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

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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 thalllose 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

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. Sabellids 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
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 symbiobio 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 *Pseudobranchioma 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. wellsii* (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), phaeophyceaean 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 Curaçao and the Eastern Caribbean island of St. Eustatius (Table 1).
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 *Oribicella 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).
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 | Curacao | 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 |
| *Heliosertis 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 |
| *Meandrina meandrites* (Linnaeus, 1758) | a,c | e | f |
| **Merulinidae** | | | |
| *Dendrogyra cylindrus* (Ehrenberg, 1834) | a | - | - |
| *Orbicella annularis* (Ellis & Solander, 1786) | a | - | f |
| *Orbicella faveolata* (Ellis & Solander, 1786) | a | e | - |
| *Orbicella franksi* (Gregory, 1895) | a,b,d | e | f |
| **Montastraeidae** | | | |
| *Montastrea cavernosa* (Linnaeus, 1767) | a,b | - | - |
| **Pocilloporidae** | | | |
| *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: Asciacea** | | | |
| **Didemnidae** | | | |
| *Trididemnum solidum* (Van Name, 1902) | a,b | - | - |
| **Porifera spp.** | a | - | - |
| **Unidentified dead coral with/without algae** | a | - | - |
Figure 2. Split-crown feather dusters (*Ananoba* 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.
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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.
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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.
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.
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.
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.
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 phaeophyceae alga *Lobophora* sp. at Curaçao (2021). Arrows indicate worm tubes. The maximum width of each tube is ca. 5 mm.
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].
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.
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
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.

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