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Neutral interactions among three nonindigenous coral species in a tropical marine fouling community

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The introduction and range expansions of alien species can impact the populations of native species. Among marine benthic invasive species, there are numerous instances of alien species competing with native ones, but examples of co-existing invasives that interact or compete with each other are harder to find (e.g., Kuebbing & Nuñez, 2015). If invasive species have functionally equivalent roles in their new communities, their interactions can lead to competitive displacement when resources, such as space, become limiting (Rauschert & Shea, 2017; Russell et al., 2014).

A well studied case of congeneric marine invasives in the Atlantic is that of three sun coral species of the genus *Tubastraea* (Scleractinia: Dendrophylliidae), which are originally from the tropical Indo-Pacific. They show overlapping distribution ranges in the southwestern Atlantic, the Caribbean, and the Gulf of Mexico, where they can negatively impact native benthic communities (Creed, 2006; Lages et al., 2012; Luz & Kitahara, 2017; Miranda et al., 2016). *Tubastraea coccinea* Lesson, 1830 was the first species that invaded the Atlantic region, dated to the 1930s (Cairns, 2000), followed by *T. tagusensis* Wells, 1982, in 2000, and *T. micranthus* (Ehrenberg, 1834), in 2006 (Creed et al., 2017a). These species show an opportunistic preference for a variety of substrates and can settle on natural and man-made materials, including mussel shells, plastic nets, and flotsam (Ballesteros et al., 2018; Creed & De Paula, 2007; Faria & Kitahara, 2020; Hoeksema & Hermanto, 2018; Mantelatto et al., 2020; Mantelatto & Creed, 2015). They can rapidly overtake open spaces through asexual reproduction (Capel et al., 2017) and function as habitats for a variety of native and nonnative coral-associated organisms, some of which are parasitic and have adopted these newly introduced corals as their new hosts (Alves et al., 2020; De Paula et al., 2017; Hoeksema & ten Hove, 2017; Vinagre et al., 2018).

In addition to these *Tubastraea* species, various introduced or cryptogenic octocoral species have recently been discovered in the southwestern Atlantic and the Caribbean, including fouling corals of the genera *Stragulum* (Hoeksema et al., 2023a; Samimi-Namin et al., 2022) and

Chromonephthea sp. (Hoeksema et al., 2023b). Given the expected range expansions and potential invasiveness of nonnative coral species, the probability that, in addition to native fauna, they also face competition from one another increases, depending on their co-occurrences. Although many studies have found that invasive coral species have impacted native populations (e.g., through the displacement of native species), few have examined the mechanisms underlying these competitive interactions (e.g., Guilhem et al., 2020; Sammarco et al., 2015). Neighboring individuals belonging to different *Tubastraea* species apparently show no signs of visible interaction in laboratory settings (*T. coccinea* and *T. micranthus*; Hennessey & Sammarco, 2014) or in the field, where they have jointly invaded certain areas (*T. coccinea* and *T. tagusensis*; Barbosa et al., 2023). The generality of this apparent lack of competition among co-invading coral species is currently not well known.

Recently, four nonnative coral species were reported from a fouling community on a semisubmersible platform that had operated in the southern Gulf of Mexico for the duration of 20 years and was then moored near a coral reef in Curaçao in the southern Caribbean (Hoeksema et al., 2023b). The nonnative coral fauna consisted of two scleractinians, *T. coccinea* and *T. tagusensis*, and two octocorals, *Chromonephthea* sp. and another unidentified nephtheid. Among these species, *T. coccinea* was already known from Curaçao at depths ranging from 0.2 m down to 55 m (Cairns, 2000; Hoeksema et al., 2019; Hoeksema & ten Hove, 2017) and *T. tagusensis* was known only from the northern Gulf of Mexico at 20–40 m depth (Figueroa et al., 2019).

Tissue contact occurred among all invasive corals and no harmful consequences of such interactions were observed when *Chromonephthea* sp. occurred adjacent to a colony of *T. coccinea* (Figure 1a). Despite their contact, neither showed tissue necrosis nor any other kind of damage in the contact zone. Interspecific interactions between the two *Tubastraea* species occurred frequently and involved direct tentacle contact (Figure 1b). This interaction was similar to nonaggressive intraspecific contacts among colonies of the same species, that is, without any signs of tissue damage in the contact zone as is commonly observed in colonies that actively compete (Lang, 1973). When space for lateral growth was not available anymore, colonies of both *Tubastraea* species usually grew upward, forming large, globular colonies (Figure 1b; Hoeksema et al., 2023b), a growth pattern also seen in *Tubastraea* populations with dense cover on concrete breakwaters (Ho et al., 2017), rocky reef walls

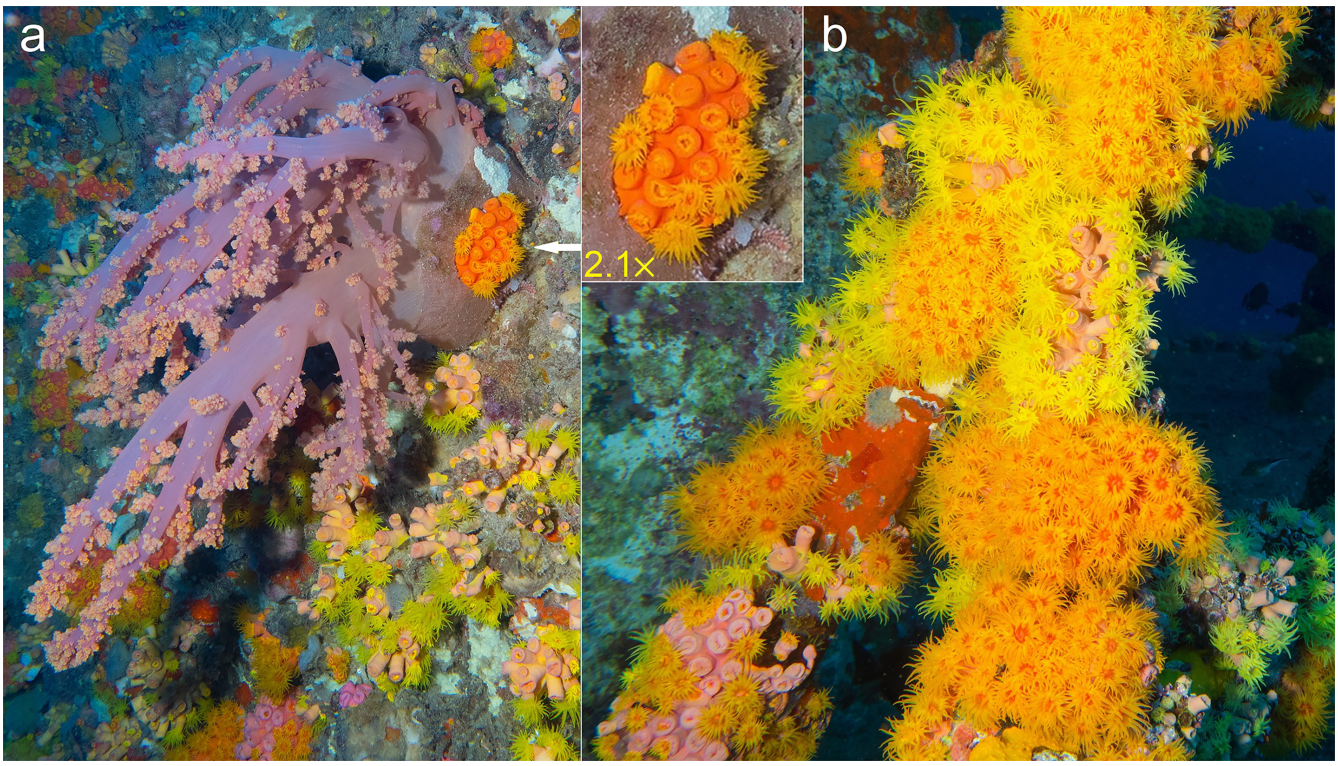

FIGURE 1 Nonindigenous corals showing neutral contact interactions on the hulls of the semisubmersible platform *Safe Regency* at Curaçao (7 May 2017). (a) A large soft coral, *Chromonephthea* sp., in direct tissue contact with an orange colony of *Tubastraea coccinea* (inset). Note the presence of various yellow coral colonies of *T. tagusensis* nearby. (b) Orange coral colonies of *T. coccinea* and yellow ones of *T. tagusensis* showing a dense intermixed assemblage with direct interspecific contact by their tentacles. Photograph credit: J. Bruijninckx.

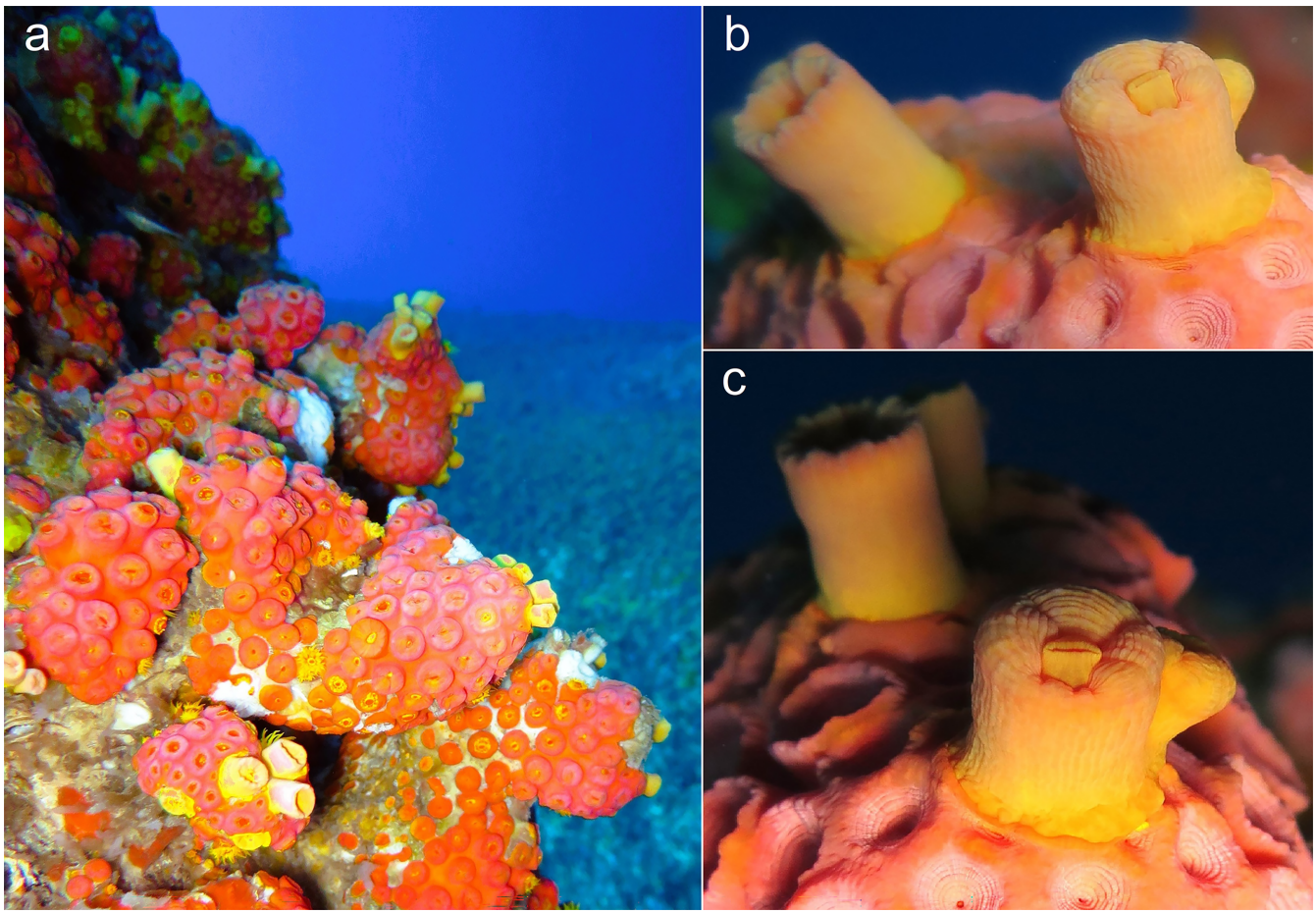

FIGURE 2 Colonies of *Tubastraea coccinea* (orange) and *T. tagusensis* (yellow) interacting by fusion on the semisubmersible platform *Safe Regency* at Curaçao, establishing a chimera (a) A cluster of fused colonies. (b, c) Long, light-colored *T. tagusensis* polyps surrounded by shorter, dark-colored *T. coccinea* polyps. Photograph credit: M. J. A. Vermeij.

(Mantelatto et al., 2011), and gas production platforms (Creed et al., 2017b).

Some neighboring colonies belonging to different coral species had fused, creating a chimeric mosaic of long *T. tagusensis* polyps surrounded by short *T. coccinea* polyps (Figure 2), further confirming earlier findings that coral colonies of different *Tubastraea* species do not harm each other (Barbosa et al., 2023; Hennessey & Sammarco, 2014). When and how this fusion could have happened in the life history of both species is unclear. Fusion of larvae is known to occur in *Tubastraea* corals (Luz et al., 2020; Mizrahi et al., 2014), which may explain how the present multispecies chimeric colonies could have developed. To our knowledge, illustrations of chimeric colonies with intermixed polyps belonging to different scleractinian species have not been published from other localities, although "mixed colonies" of *T. tagusensis* and *T. coccinea* are mentioned in a report on the removal of *Tubastraea* corals in Brazil (Creed et al., 2017b). This indicates that our case is not unique and could be more widespread but perhaps only in a nonnative setting. The colony mixing of two *Tubastraea* species differs from coral fusion involving two hydrocoral species, in which corals of the genus *Stylaster* (family Stylasteridae) settle on corals of the genus *Millepora* (family Milleporidae) (Fourreau et al., 2024; Montano et al., 2020).

The introduction and colonization of Caribbean reefs by new nonnative reef fauna seem inevitable as long as semisubmersible platforms are allowed to moor close to coral reefs, rocky shores, and breakwaters. The nearshore presence of semisubmersible platforms not only offers the opportunity to observe and study the development of nonnative marine communities and the interactions between nonnative and native organisms, but also to observe and study nonnatives themselves in their newly occupied habitats. The ability of invasive *Tubastraea* species to coexist in dense mixed assemblages, partially consisting of chimeric colonies, is in stark contrast with the competitive hierarchy that typifies native Caribbean corals (Lang, 1973) and could contribute to their success as invaders of a variety of benthic landscapes in their nonnative range.

AUTHOR CONTRIBUTIONS

Bert W. Hoeksema identified the project, contributed to the field sampling and the species identification, and produced the first manuscript draft. Kaveh Samimi-Namin contributed to the species identification and to the writing. Mark J. A. Vermeij contributed to the field sampling and to the writing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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REFERENCES

Alves, J., E. Neves, and R. Johnsson. 2020. "Two New *Amphilochida* (Amphipoda: Amphilochidea) Associated with the Bioinvasive *Tubastraea coccinea* from Todos-os-Santos Bay, Bahia State, Brazil." *Zootaxa* 4743: 21–34.

Ballesteros, L. V., J. L. Matthews, and B. W. Hoeksema. 2018. "Pollution and Coral Damage Caused by Derelict Fishing Gear on Coral Reefs around Koh Tao, Gulf of Thailand." *Marine Pollution Bulletin* 135: 1107–16.

Barbosa, A. C. C., C. Vinagre, M. V. Kitahara, and A. A. V. Flores. 2023. "Priority Effects, Environmental Filtering and Neutral Coexistence Explain Large-to Small-Scale Distribution of Invasive Sun Corals in the SW Atlantic." *Marine Ecology Progress Series* 707: 31–42.

Cairns, S. D. 2000. "A Revision of the Shallow-Water Azooxanthellate Scleractinia of the Western Atlantic." *Studies of the Natural History of the Caribbean Region* 125: 1–235.

Capel, K. C. C., R. J. Toonen, C. T. Rachid, J. C. Creed, M. V. Kitahara, Z. Forsman, and C. Zilberberg. 2017. "Clone Wars: Asexual Reproduction Dominates in the Invasive Range of *Tubastraea* spp. (Anthozoa: Scleractinia) in the South-Atlantic Ocean." *PeerJ* 5: e3873.

Creed, J. C. 2006. "Two Invasive Alien Azooxanthellate Corals, *Tubastraea coccinea* and *Tubastraea tagusensis*, Dominate the Native Zooxanthellate *Mussismilia hispida* in Brazil." *Coral Reefs* 25: 350.

Creed, J. C., and A. F. De Paula. 2007. "Substratum Preference during Recruitment of Two Invasive Alien Corals onto Shallow-Subtidal Tropical Rocky Shores." *Marine Ecology Progress Series* 330: 101–111.

Creed, J. C., D. Fenner, P. Sammarco, S. Cairns, K. Capel, A. O. R. Junqueira, I. Cruz, et al. 2017a. "The Invasion of the Azooxanthellate Coral *Tubastraea* (Scleractinia: Dendrophylliidae) throughout the World: History, Pathways and Vectors." *Biological Invasions* 19: 283–305.

Creed, J. C., A. O. R. Junqueira, B. G. Fleury, M. C. Mantelatto, and S. S. Oigman-Pszczol. 2017b. "The Sun-Coral Project: The First Social-Environmental Initiative to Manage the Biological Invasion of *Tubastraea* spp. in Brazil." *Management of Biological Invasions* 8: 181–195.

De Paula, A. F., B. G. Fleury, B. G. Lages, and J. C. Creed. 2017. "Experimental Evaluation of the Effects of Management of Invasive Corals on Native Communities." *Marine Ecology Progress Series* 572: 141–154.

Faria, L. C., and M. V. Kitahara. 2020. "Invasive Corals Hitchhiking in the Southwestern Atlantic." *Ecology* 101: e03066.

Figueroa, D. F., A. McClure, N. J. Figueroa, and D. W. Hicks. 2019. "Hiding in Plain Sight: Invasive Coral *Tubastraea tagusensis* (Scleractinia:Hexacorallia) in the Gulf of Mexico." *Coral Reefs* 38: 395–403.

Fourreau, C. J. L., D. Pica, E. A. Jamodiong, G. M. Castelló, I. Mizukami, and J. D. Reimer. 2024. "*Millepora* spp. as Substrates of their Hydrozoan Counterparts *Stylaster* sp. in the Pacific Ocean." *Diversity* 16: 142.

Guilhem, I. F., B. P. Masi, and J. C. Creed. 2020. "Impact of Invasive *Tubastraea* spp. (Cnidaria: Anthozoa) on the Growth of the Space Dominating Tropical Rocky-Shore Zoantharian *Palythoa caribaeorum* (Duchassaing and Michelotti, 1860)." *Aquatic Invasions* 15: 98–113.

Hennessey, S. M., and P. W. Sammarco. 2014. "Competition for Space in Two Invasive Indo-Pacific Corals—*Tubastraea micranthus* and *Tubastraea coccinea*: Laboratory Experimentation." *Journal of Experimental Marine Biology and Ecology* 459: 144–150.

Ho, M. J., C. M. Hsu, and C. A. Chen. 2017. "Wall of Orange Cup Coral, *Tubastraea coccinea*, at the Inlet Breakwaters of a Nuclear Power Plant, Southern Taiwan." *Marine Biodiversity* 47: 163–64.

Hoeksema, B. W., and B. Hermanto. 2018. "Plastic Nets as Substrate for Reef Corals in Lembeh Strait, Indonesia." *Coral Reefs* 37: 631.

Hoeksema, B. W., A. F. Hiemstra, and M. J. A. Vermeij. 2019. "The Rise of a Native Sun Coral Species on Southern Caribbean Coral Reefs." *Ecosphere* 10: e02942.

Hoeksema, B. W., M. P. Meijer zu Schlochtern, K. Samimi-Namin, and C. S. McFadden. 2023a. "In the Aftermath of Hurricane Irma: Colonisation of a 4-Year-Old Shipwreck by Native and Non-native Corals, Including a New Cryptogenic Species for the Caribbean." *Marine Pollution Bulletin* 188: 112576.

Hoeksema, B. W., K. Samimi-Namin, C. S. McFadden, R. M. Rocha, L. P. van Ofwegen, A. F. Hiemstra, and M. J. A. Vermeij. 2023b. "Non-native Coral Species Dominate the Fouling Community on a Semi-Submersible Platform in the Southern Caribbean." *Marine Pollution Bulletin* 194: 115354.

Hoeksema, B. W., and H. A. ten Hove. 2017. "The Invasive Sun Coral *Tubastraea coccinea* Hosting a Native Christmas Tree

Worm at Curaçao, Dutch Caribbean." *Marine Biodiversity* 47: 59–65.

Kuebbing, S. E., and M. A. Nuñez. 2015. "Negative, Neutral, and Positive Interactions among Nonnative Plants: Patterns, Processes, and Management Implications." *Global Change Biology* 21: 926–934.

Lages, B. G., B. G. Fleury, A. M. Hovell, C. M. Rezende, A. C. Pinto, and J. C. Creed. 2012. "Proximity to Competitors Changes Secondary Metabolites of Non-indigenous Cup Corals, *Tubastraea* spp., in the Southwest Atlantic." *Marine Biology* 159: 1551–59.

Lang, J. 1973. "Interspecific Aggression by Scleractinian Corals. 2. Why the Race Is Not Only to the Swift." *Bulletin of Marine Science* 23: 260–279.

Luz, B. L. P., M. Di Domenico, A. E. Migotto, and M. V. Kitahara. 2020. "Life-History Traits of *Tubastraea coccinea*: Reproduction, Development, and Larval Competence." *Ecology and Evolution* 10: 6223–38.

Luz, B. L. P., and M. V. Kitahara. 2017. "Could the Invasive Scleractinians *Tubastraea coccinea* and *T. tagusensis* Replace the Dominant Zoantharian *Palythoa caribaeorum* in the Brazilian Subtidal?" *Coral Reefs* 36: 875.

Mantelatto, M. C., and J. C. Creed. 2015. "Non-indigenous Sun Corals Invade Mussel Beds in Brazil." *Marine Biodiversity* 45: 605–6.

Mantelatto, M. C., J. C. Creed, G. G. Mourão, A. E. Migotto, and A. Lindner. 2011. "Range Expansion of the Invasive Corals *Tubastraea coccinea* and *Tubastraea tagusensis* in the Southwest Atlantic." *Coral Reefs* 30: 397.

Mantelatto, M. C., A. A. Póvoa, L. F. Skinner, F. V. de Araujo, and J. C. Creed. 2020. "Marine Litter and Wood Debris as Habitat and Vector for the Range Expansion of Invasive Corals (*Tubastraea* spp.)." *Marine Pollution Bulletin* 160: 111659.

Miranda, R. J., I. C. Cruz, and F. Barros. 2016. "Effects of the Alien Coral *Tubastraea tagusensis* on Native Coral Assemblages in a Southwestern Atlantic Coral Reef." *Marine Biology* 163: 45.

Mizrahi, D., S. A. Navarrete, and A. A. V. Flores. 2014. "Groups Travel Further: Pelagic Metamorphosis and Polyp Clustering Allow Higher Dispersal Potential in Sun Coral Propagules." *Coral Reefs* 33: 443–48.

Montano, S., J. D. Reimer, V. N. Ivanenko, J. E. García-Hernández, G. W. N. M. van Moorsel, P. Galli, and B. W. Hoeksema. 2020. "Widespread Occurrence of a Rarely Known Association between the Hydrocorals *Stylaster roseus* and *Millepora alcicornis* at Bonaire, Southern Caribbean." *Diversity* 12: 218.

Rauschert, E. S. J., and K. Shea. 2017. "Competition between Similar Invasive Species: Modeling Invasional Interference across a Landscape." *Population Ecology* 59: 79–88.

Russell, J. C., N. S. Sataruddin, and A. D. Heard. 2014. "Over-Invasion by Functionally Equivalent Invasive Species." *Ecology* 95: 2268–76.

Samimi-Namin, K., L. P. van Ofwegen, B. W. Hoeksema, L. C. Woodall, M. Meijer zu Schlochtern, and C. S. McFadden. 2022. "New Records of the Cryptogenic Soft Coral Genus *Stragulum* (Tubiporidae) from the Eastern Caribbean and the Persian Gulf." *Diversity* 14: 909.

Sammarco, P. W., S. A. Porter, M. Genazzio, and J. Sinclair. 2015. "Success in Competition for Space in Two Invasive Coral Species in the Western Atlantic – *Tubastraea micranthus* and *T. coccinea*." *PLoS One* 10: e0144581.

Vinagre, C., R. Silva, V. Mendonça, A. A. Flores, A. Baeta, and J. C. Marques. 2018. "Food Web Organization Following the Invasion of Habitat-Modifying *Tubastraea* spp. Corals Appears to Favour the Invasive Borer Bivalve *Leiosolenus aristatus*." *Ecological Indicators* 85: 1204–9.

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