**, *36*, 1661–1670. [CrossRef]
- 50. Nogueira, J.M.M.; Amaral, A.C.Z. *Amphicorina schlenzae*, a small sabellid (Polychaeta, Sabellidae) associated with a stony coral on the coast of Sao Paulo State, Brazil. *Bull. Mar. Sci.* **2000**, *67*, 617–624.
- 51. Tovar-Hernández, M.A.; ten Hove, H.A.; Vinn, O.; Zatoń, M.; de León-González, J.A.; García-Garza, M.E. Fan worms (Annelida: Sabellidae) from Indonesia collected by the Snellius II Expedition (1984) with descriptions of three new species and tube microstructure. *PeerJ* 2020, 8, e9692. [CrossRef]
- 52. Benzoni, F.; Arrigoni, R.; Stefani, F.; Reijnen, B.T.; Montano, S.; Hoeksema, B.W. Phylogenetic position and taxonomy of *Cycloseris explanulata* and *C. wellsi* (Scleractinia: Fungiidae): Lost mushroom corals find their way home. *Contrib. Zool.* **2012**, *81*, 125–146. [CrossRef]

Diversity 2022, 14, 332 18 of 19

53. Nishi, E.; Gil, J.; Tanaka, K.; Kupriyanova, E.K. *Notaulax yamasui* sp. n. (Annelida, Sabellidae) from Okinawa and Ogasawara, Japan, with notes on its ecology. *ZooKeys* **2017**, *660*, 1–16. [CrossRef]

- 54. Tovar-Hernández, M.A.; Pineda-Vera, A. Taxonomía y estrategias reproductivas del poliqueto sabélido *Bispira brunnea* (Treadwell, 1917) del Caribe Mexicano. *Cienc. Mar.* **2008**, *21*, 3–14.
- 55. Nishi, E.; Nishihira, M. Use of annual density banding to estimate longevity of infauna of massive corals. *Fish. Sci.* **1999**, *65*, 48–56. [CrossRef]
- 56. van der Meij, S.E.T.; Fransen, C.H.J.M.; Pasman, L.R.; Hoeksema, B.W. Phylogenetic ecology of gall crabs (Cryptochiridae) as associates of mushroom corals (Fungiidae). *Ecol. Evol.* **2015**, *5*, 5770–5780. [CrossRef]
- 57. Klompmaker, A.A.; Portell, R.W.; van der Meij, S.E.T. Trace fossil evidence of coral-inhabiting crabs (Cryptochiridae) and its implications for growth and paleobiogeography. *Sci. Rep.* **2016**, *6*, 23443. [CrossRef]
- 58. Terrana, L.; Caulier, G.; Todinanahary, G.; Lepoint, G.; Eeckhout, I. Characteristics of the infestation of *Seriatopora* corals by the coral gall crab *Hapalocarcinus marsupialis* Stimpson, 1859 on the great reef of Toliara, Madagascar. *Symbiosis* **2016**, *69*, 113–122. [CrossRef]
- 59. Hoeksema, B.W.; Butôt, R.; García-Hernández, J.E. A new host and range record for the gall crab *Fungicola fagei* as a symbiont of the mushroom coral *Lobactis scutaria* in Hawai'i. *Pac. Sci.* **2018**, 72, 251–261. [CrossRef]
- 60. Chan, B.K.K.; Wong, K.J.H.; Cheng, Y.R. Biogeography and host usage of coral-associated crustaceans: Barnacles, copepods, and gall crabs as model organisms. In *The Natural History of the Crustacea: Evolution and Biogeography of the Crustacea*; Thiel, M., Poore, G.C., Eds.; Oxford University Press: Oxford, UK, 2020; Volume 8, pp. 183–215. [CrossRef]
- 61. 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]
- 62. Bruce, A.J. Notes on some Indo-Pacific Pontoniinae. XIV. Observations on *Paratypton siebenrocki* Balss. *Crustaceana* **1969**, *17*, 171–186. [CrossRef]
- 63. Scott, P.J.B.; Reiswigh, M.; Marcottbe, M. Ecology, functional morphology, behaviour, and feeding in coral- and sponge-boring species of *Upogebia* (Crustacea: Decapoda: Thalassinidea). *Can. J. Zool.* **1988**, *66*, 483–495. [CrossRef]
- 64. Scott, P.J.B. Distribution, habitat and morphology of the Caribbean coral-and rock-boring bivalve, *Lithophaga bisulcata* (d'Orbigny) (Mytilidae: Lithophaginae). *J. Molluscan Stud.* **1988**, 54, 83–95. [CrossRef]
- Kleemann, K. Boring and growth in chemically boring bivalves from the Caribbean, Eastern Pacific and Australia's Great Barrier Reef. Senckenb. Marit. 1990, 22, 101–154.
- 66. Chan, B.K.K.; Tan, J.C.H.; Ganmanee, M. Living in a growing host: Growth pattern and dwelling formation of the scallop *Pedum spondyloideum* in massive *Porites* spp. corals. *Mar. Biol.* **2020**, *167*, 95. [CrossRef]
- 67. Scaps, P. Association between the scallop *Pedum spondyloideum* (Bivalvia: Pteriomorphia: Pectinidae) and scleractinian corals from Nosy Be, Madagascar. *Cah. Biol. Mar.* **2020**, *61*, 73–80. [CrossRef]
- 68. Gittenberger, A.; Gittenberger, E. Cryptic, adaptive radiation of endoparasitic snails: Sibling species of *Leptoconchus* (Gastropoda: Coralliophilidae) in corals. *Org. Divers. Evol.* **2011**, *11*, 21–41. [CrossRef]
- 69. Dojiri, M. *Isomolgus desmotes*, new genus, new species (Lichomolgidae), a gallicolous poecilostome copepod from the scleractinian coral *Seriatopora hystrix* Dana in Indonesia, with a review of gall-inhabiting crustaceans of anthozoans. *J. Crust. Biol.* **1988**, 8, 99–109. [CrossRef]
- 70. Kim, I.-H.; Yamashiro, H. Two species of poecilostomatoid copepods inhabiting galls on scleractinian corals in Okinawa, Japan. *J. Crust. Biol.* **2007**, *27*, 319–326. [CrossRef]
- 71. Ivanenko, V.N.; Moudrova, S.V.; Bouwmeester, J.; Berumen, M.L. First report of tubular corallites on *Stylophora* caused by a symbiotic copepod crustacean. *Coral Reefs* **2014**, *33*, 637. [CrossRef]
- 72. Shelyakin, P.V.; Garushyants, S.K.; Nikitin, M.A.; Mudrova, S.V.; Berumen, M.; Speksnijder, A.G.; Hoeksema, B.W.; Fontaneto, D.; Gelfand, M.S.; Ivanenko, V.N. Microbiomes of gall-inducing copepod crustaceans from the corals *Stylophora pistillata* (Scleractinia) and *Gorgonia ventalina* (Alcyonacea). *Sci. Rep.* **2018**, *8*, 11563. [CrossRef] [PubMed]
- 73. Grygier, M.J.; Cairns, S.D. Suspected neoplasms in deep-sea corals (Scleractinia: Oculinidae: *Madrepora* spp.) reinterpreted as galls caused by *Petrarca madreporae* n. sp. (Crustacea: Ascothoracida: Petrarcidae). *Dis. Aquat. Org.* **1996**, 24, 61–69. [CrossRef]
- 74. Tachikawa, H.; Grygier, M.J.; Cairns, S.D. Live specimens of the parasite *Petrarca madreporae* (Crustacea: Ascothoracida) from the deep-water coral *Madrepora oculata* in Japan, with remarks on the development of its spectacular galls. *J. Mar. Sci. Technol.* **2020**, 28, 58–64. [CrossRef]
- 75. Chan, B.K.K.; Dreyer, N.; Gale, A.S.; Glenner, H.; Ewers-Saucedo, C.; Pérez-Losada, M.; Kolbasov, G.A.; Crandall, K.A.; Høeg, J.T. The evolutionary diversity of barnacles, with an updated classification of fossil and living forms. *Zool. J. Linn. Soc.* 2021, 193, 789–846. [CrossRef]
- 76. Bergsma, G.S. Tube-dwelling coral symbionts induce significant morphological change in *Montipora*. *Symbiosis* **2009**, *49*, 143–150. [CrossRef]
- 77. Bergsma, G.S.; Martinez, C.M. Mutualist-induced morphological changes enhance growth and survival of corals. *Mar. Biol.* **2011**, 158, 2267–2277. [CrossRef]
- 78. Manca, F.; Puce, S.; Caragnano, A.; Maggioni, D.; Pica, D.; Seveso, D.; Galli, P.; Montano, S. Symbiont footprints highlight the diversity of scleractinian-associated *Zanclea* hydrozoans (Cnidaria, Hydrozoa). *Zool. Scr.* **2019**, *48*, 399–410. [CrossRef]

Diversity 2022, 14, 332 19 of 19

79. Maggioni, D.; Arrigoni, R.; Seveso, D.; Galli, G.; Berumen, M.L.; Denis, V.; Hoeksema, B.W.; Huang, D.; Manca, F.; Pica, D.; et al. Evolution and biogeography of the *Zanclea*-Scleractinia symbiosis. *Coral Reefs* **2020**. [CrossRef]

- 80. Maggioni, D.; Saponari, L.; Seveso, D.; Galli, P.; Schiavo, A.; Ostrovsky, A.N.; Montano, S. Green fluorescence patterns in closely related symbiotic species of *Zanclea* (Hydrozoa, Capitata). *Diversity* **2020**, *12*, 78. [CrossRef]
- 81. Colgan, M.W. Growth rate reduction and modification of a coral colony by a vermetid mollusc *Dendropoma maxima*. In Proceedings of the 5th International Coral Reef Congress, Tahiti, French Polynesia, 27 May–1 June 1985; Volume 6, pp. 205–210.
- 82. Zvuloni, A.; Armoza-Zvuloni, R.; Loya, Y. Structural deformation of branching corals associated with the vermetid gastropod *Dendropoma maxima*. *Mar. Ecol. Prog. Ser.* **2008**, *363*, 103–108. [CrossRef]
- 83. Shima, J.S.; McNaughtan, D.; Strong, A.T. Vermetid gastropods mediate within-colony variation in coral growth to reduce rugosity. *Mar. Biol.* **2015**, *162*, 1523–1530. [CrossRef]
- 84. Elliott, J.; Patterson, M.; Vitry, E.; Summers, N.; Miternique, C. Morphological plasticity allows coral to actively overgrow the aggressive sponge *Terpios hoshinota* (Mauritius, Southwestern Indian Ocean). *Mar. Biodivers.* **2016**, *46*, 489–493. [CrossRef]
- 85. García-Hernández, J.E.; van Moorsel, G.W.N.M.; Hoeksema, B.W. Lettuce corals overgrowing tube sponges at St. Eustatius, Dutch Caribbean. *Mar. Biodivers.* **2017**, *47*, 55–56. [CrossRef]
- 86. Hoeksema, B.W.; ten Hove, H.A.; Berumen, M.L. A three-way association causing coral injuries in the Red Sea. *Bull. Mar. Sci.* **2018**, *94*, 1525–1526. [CrossRef]
- 87. Samimi Namin, K.; Risk, M.J.; Hoeksema, B.W.; Zohari, Z.; Rezai, H. Coral mortality and serpulid infestations associated with red tide, in the Persian Gulf. *Coral Reefs* **2010**, 29, 509. [CrossRef]
- 88. Benzoni, F.; Galli, P.; Pichon, M. Pink spots on Porites: Not always a coral disease. Coral Reefs 2010, 29, 153. [CrossRef]
- 89. Benzoni, F.; Basso, D.; Caragnano, A.; Rodondi, G. *Hydrolithon* spp. (Rhodophyta, Corallinales) overgrow live corals (Cnidaria, Scleractinia) in Yemen. *Mar. Biol.* **2011**, *158*, 2419–2428. [CrossRef]
- 90. Kubomura, T.; Wee, H.B.; Reimer, J.D. Investigating incidence and possible causes of pink and purple pigmentation response in hard coral genus *Porites* around Okinawajima Island, Japan. *Reg. Stud. Mar. Sci.* **2021**, *41*, 101569. [CrossRef]
- 91. Ladd, M.C.; Shantz, A.A.; Burkepile, D.E. Newly dominant benthic invertebrates reshape competitive networks on contemporary Caribbean reefs. *Coral Reefs* **2019**, *38*, 1317–1328. [CrossRef]
- 92. Hoeksema, B.W.; Lau, Y.W.; ten Hove, H.A. Octocorals as secondary hosts for Christmas tree worms off Curação. *Bull. Mar. Sci.* **2015**, *91*, 489–490. [CrossRef]
- 93. Bak, R.P.M.; Sybesma, J.; van Duyl, F.C. The ecology of the tropical compound ascidian *Trididemnum solidum*. II. Abundance, growth and survival. *Mar. Ecol. Prog. Ser.* **1981**, *6*, 43–52. [CrossRef]
- 94. Sommer, B.; Harrison, P.L.; Scheffers, S.R. Aggressive colonial ascidian impacting deep coral reefs at Bonaire, Netherlands Antilles. *Coral Reefs* **2010**, *29*, 245. [CrossRef]
- 95. Hoeksema, B.W.; García-Hernández, J.E.; van Moorsel, G.W.N.M.; Olthof, G.; ten Hove, H.A. Extension of the recorded host range of Caribbean Christmas tree worms (*Spirobranchus* spp.) with two scleractinians, a zoantharian, and an ascidian. *Diversity* **2020**, *12*, 115. [CrossRef]
- 96. Hoeksema, B.W.; ten Hove, H.A.; Berumen, M.L. Christmas tree worms evade smothering by a coral-killing sponge in the Red Sea. *Mar. Biodivers.* **2016**, *48*, 15–16. [CrossRef]
- 97. García-Hernández, J.E.; Hoeksema, B.W. Sponges as secondary hosts for Christmas tree worms at Curação. *Coral Reefs* **2017**, 36, 1243. [CrossRef]
- 98. Nugues, M.M.; Bak, R.P.M. Differential competitive abilities between Caribbean coral species and a brown alga: A year of experiments and a long-term perspective. *Mar. Ecol. Prog. Ser.* **2006**, *315*, 75–86. [CrossRef]
- 99. Nugues, M.M.; Bak, R.P.M. Long-term dynamics of the brown macroalga *Lobophora variegata* on deep reefs in Curação. *Coral Reefs* **2008**, 27, 389–393. [CrossRef]
- 100. Kicklighter, C.E.; Hay, M.E. To avoid or deter: Interactions among defensive and escape strategies in sabellid worms. *Oecologia* **2007**, *151*, 161–173. [CrossRef]
- 101. Stabili, L.; Schirosi, R.; Di Benedetto, A.; Merendino, A.; Villanova, L.; Giangrande, A. First insights into the biochemistry of Sabella spallanzanii (Annelida: Polychaeta) mucus: A potentially unexplored resource for applicative purposes. J. Mar. Biol. Assoc. U. K. 2011, 91, 199–208. [CrossRef]
- 102. Giangrande, A.; Licciano, M.; Schirosi, R.; Musco, L.; Stabili, L. Chemical and structural defensive external strategies in six sabellid worms (Annelida). *Mar. Ecol.* **2014**, *35*, 36–45. [CrossRef]
- 103. Stabili, L.; Schirosi, R.; Licciano, M.; Giangrande, A. Role of *Myxicola infundibulum* (Polychaeta, Annelida) mucus: From bacterial control to nutritional home site. *J. Exp. Mar. Biol. Ecol.* **2014**, *461*, 344–349. [CrossRef]
- 104. Coutinho, M.C.L.; Teixeira, V.L.; Santos, C.S.G. A review of "Polychaeta" chemicals and their possible ecological role. *J. Chem. Ecol.* **2018**, 44, 72–94. [CrossRef]
- 105. Barton, J.A.; Bourne, D.G.; Humphrey, C.M.; Hutson, K.S. Parasites and coral-associated invertebrates that impact coral health. *Rev. Aquac.* 2020, 12, 2284–2303. [CrossRef]
- 106. Adhavan, D.; Prakash, S.; Kumar, A. Tube dwelling gastropod an indicator of coral reef status at the tropical reef of Palk Bay region, southeast coast of India. *Ind. J. Geo Mar. Sci.* **2021**, *50*, 585–587.
- 107. Liu, J.C.W.; Hoeg, J.T.; Chan, B.K.K. How do coral barnacles start their life in their hosts? Biol. Lett. 2016, 12, 20160124. [CrossRef]
- 108. Yu, M.-C.; Dreyer, N.; Kolbasov, G.A.; Høeg, J.T.; Chan, B.K.K. Sponge symbiosis is facilitated by adaptive evolution of larval sensory and attachment structures in barnacles. *Proc. R. Soc. B* **2020**, 287, 20200300. [CrossRef]