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The rise of a native sun coral species on southern Caribbean coral reefs

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Abstract. In contrast with a general decline of Caribbean reef corals, a previously rare sun coral is increasing in abundance within shallow coral communities on Curaçao. This azooxanthellate scleractinian was identified as *Cladopsammia manuelensis,* which has an amphi-Atlantic distribution. Over the last decade, *C. manuelensis* has increased abundance along the leeward coast of Curaçao (southern Caribbean) between depths of 4 and 30 m. This species was initially not noticed because it resembles the invasive coral *Tubastraea coccinea*, which was introduced to Curaçao from the Indo-Pacific around 1940. However, in contrast to *T. coccinea, C. manuelensis* was previously only present on deeper reef sections (>70 m) of Caribbean reefs. Our observations illustrate how the sudden increase in abundance of a previously unnoticed, apparently cryptogenic species could result from natural dynamics on present-day reefs, but also could easily be mistaken for an invasive species. The finding that deep reef sections can harbor species capable of colonizing shallower reef zones highlights the importance of thorough inventories of reef communities across large depth ranges, which can help us to discriminate between range increases of native species and the arrival of invasives.

Key words: bathymetric distribution; *Cladopsammia;* coral reefs; cryptogenic; deep water; Dendrophylliidae; invasive; native; *Rhizopsammia; Tubastraea;*.

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Indo-Pacific corals of the genus *Tubastraea* (Scleractinia: Dendrophylliidae) have become introduced to the Caribbean for decades (Creed et al. 2017). Because their expanded tentacles appear like yellow, radiating sun rays, they are often named sun corals. So far, three *Tubastraea* species have been observed in the tropical and subtropical West Atlantic, most probably introduced as fouling organisms on ships and oil platforms (Creed et al. 2017). Unlike many other reef-building corals, *Tubastraea* species are not restricted to shallow depths as they lack symbiotic algae (zooxanthellae) and solely depend on planktonic food for nutrition (Goreau et al. 1971).

The first introduced *Tubastrea* species, *T. coccinea* Lesson, 1829, arrived in the Caribbean at Curaçao and Puerto Rico around 1940 and subsequently expanded its range northward to Georgia (USA) and southward to southern Brazil (Cairns 2000, Creed et al. 2017). The second species, *T. tagusensis* Wells, 1982, has become widespread along the Brazilian coastline since 2002 (Creed et al. 2017) and has recently been reported from the Gulf of Mexico (Figueroa et al. 2019). Both species form clumps of polyps with dark- and light-orange calyces, respectively (Mantelatto et al. 2011). The third introduced species, *T. micranthus* (Ehrenberg, 1834), has been observed as fouling benthos on oil rigs in the Gulf of Mexico since 2006 and possesses a branching morphology with green calyces and tentacles (Sammarco et al. 2010, Creed et al. 2017). Along the coastline of Brazil, the first two are now considered nuisance species because they outcompete native corals (dos Santos et al. 2013, Miranda et al. 2016).

During reef surveys (2014–2017) along the leeward side of Curaçao (southern Caribbean), a previously unnoticed, but presently common sun coral species was observed at 23 out of 32 (72%) dive locations (Figs. 1, 2; Appendix S1: Table S1). Its sudden increase in abundance in shallow water at Curaçao had already been described by Engelen et al. (2018), who identified the species as *Rhizopsammia goesi* (Lindström 1877). The new species looked very similar to co-occurring *T. coccinea*, because both species have distinctive yellow tentacles. However, under artificial light the color of the new species' calyces varies from gray to brick red or dark orange, which differs from the uniform dark orange commonly seen in *T. coccinea* (Fig. 1; Appendix S1). Young polyps of the newly seen species taper toward the base, where they bud off from the basis of older polyps (Fig. 1c–f, j) or from root-like stolons (Fig. 1a, d, k, l), which eventually form a basal plate (Fig. 1k). In between polyps, the basal plate may become overgrown by algae, disguising the coral's colonial architecture (Fig. 1g, l). Both species were commonly found on reefs, on shipwrecks, and underneath rocky overhangs: *T. coccinea* at 0.2–55 m depth and the new species at 4–30 m (Appendix S1).

Septa of the new species appear to be more pronounced than those of *T. coccinea* (Fig. 2a). In dead polyps (Fig. 2b), septa of the new species show a bifurcating pattern according to the Pourtalès plan (Cairns 1994), which does not occur in *Tubastraea* (Fig. 2c). The septal pattern and the presence of stolons indicate that this species belongs to either the genus *Cladopsammia* or *Rhizopsammia*, which are both phylogenetically closely related to *Tubastraea* (Cairns 2001, Arrigoni et al. 2014). Genetic information on Atlantic *Cladopsammia* and *Rhizopsammia* is currently not available, but a preliminary molecular analysis based on the mitochondrial marker cytochrome c oxidase subunit I (COI) revealed that the species found on Curaçao is very closely related to both *Cladopsammia gracilis* (Milne Edwards & Haime, 1848) and *Rhizopsammia wettsteini* (Scheer & Pillai, 1983) from the Red Sea (A.-F. Hiemstra, *unpublished data*). The stolons of *Cladopsammia* merge into a basal plate (like in Fig. 1k) but not in *Rhizopsammia*; though this difference is hard to observe in juveniles (Cairns 2000, Cairns and Kitahara 2012; Fig 1a) making young individuals of both genera almost impossible to identify.

In the Caribbean, two species are already present that fulfill aforementioned morphological characters and taxonomic relatedness to the species from the Red Sea: *Cladopsammia manuelensis* (Chevalier, 1966) and *R. goesi* (Lindström 1877). Both species occur at mesophotic depths or deeper. The bathymetric range of the amphi-Atlantic *C. manuelensis* is 70–366 m (Cairns 2000). Its earliest West Atlantic records (since 1958) are from the Gulf of Mexico, while specimens from Curaçao were first collected with manned submersibles from 143 to 330 m depth in 2000 and 2013, respectively (https://collections.nmnh.si.edu/search/iz/). Fossils of East Atlantic *C. manuelensis* were found in the Pleistocene of West Africa (Cairns 2000), and since there are several scleractinian coral species with a natural amphi-Atlantic distribution (Cairns 2000, Nunes et al. 2011), there is no reason to assume that this species was recently introduced in the western Atlantic.

Rhizopsammia goesi is a deep-water species native to the Caribbean: Museum specimens have been collected from 75 to 275 depth at St. Martin in the eastern Caribbean (Lindström 1877) and from 73 to 152 m depth in the Colombian Caribbean (Santodomingo et al. 2013), and it has been observed at depths exceeding 30 m in the Bahamas and Cayman Islands (Slattery and Lesser 2019). Rather than yet another introduced dendrophylliid, the new coral increasing in abundance within shallow-water coral communities is likely one of two species that are native to deep water in the Caribbean as already proposed by Engelen et al. (2018). However, in contrast to Engelen et al. (2018) and Hoeksema and ten Hove (2017), who identified the species as *R. goesi*, we identified the species as *C. manuelensis*

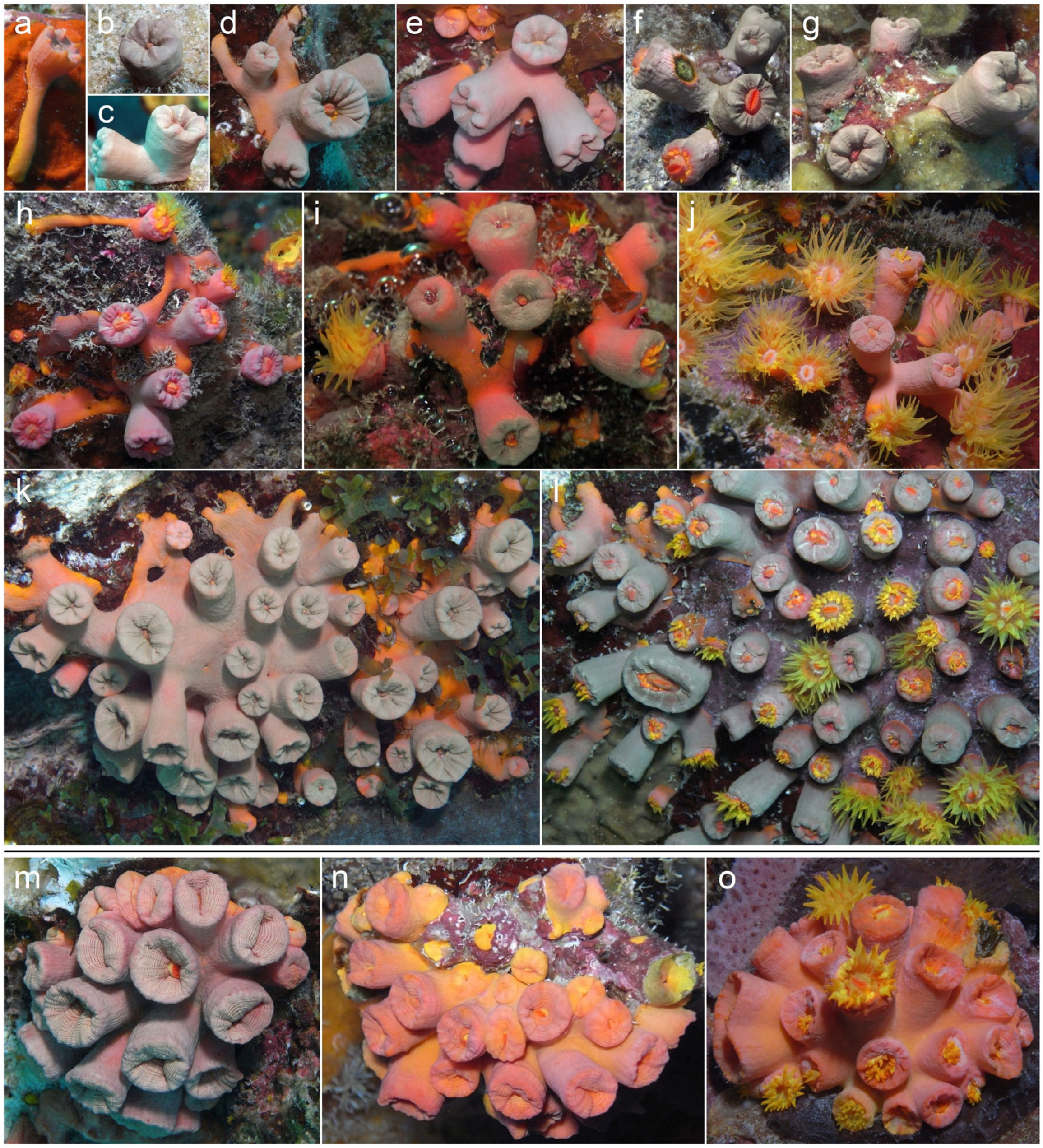

Fig. 1. *Cladopsammia manuelensis* (a–l) and invasive *Tubastraea coccinea* (m–o) at various localities (with depths) at Curaçao, southern Caribbean (2014–2017). (a) Snake Bay, 16 m. (b, c) Marie Pampoen, 17 m. (d, j) Hilton, Piscadera Bay, 12 m. (e) Caracas Bay, 9 m. (f, g) Water Factory, 16 m. (h, i) Caracas Bay, 20 m. (k, m) Carmabi, Piscadera Bay, 3 m. (l) Tugboat, Caracas Bay, 4 m. (n) Superior Producer shipwreck, 30 m. (o) Hilton, Piscadera Bay, 1 m (on a concrete pillar).

based on the presence of a basal plate, which is visible in some of the larger specimens (Fig. 1; Appendix S1) but is absent in *R. goesi* (Cairns 2000). Previously, the basal plate was not noticed because corals were too young and it had not yet developed or because it was covered by algae.

Corals of *C. manuelensis* were recently also discovered in Haiti, where they were abundant

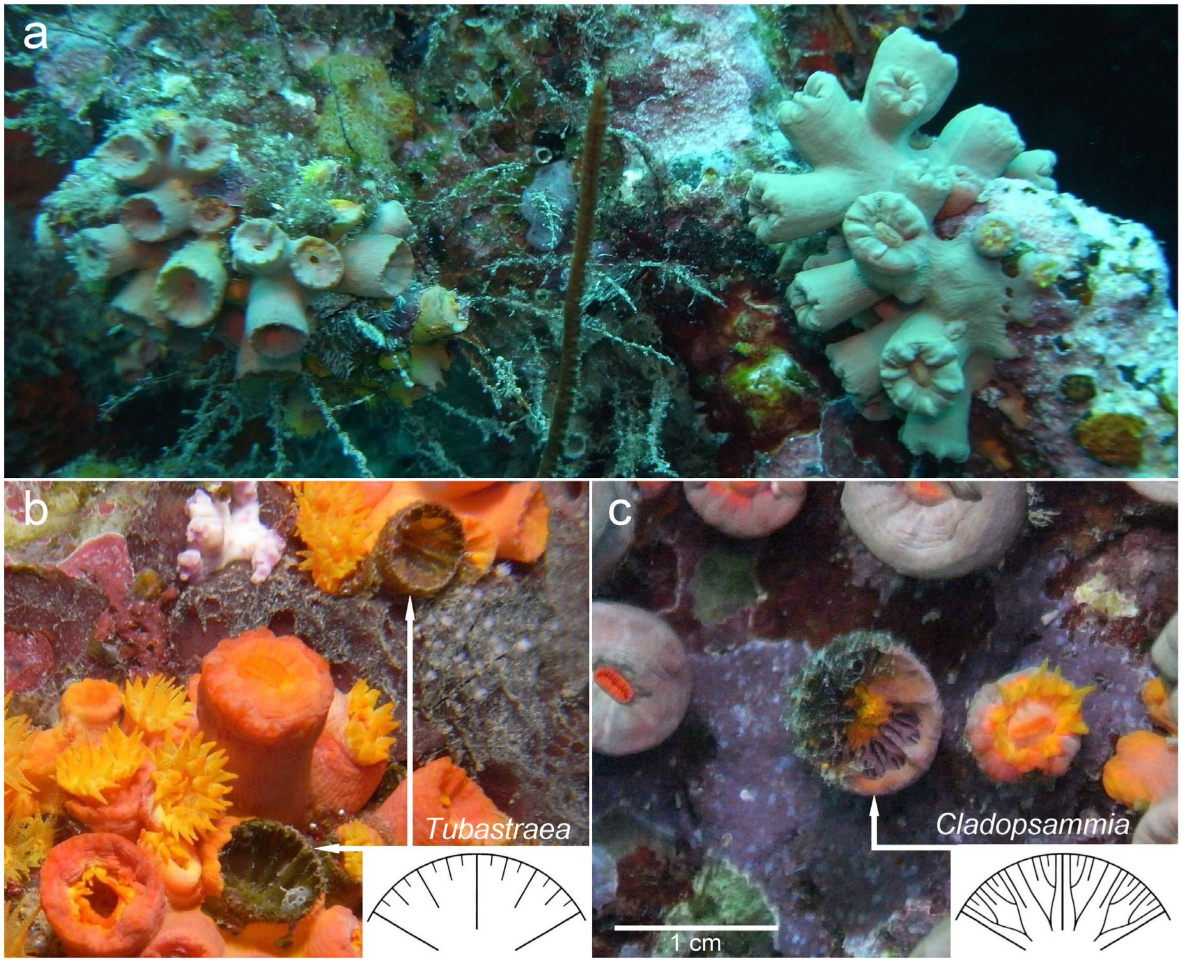

Fig. 2. *Tubastraea coccinea* (left) and *Cladopsammia manuelensis* (right) at Curaçao. (a) Underexposed picture showing green color of both species at 24 m depth on Superior Producer shipwreck. (b, c) Use of artificial light reveals true colors and septal arrangement inside dead calyces (schemes after Cairns 1994): (a) regular, (b) Pourtalès plan.

in shallow reef communities at eight out of 32 (25%) dive sites (Kramer et al. 2016). Observations from Haiti (Kramer et al. 2016: Fig. 64) clearly show that the species is identical to that on Curaçao and probably represent the first record of *C. manuelensis* occurring within shallow Caribbean reef communities (Kramer et al. 2016; J. Lang and S. Williams, *personal communication*). Finally, approximately 100 colonies were observed across 51 sites at Aruba in May 2019 (see, e.g., Appendix S1: Fig. S16), an island located only 75 km west of Curaçao.

A plausible hypothetical scenario for the appearance of *C. manuelensis* within shallow reef communities on Curaçao is that this native deep-water species has started to colonize shallower habitats due to recent, but unidentified, changes in environmental conditions. Earlier detection at Curaçao may have been hindered because of *Cladopsammia*'s resemblance to *Tubastraea* (Figs. 1, 2). The fact that it is easily confused with an introduced, already established dendrophylliid species can also explain why it has not yet been reported from shallow reef communities in other Caribbean localities apart from Haiti, Curaçao, and Aruba. Moreover, an upward migration may not have taken place everywhere in the Caribbean. For instance, despite a search for *C. manuelensis* at St. Eustatius (eastern Caribbean) in 2015, in particular on shipwrecks and underneath rocky overhangs, it was not found here (Hoeksema and van Moorsel 2016).

The rise of *C. manuelensis* on shallow Curaçaoan reefs and certain other islands within the Caribbean is remarkable considering the decrease in abundance of many other coral species in recent decades (de Bakker et al. 2016). Additional research is needed to find out what has caused the expansion of *C. manuelensis* on Caribbean coral reefs and how this relates to the ecological role and geographic expansion of sun coral species in the western Atlantic. Moreover, the present case indicates that in future studies on the origin of cryptogenic reef species, we should not only consider introductions from elsewhere, but also bathymetric range expansions of native species previously only recorded from greater depths.

Acknowledgments

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2942/full

Supporting Information. Bert W. Hoeksema, Auke-Florian Hiemstra, Mark J.A. Vermeij. 2019. The rise of a native sun coral species on southern Caribbean coral reefs. *Ecosphere.*

Table S1. Localities surveyed at Curaçao (2014–2017) arranged from north to south with presence (+) / absence (-) records of *Cladopsammia manuelensis.*

1. Playa Kalki	12°22'29"N, 69°09'30"W	+
2. Playa Jeremi	12°19'45"N, 69°09'05"W	-
3. Playa Lagun	12°19'02"N, 69°09'09"W	-
4. St. Martha Bay	12°16'02"N, 69°07'43"W	-
5. Playa Grandi	12°14'56"N, 69°06'31"W	+
6. Valentijn's Bay, Playa Cas Abao	12°13'55"N, 69°05'44"W	+
7. Porto Mari	12°13'07"N, 69°05'09"W	-
8. Daaibooi Bay	12°12'41"N, 69°05'13"W	+
9. Habitat (Coral Estate)	12°11'54"N, 69°04'45"W	-
10. Komomo Beach, Vaarsen Bay	12°09'38"N, 69°00'20"W	+
11. St. Michiel's Bay	12°08'53"N, 69°00'00"W	-
12. Snake Bay	12°08'21"N, 68°59'53"W	+
13. Blue Wall	12°08'06"N, 68°59'16"W	+
14. Blue Bay	12°08'02"N, 68°59'07"W	+
15. Buoy 1, Piscadera Bay	12°07'23"N, 68°58'14"W	-
16. Carmabi, Piscadera Bay	12°07'20"N, 68°58'08"W	+
17. Hilton	12°07'17"N, 68°58'09"W	+
18. Crash site	12°07'05"N, 68°58'05"W	+
19. Parasasa Beach	12°06'57"N, 68°57'55"W	+
20. Water Factory	12°06'33"N, 68°57'15"W	+
21. Double Reef	12°06'27"N, 68°56'56"W	+
22. Holiday Beach	12°06'25"N, 68°56'48"W	+
23. Superior Producer shipwreck	12°06'18"N, 68°56'36"W	+
24. Atlantis	12°05'41"N, 68°54'44"W	+
25. Playa Mari Pampoen	12°05'24"N, 68°54'19"W	+
26. Substation Curaçao	12°05'04"N, 68°53'54"W	+
27. Jan Thiel Bay, south	12°04'28"N, 68°52'50"W	-
28. Tugboat, Caracas Bay	12°04'05"N, 68°51'44"W	+
29. Director's Bay	12°03'59"N, 68°51'38"W	-
30. Punto Pico	12°03'59"N, 68°51'13"W	+
31. Punda, entry port	12°02'34"N, 68°44'17"W	+
32. Klein Curaçao	11°59'04"N, 68°38'41"W	+

Photographic records of *Cladopsammia manuelensis* (Chevalier, 1966) and the invasive *Tubastraea coccinea* Lesson, 1829 at Curaçao (2014–2017).

Fig. S1. Playa Kalki (12°22'29"N, 69°09'30"W), February 2015; colony of *C. manuelensis* on rocky substrate at 10 m depth.

Fig. S2. Snake Bay (12°08'21"N, 68°59'53"W), June 2017. (a, b) Polyps of *C. manuelensis* on rocky substrate at 16–17 m depth.

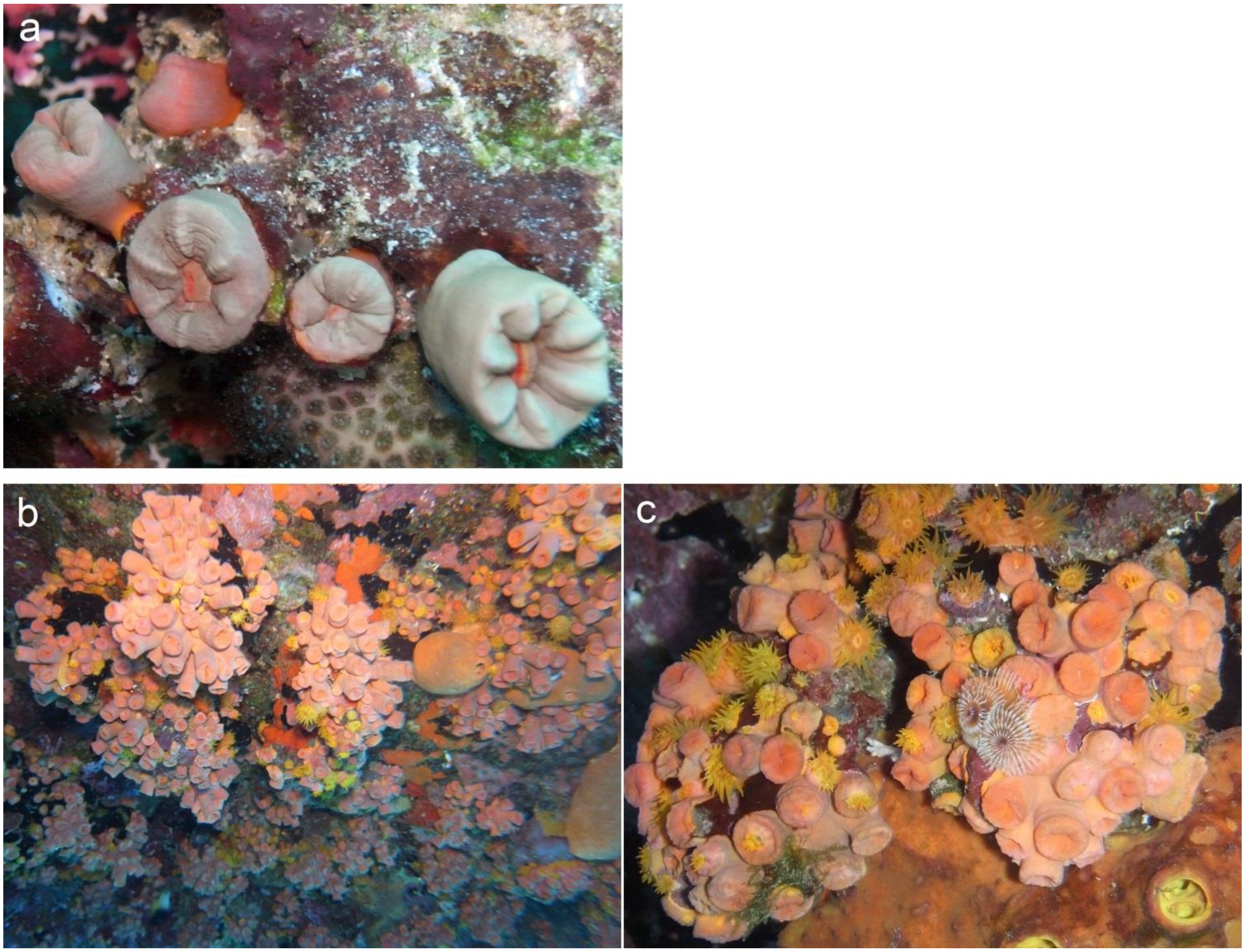

Fig. S3. Blue Wall (12°08'06''N, 68°59'16''W), June 2017. (a) Polyps of *C. manuelensis* on rocky substrate at 11 m depth. (b, c) Aggregation of *T. coccinea* underneath an overhang at 6 m depth.

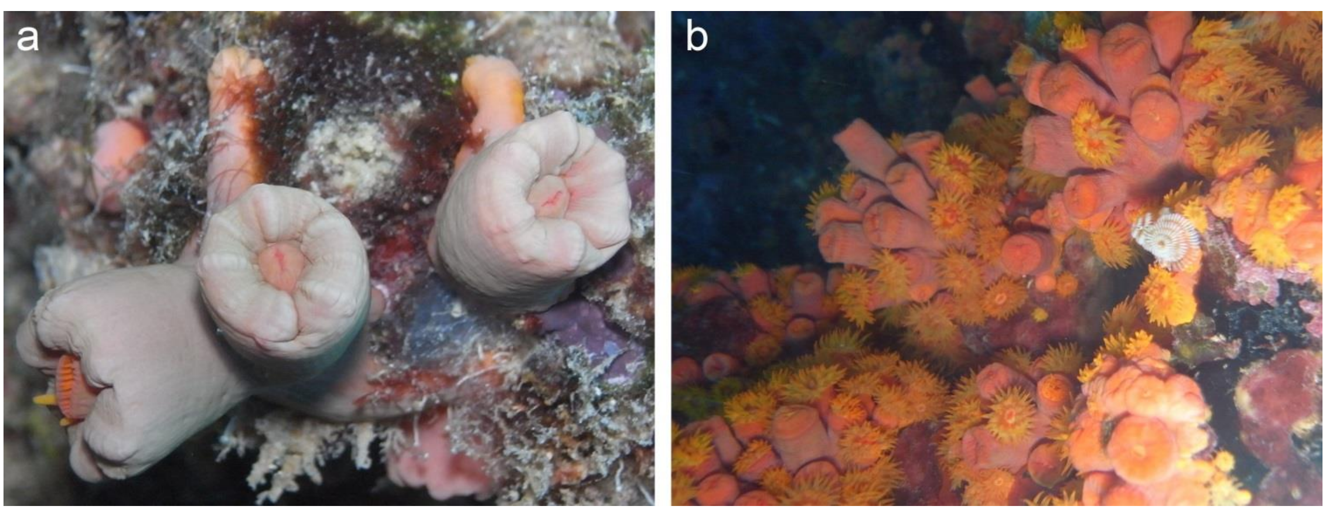

Fig. S4. Blue Bay (12°08'02''N, 68°59'07''W). (a) Polyps of *C. manuelensis* on rocky substrate at 5 m depth (June 2017). (b) Aggregation of *T. coccinea* underneath an overhang at <1 m depth (March 2014).

Fig. S5. Carmabi, Piscadera Bay (12°07'20''N, 68°58'08''W), coral colonies at 3 m depth underneath a small floating dock (pontoon) made of steel June 2017. (a, b) Colonies of *C. manuelensis*, (c) A colony of *T. coccinea*.

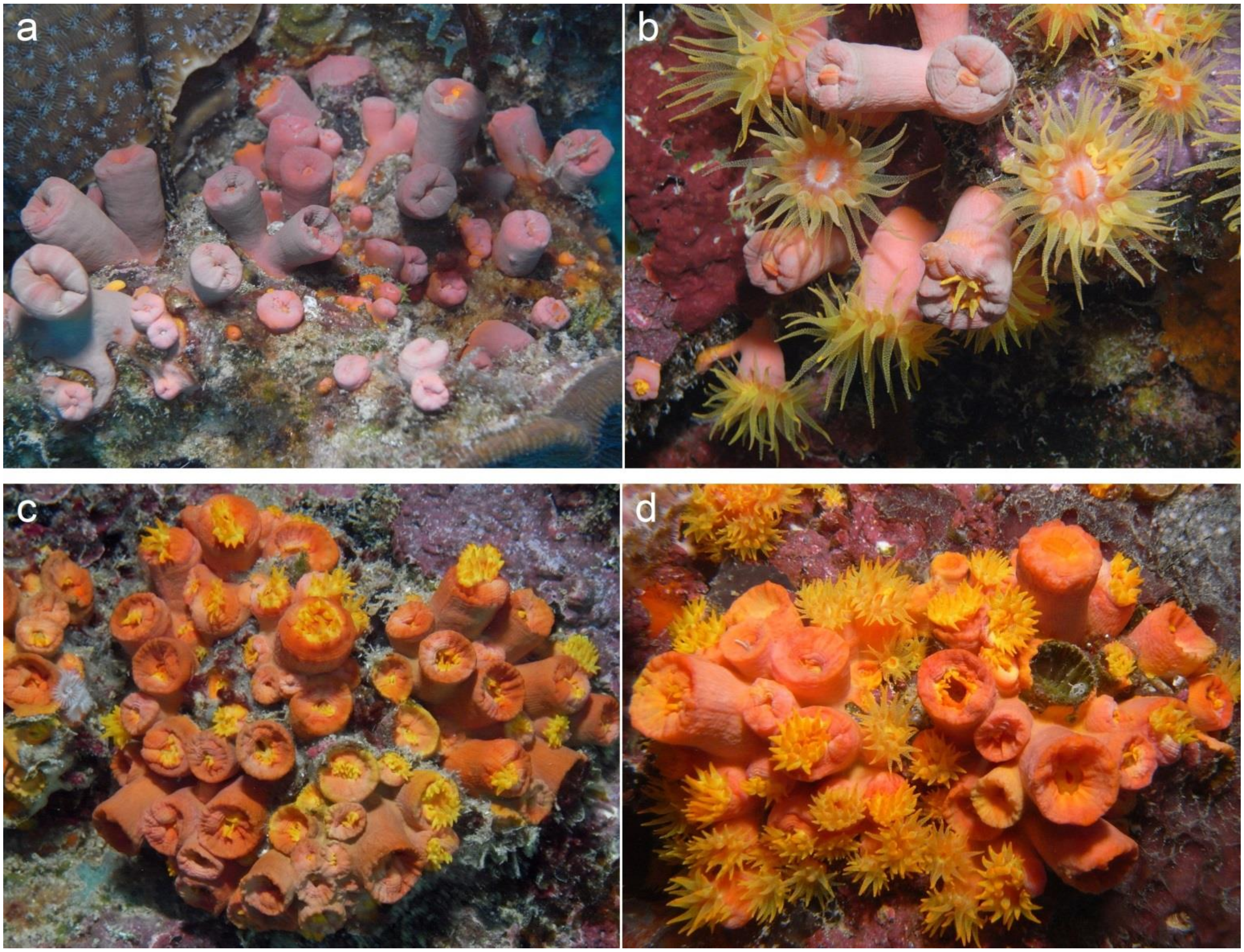

Fig. S6. Hilton (12°07'17''N, 68°58'09''W), rocky substrate. (a, b) Colonies of *C. manuelensis* at 12 m depth (February 2015, February 2017). (c, d) Colonies of *T. coccinea* underneath an overhang < 1 m depth (February 2015 February 2017).

Fig. S7. Parasasa Beach (12°06'57''N, 68°57'55''W), rocky substrate, June 2017. Colony of *C. manuelensis* at 20 m depth.

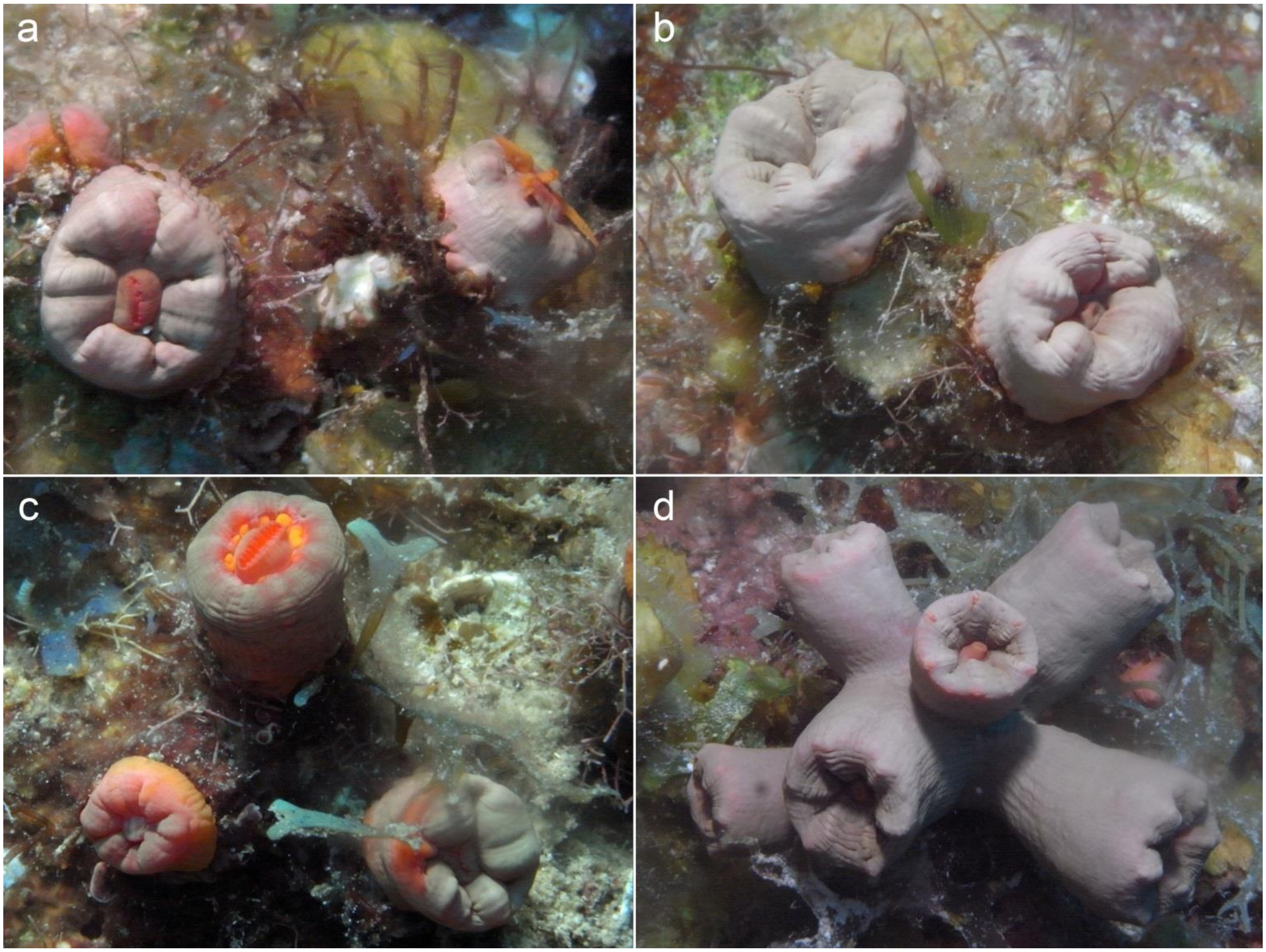

Fig. S8. Water Factory (12°06'33''N, 68°57'15''W), rocky substrate, 16–18 m depth, February 2016. (a–d) Colonies of *C. manuelensis*.

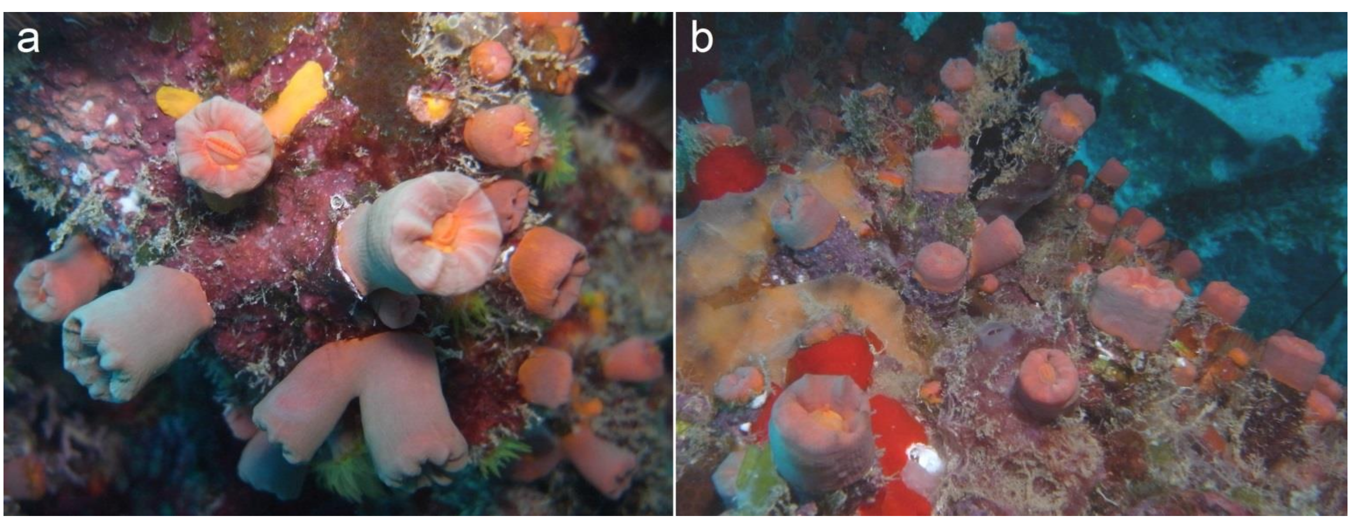

Fig. S9. Playa Mari Pampoen (12°05'24''N, 68°54'19''W), rocky substrate, February 2017. (a, b) Polyps of *C. manuelensis* at 17 m depth.

Fig. S10. Superior Producer shipwreck (12°06'18''N, 68°56'36''W). (a, b) Colonies of *R. goesi* at 23 m depth (March 2014) and (c) at 30 m (February 2017). Colonies of *C. manuelensis* at (d) 15 m, (e) 20 m (both March 2014), (f) at 30 m depth (February 2017).

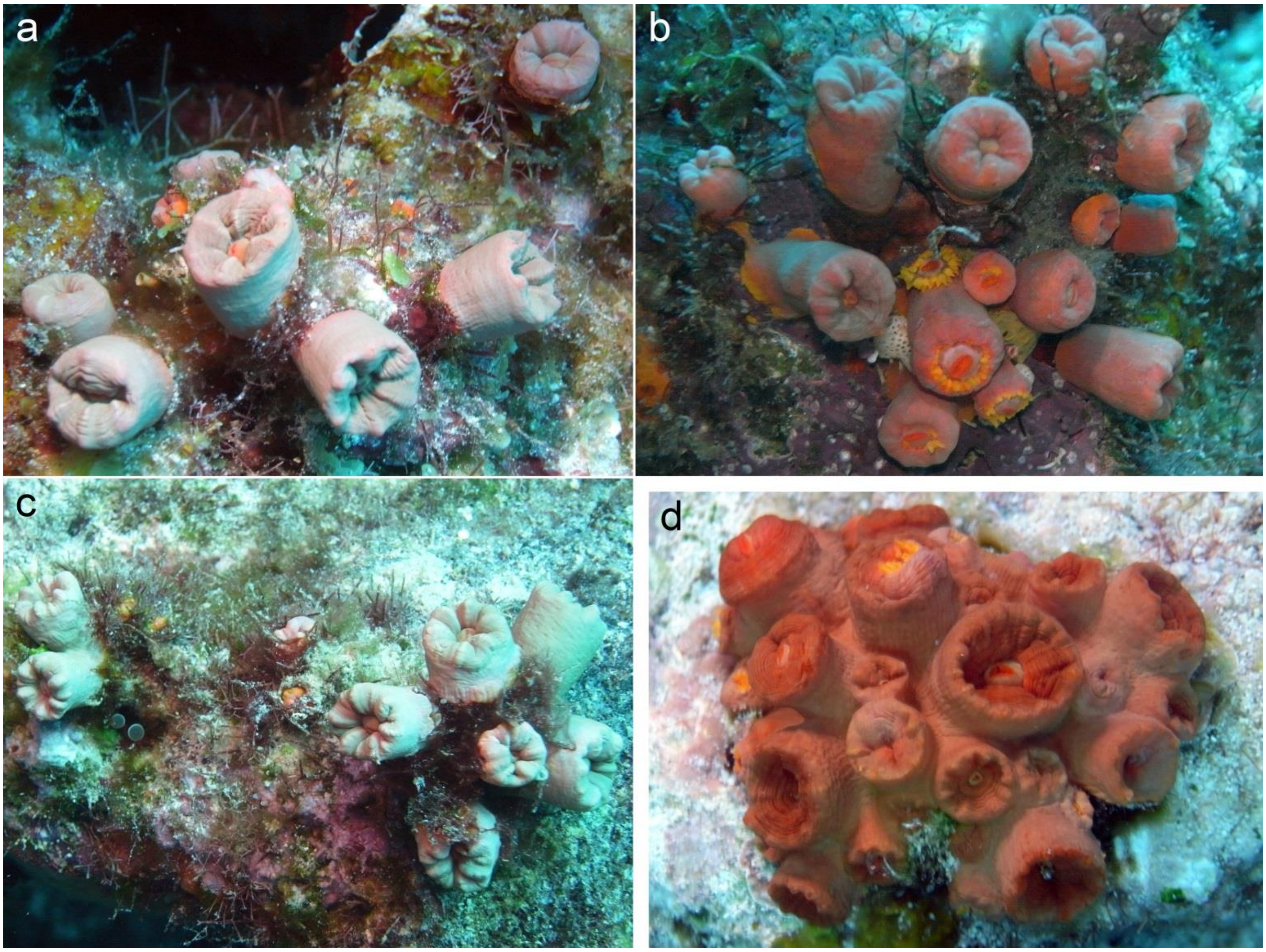

Fig. S11. Substation Curaçao (12°05'04"N, 68°53'54"W), rocky substrate. (a, b) Colonies of *Rhizopsammia* sp. on a reef slope at 6 m depth (February 2015). (c) Same species on a reef slope at 7 m depth (March 2014) (d) Colony of *T. coccinea* on a reef flat at 5 m depth (March 2014).

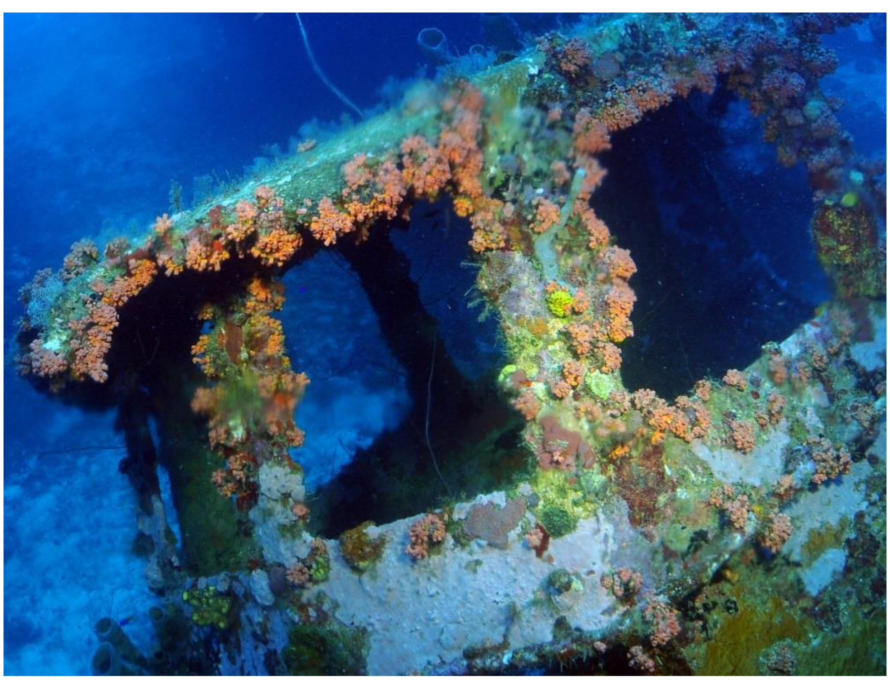

Fig. S12. Substation Curaçao (12°05'04"N, 68°53'54"W), March 2017. Aggregation of *T. coccinea* conies on a tugboat wreck at 55 m depth. Photo credit: Bruce Brandt taken from manned submersible *Curasub*.

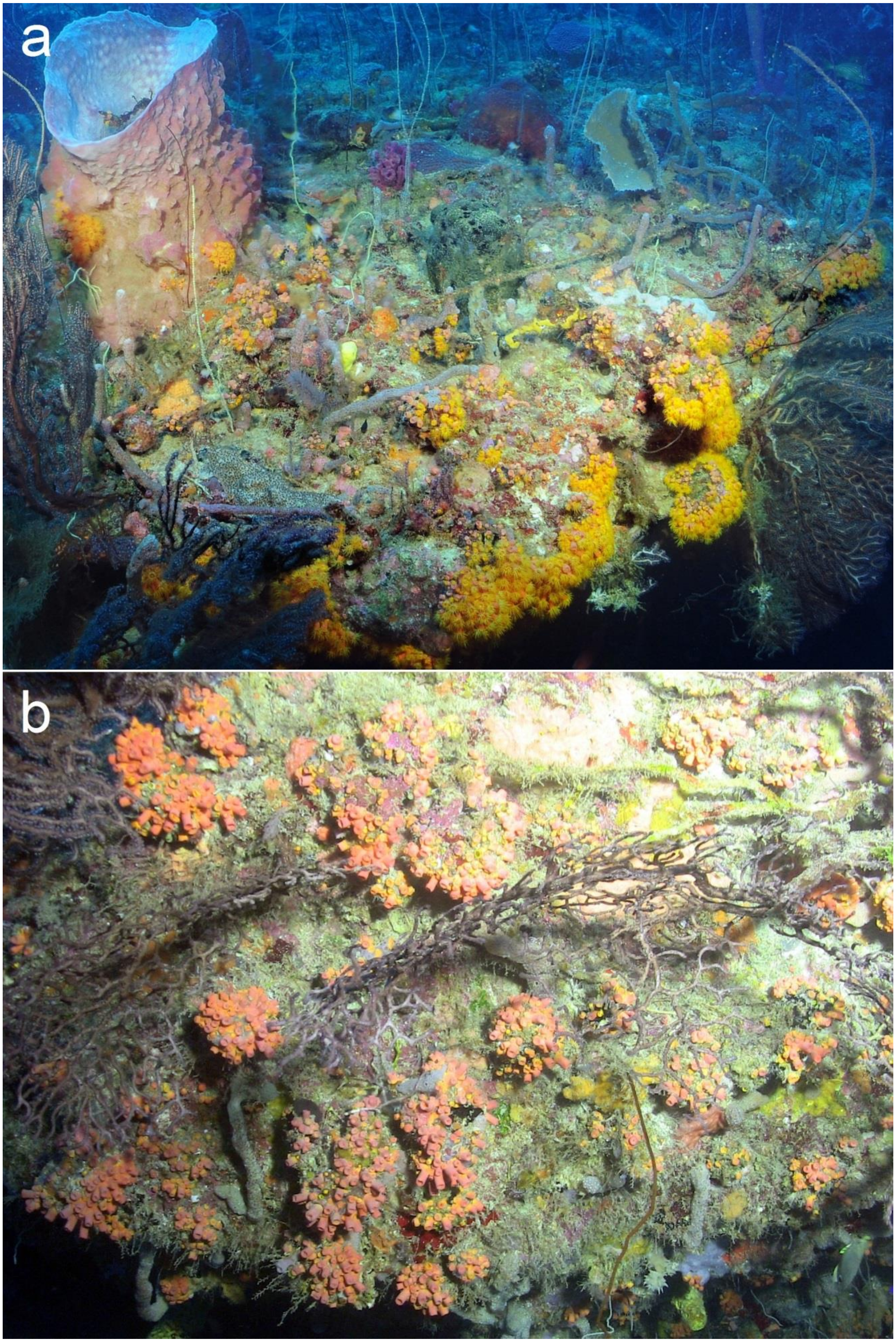

Fig. S13. Substation Curaçao (12°05'04"N, 68°53'54"W), March 2017. (a, b) Aggregation of *T. coccinea* colonies on an overhang at 55 m depth. Photo credit: Bruce Brandt taken from manned submersible *Curasub*.

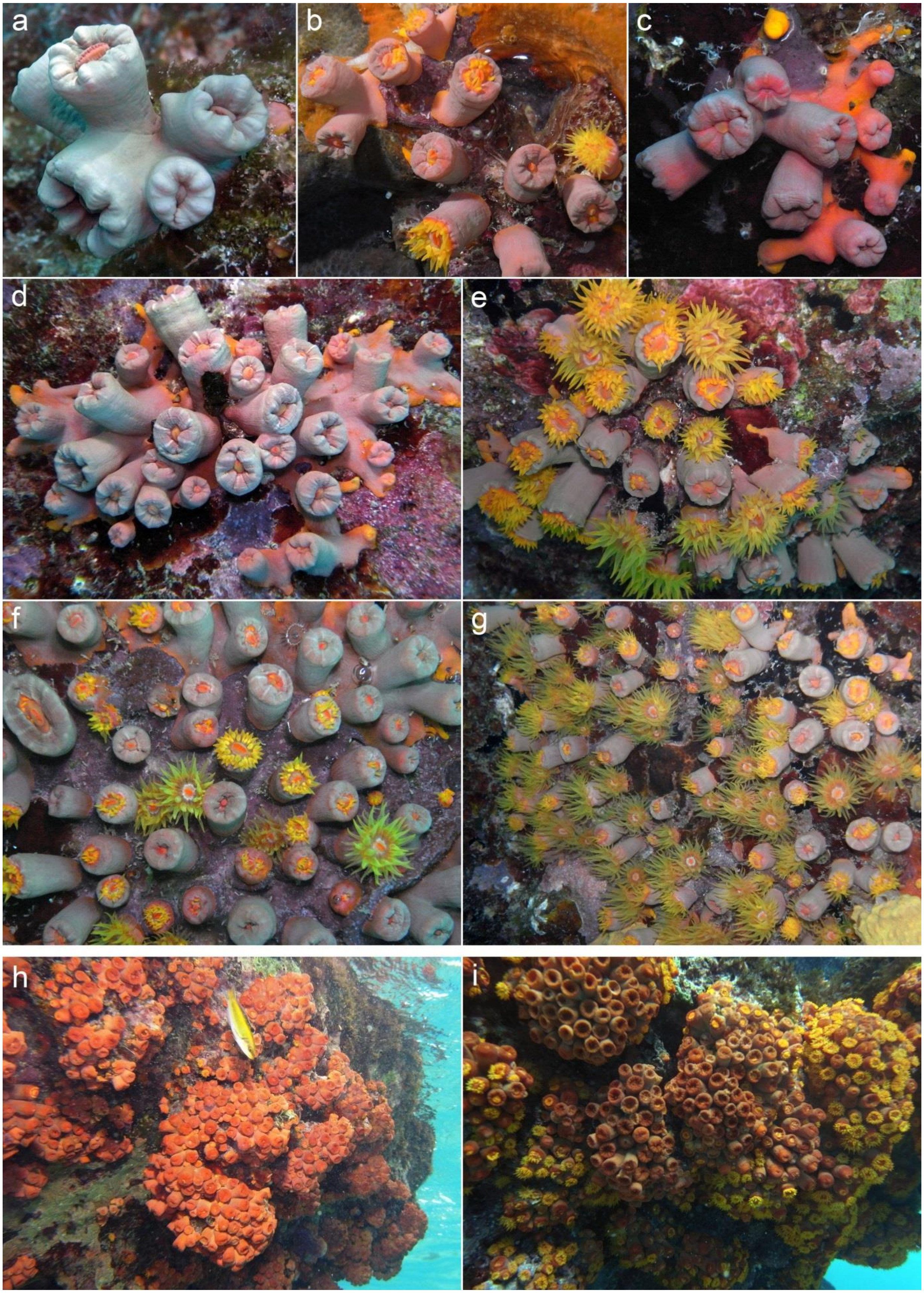

Fig. S14. Caracas Bay (12°04'05''N, 68°51'44''W), February and June 2017. (a–c) Polyps of *C. manuelensis* on rocky substrate at 9, 20, and 20 m depth, respectively (June 2017). (d–g) Same species on and inside small tugboat wreck at 4 m depth. (h, i) Aggregations of *T. coccinea* underneath rocky overhangs at 0.3 m depth.

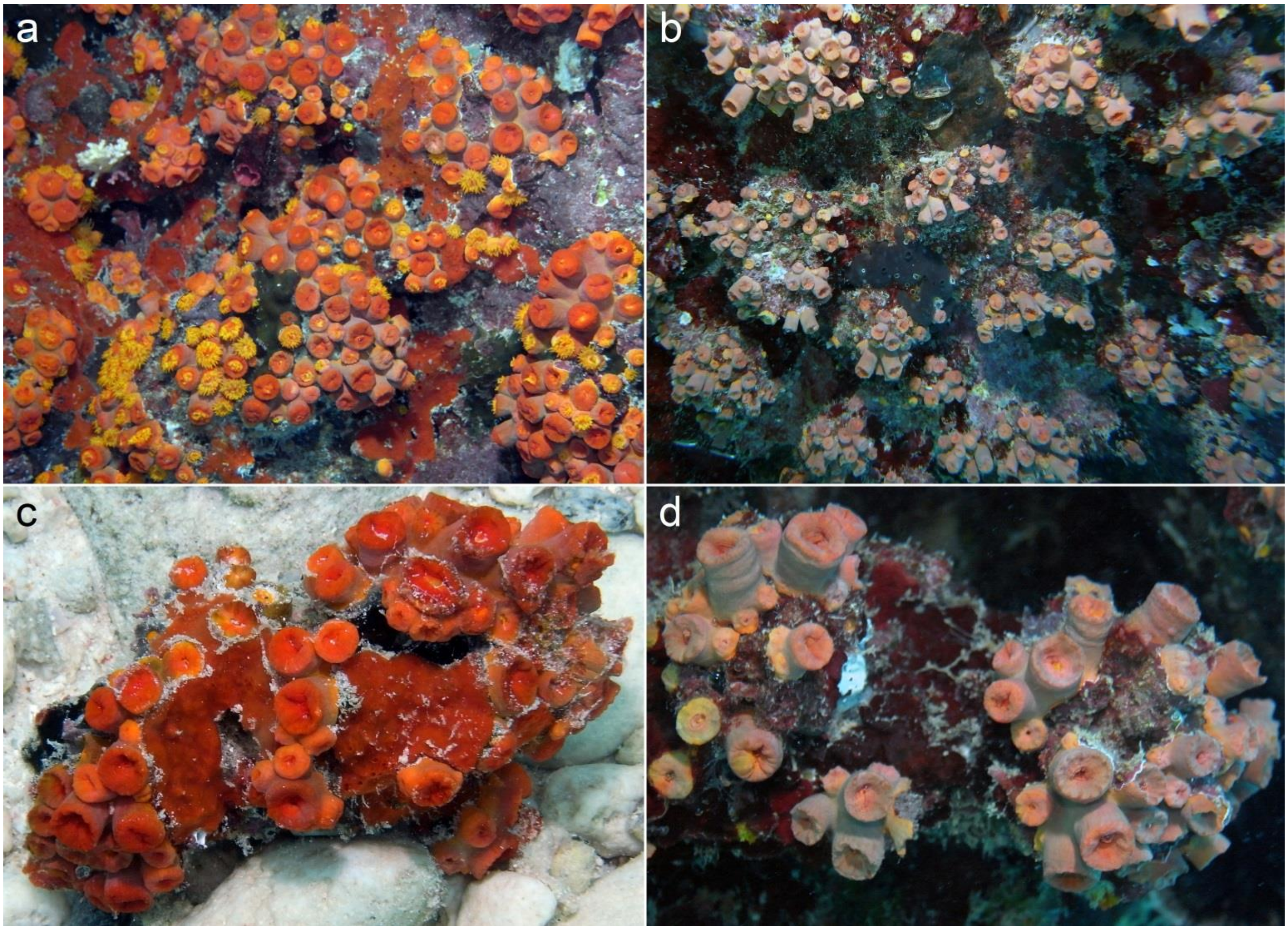

Fig. S15. Director’s Bay (12°03'59"N, 68°51'38"W), February 2017. Colonies of *T. coccinea* underneath overhangs (a) at 2 m and (b–d) at 6 m depth. The loose fragment on the bottom (c) has dropped 4 m downward from the overhang ceiling at 2 m depth.

Fig. S16. Colony of *C. manuelensis* at Aruba (May 2019). About 100 colonies were observed at 51 reef sites in 5x30 m^2 transects at 10 m depth with each site 700 m from the next one along the entire leeward coast of Aruba in May 2019.