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# The invasive soft coral *Xenia umbellata* has been confirmed in Cuban waters

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ABSTRACT.—Biological invasions rank among the most severe threats to vulnerable ecosystems because invasive species often outcompete native organisms, frequently resulting in local extinctions. This is especially concerning for Caribbean reef ecosystems, which have been declining under continuous and emerging pressures, and where reports of allochthonous octocoral species have been increasing. Octocoral colonies with unusual morphology were detected in September 2022 and October 2023 in two coastal areas east of Havana, Cuba, and tentatively identified as invasive *Unomia stolonifera*, an Indo-Pacific octocoral first reported in the Caribbean off Venezuela in the early 2000s. We applied molecular barcoding (16S/ND2, mtMutS, COI, 28S) to verify the taxonomic identification of the octocorals. These analyses unequivocally identified the sampled colony as *Xenia umbellata*, an octocoral native to the Red Sea. *Xenia umbellata* was first detected in Puerto Rico in October 2023 and has since been found on reefs along its southern coast. Both invasive octocorals pose serious environmental concerns due to their stress tolerance, totipotentiality, propagation capacity, and negative interactions with native benthic fauna. Attempts to eradicate the octocoral colonies from Cuban waters have had apparent success, helping to control further expansion. The introduction of *X. umbellata* to Cuba is likely linked to the aquarium trade, biofouling through hull fouling and floating debris, or ballast water. The presence of either invasive species in the Caribbean is a serious environmental concern, underscoring the need for continued surveillance and rapid response to prevent further spread across the region.


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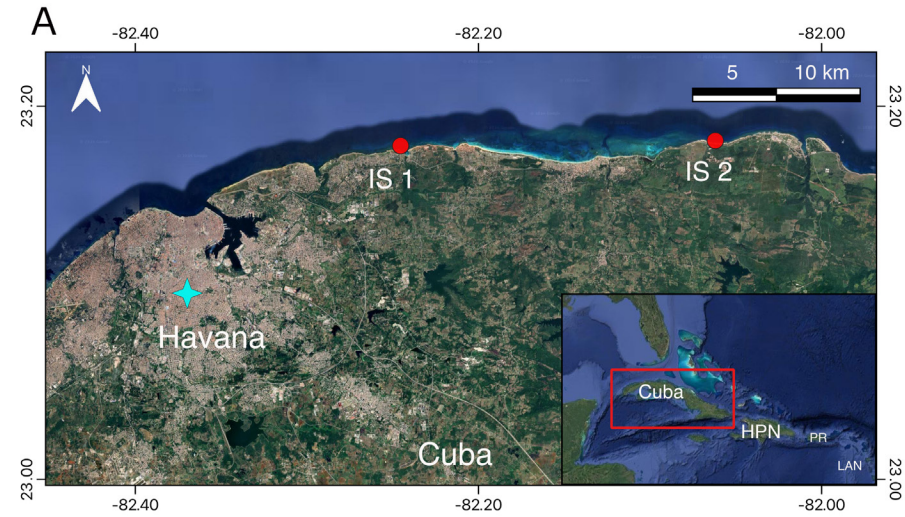
In September 2022 scientists from the Center of Marine Research at the University of Havana (CIM-UH) observed several colonies of an atypical crustose octocoral during an ecological assessment for "Habana Sumergida" (Underwater Havana). Gross morphological characteristics showed similarity to *Unomia stolonifera* (Gohar, 1938) (Malacalcyonacea: Xeniidae), an invasive soft coral species already present in Venezuela (Ruiz-Allais et al. 2014, 2021, Espinosa et al. 2023). The colonies covered approximately 1 $m^2$ of benthos and were found at a depth of between 8 and 10 m in the Bacuranao Inlet, Habana del Este municipality (23°10′47.4″N, 82°14′39.7″W; Fig. 1A). The stolons were attached to a rocky matrix, encrusted with a layer of calcareous red algae. Samples of these octocorals were collected and preserved by the Institute of Marine Sciences (ICIMAR) in 4% formalin and deposited in the collections of the National Aquarium of Cuba and CIM-UH.

Eradication efforts were permitted by the Oficina de Regulación y Seguridad Ambiental, Havana, and initiated immediately to stave off the ecological damage in Cuba experienced in past octocoral invasions of the Caribbean, such as the *U. stolonifera* colonization of Venezuelan waters (Ruiz-Allais et al. 2014, 2021). Invasive corals were detached with knives and carried away in nylon bags (Espinosa et al. 2023). Despite the eradication of these initial colonies, subsequent reef surveys of Bacuranao Inlet (on 17 and 23 February, and 13 March, 2023) found that the octocoral patch had regrown and expanded near the original sighting location. The reestablished patch overgrew a small portion of the channel's western reef on the wall and surface of a surge channel. There have been no recent visits by members of CIM-UH to the area; however, knowledgeable local underwater fishermen and divers who frequent Bacuranao Inlet have not reported additional colonies.

In response to a soft coral sighting by recreational diver Mitch Morales, the study area was expanded to include Boca de Calderas, Mayabeque (23°10′57.14″N, 82°3′39.21″W; Fig. 1A). This second phase was conducted by a team of specialists and divers staffed by members of the Antonio Núñez Jiménez Foundation for Nature and Humanity (FANJ), ICIMAR, CIM-UH, and the Rincón de Guanabo Protected Natural Landscape (PNPRdG). Carried out on 5 October, 2023, this survey revealed a second aggregate of octocorals morphologically similar to the first (Fig. 1B), but roughly 19 km from the Bacuranao site to the east of the city of Havana. The Boca de Calderas aggregates were more extensive than those at Bacuranao, spread over an estimated area of 150 $m^2$. The aggregations extended about 30 m along the edge of the first submarine terrace at depths of 8–13 m. Within this area, three to five soft coral aggregations were observed, each occupying a surface area of 5 to 6 $m^2$. The main aggregation covered about 4 $m^2$, extending over rocks, corals and other substrata (Fig. 1B); because of this three-dimensional structure, the actual area covered may be nearly double that of its two-dimensional projection. Each soft coral aggregate typically covered over 95% of the occupied area. These colonies were treated with chlorine tablets and covered with nylon (black plastic sheeting). While not completely eradicated, their distribution has not increased.

Espinosa et al. (2023) tentatively identified the invasive octocorals in Cuba as *U. stolonifera* based on morphological characteristics; however, they emphasized that definitive identification would require DNA analyses from the colonies. Contemporary surveys in Puerto Rican waters reported two new allochthonous octocoral species belonging to the family Xeniidae (Toledo-Rodriguez et al. 2025a,b). These parallel octocoral invasions prompted communication and collaboration



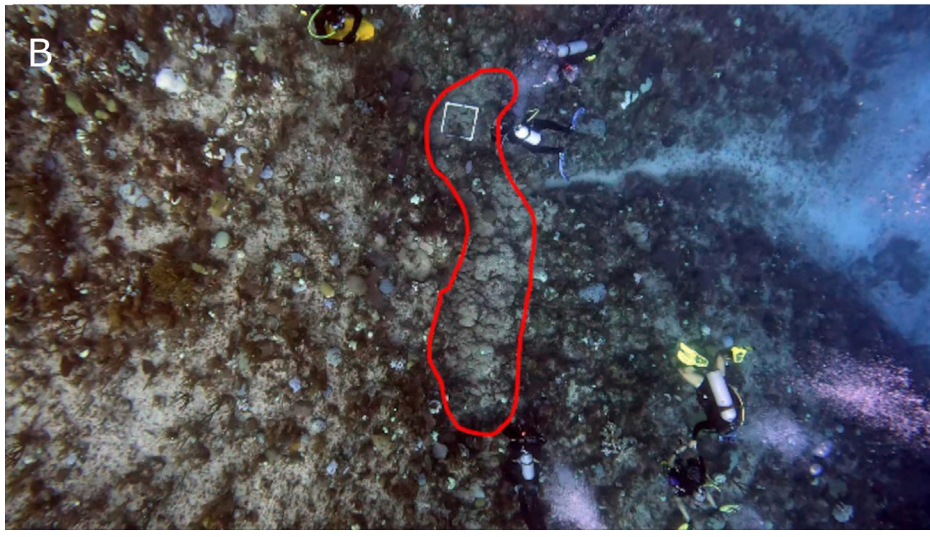




Figure 1. (A) Map showing the geographic location of established colonies of *Xenia umbellata* along the northwestern coast of Cuba. Location of two invasion sites: Bacuranao (IS 1) and Boca de Calderas (IS 2). Inset showing the location of Cuba within the Greater Caribbean. (B) Approximate outline (in red) of the main octocoral aggregate found in Boca de Calderas, Mayabeque, 5 October, 2023. Several divers can be seen surveying the site. As reference, the size of the white quadrat is 50 × 50 cm. HPN: Hispaniola, PR: Puerto Rico, LAN: Lesser Antilles. Photo credit: J Espinosa Sáez, R Estrada Estrada, A Martínez Pérez, Y del Carmen Luguera González. Modified from Google Maps, 2006.

between the various stakeholders within the affected jurisdictions. It was determined that the correct taxonomic identification of the invasive species was of paramount importance to the implementation of an effective management plan. This knowledge informs the selection of appropriate response actions, offering insight into potential introduction pathways or modes of propagation, and reducing the risk of ineffective or misdirected interventions that may further compromise the coastal ecosystem.

However, identifying xeniid species can be complicated when based solely on external and internal morphology. Overlapping shapes of colony forms, stalk growth patterns, and characteristics of the pinnate tentacles make them difficult to distinguish visually, especially in the field. Unlike most other octocoral taxa that can be identified from the characteristic shapes and distribution of sclerites (calcitic skeletal elements), the sclerites of xeniids are very homogeneous and exhibit few species-specific characters that can be observed under light microscopy (Halász et al. 2019). These limitations emphasize the importance of integrative taxonomy, which requires molecular analyses. In this study, we employed multilocus barcoding to clarify the taxonomic identity of a colony sampled from Boca de Calderas, east of Havana.

## Methods

Sampling Sites.—During surveys conducted by personnel from ICIMAR, FANJ, CIM-UH, and PNPRdG, one colony was sampled for genetic barcoding at Boca de Calderas, Mayabeque Province, near PNPRdG Rincón de Guanabo (23°10′57.14″N, 82°3′39.21″W). The tissue sample was sent to personnel of the Puerto Rico Department of Natural and Environmental Resources, who then distributed it to the McFadden Laboratory, Harvey Mudd College, and the Marine Genomic Biodiversity Lab at the University of Puerto Rico, Mayagüez for molecular identification.

DNA Procedures and Analysis.—From one polyp, 4–5 tentacles were excised using sterile tweezers and a scalpel, then used as a tissue source for DNA extraction. DNA extraction was performed using the Qiagen DNeasy Blood and Tissue kit following the manufacturer's protocol, or Qiagen DNeasy PowerSoil® kit with an additional homogenization step consisting of three sets of 20 s, with 1-min intervals on ice between the sets to maximize DNA yield. PCR amplifications of three mitochondrial regions (16S/ND2, mtMutS, COI) and the nuclear large ribosomal subunit (28S rDNA) were done using the primers listed in Koido et al. (2022). For the PCR amplifications, we followed the protocol in Toledo-Rodriguez et al. (2025a). Amplified DNA was sequenced in both directions in an Applied Biosystems SeqStudio Genetic Analyzer using the BigDye 3.1 Terminator Cycle chemistry. The DNA traces were inspected for quality and accuracy in CodonCode Aligner v10.0.2 (CodonCode Corp.). GenBank accession numbers for the generated sequences are: 16S/ND2 (QB136112), mtMutS (QB136111), COI (QB137842), and 28S (QB131188). The resulting DNA sequences were concatenated and then aligned in MAFFT v.7 (Katoh and Standley 2013) with default parameters. We compared the DNA sequences from Cuba with 31 published xeniid sequences in a phylogenetic analysis. The analyses included selected 16S/ND2, mtMutS, COI, and 28S sequences from McFadden et al. (2017) and Benayahu et al. (2021; Supplementary Table S1). A maximum likelihood (ML) tree was constructed using raxmlGUI 2.0.17 (Stamatakis 2014, Edler et al. 2021) and rooted on the *Xenia*–*Ovabunda* branch.

First, the program modeltest-ng (Darriba et al. 2020) was used in raxmlGUI to estimate the best nucleotide substitution model for the concatenated data. The best nucleotide substitution model (TPM3uf+I) for the alignment was selected using the Akaike Information Criterion. Then, an ML + thorough bootstrap search for the best tree was conducted in raxml-ng (Kozlov et al. 2019). Clade support was assessed with 100 nonparametric bootstrap replicates (Felsenstein 1985). The best-scoring ML tree




Figure 2. (A) Partial view of an aggregate of *Xenia umbellata*, (B) colonies of *Xenia umbellata* showing contracted polyps, and (C and D) polyp details of *Xenia umbellata* in Boca de Calderas, Mayabeque, 5 October, 2023. Photo credit: J Espinosa Sáez, R Estrada Estrada, A Martínez Pérez, Y del Carmen Luguera González.

with bootstrap values was viewed and edited in FigTree 1.4.4, then imported into Adobe Illustrator 30.2.1 to improve visualization.

## Results

Photographs of the Cuban xeniid colonies taken in situ (Fig. 2A–D) show all polyps localized to the tops of the colony stalks, a diagnostic character of the genus *Xenia*. In contrast, *U. stolonifera* exhibits isolated polyps on the stalks and base of the colony (Benayahu et al. 2021). In addition, sequences obtained for each of four loci used for DNA barcoding of octocorals (16S/ND2 = 710 bp; mtMutS = 714 bp; COI = 771 bp; 28S rDNA = 708 bp, a total of 2,903 bp) were 100% identical to barcodes published previously for *Xenia umbellata* from the Red Sea and from the invasive population in Puerto Rico (Fig. 3).

## Discussion

The occurrence of invasive octocorals from the family Xeniidae is evident in the wider Caribbean and causes increasing concerns in the Greater Antilles (Ruiz-Allais et al. 2014, 2021, Espinosa et al. 2023, Toledo-Rodriguez et al. 2025a,b, Veglia et al. 2025). Since the detection of xeniid colonies in Cuban waters, initially identified

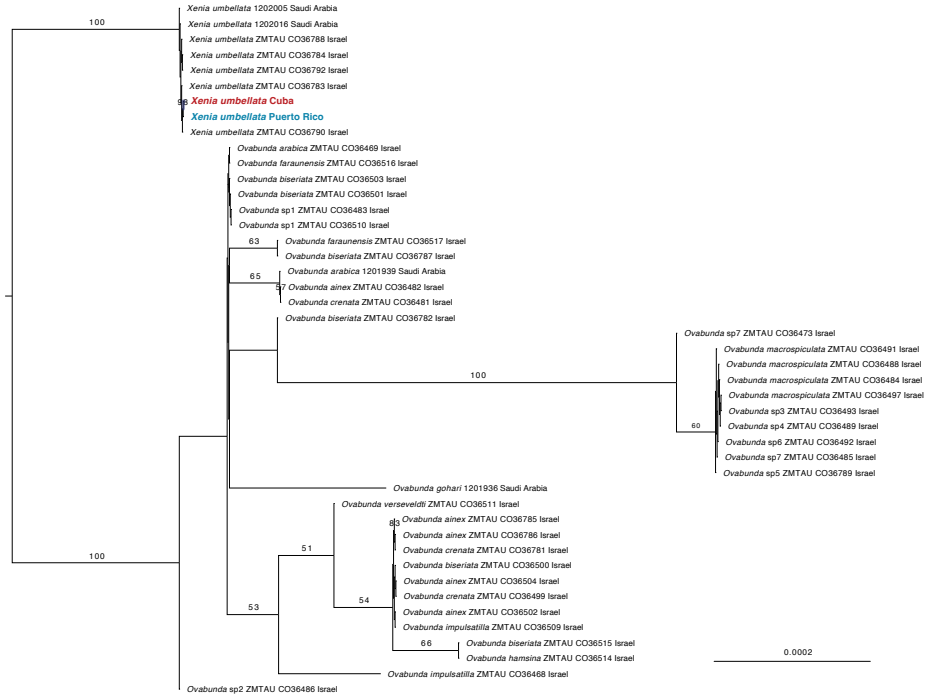



Figure 3. A maximum likelihood tree based on concatenated sequences of mtMutS, 16S/ND2, COI, and 28S gene regions showing the phylogenetic placement of invasive xeniid corals in Cuba (in bold red) and in Puerto Rico (in bold blue) within the *Xenia umbellata* clade. The tree was rooted on the *Xenia-Ovabunda* branch. Numbers on clades represent nonparametric bootstrap values (Bp > 50). Voucher information follows the specimen's name (see McFadden et al. 2017 and Supplementary Table S1).

morphologically as *U. stolonifera*, an immediate response was executed to limit further spread and potential ecological impact. This response was motivated by the ecological impacts reported in Venezuela, where *U. stolonifera* rapidly expanded and monopolized benthic habitats (Ruiz-Allais et al. 2014, 2021). More recently, similar concerns emerged in Puerto Rico following reports of invasive octocoral colonies initially presumed to be *U. stolonifera*. Molecular and morphological analyses later confirmed these colonies as two separate species of pulsing corals, *X. umbellata* (Toledo-Rodriguez et al. 2025a, Veglia et al. 2025) and *Latissimia ningalooensis* (Toledo-Rodriguez et al. 2025b). Here, using identical approaches applied to Puerto Rico specimens, we examined four DNA regions to confirm unequivocally that the invasive Cuban species is not *U. stolonifera* as originally reported (Espinosa et al. 2023), but is instead identified as *X. umbellata*.

The phylogenetic footprint of *X. umbellata* is unique within Xeniidae (McFadden et al. 2017) and standard DNA barcode sequencing can provide definitive evidence for the presence of the species in the area (McFadden et al. 2019). Our results indicate that *X. umbellata* may be more widespread in the region than previously thought. Whether through artificial means (e.g., hull fouling, ballast water, releases from aquaria, rafting) or potential dispersal of larval propagules, additional populations may occur along the coasts of the Dominican Republic and Haiti, or in other locations in the Caribbean. This discovery of *X. umbellata* in Cuba and Puerto Rico

has changed the prevailing narrative regarding soft coral invasion in the Caribbean. Rather than addressing a single-species scenario—*U. stolonifera*, which has rapidly expanded in Venezuela (Ruiz-Allais et al. 2014, 2021)—the region is now confronted with the introduction of multiple species: *X. umbellata* (Toledo-Rodriguez et al. 2025a, Veglia et al. 2025) and *L. ningalooensis* (Toledo-Rodriguez et al. 2025b) in Puerto Rico, and *X. umbellata* in Cuba (this study). This represents a conservative scenario, given that invasive soft corals will most likely continue expanding beyond these three Caribbean territories.

The first octocoral aggregations in Cuba were discovered in Bacuranao Inlet, east of Havana, in September 2022, more than one year before colonies were first observed by recreational divers in southern Puerto Rico in October 2023. Although these Cuban aggregations are presumed to be *X. umbellata*, species identity was unequivocally confirmed only for a colony from Boca de Calderas. However, at least in Puerto Rico, the size of the aggregations suggests the initial sightings likely postdated the actual establishment of colonies. The near-simultaneous detection of *X. umbellata* in two Caribbean islands is puzzling. Commercial vessel traffic between the two islands appears to be limited or absent, which may reduce the likelihood of spread between sites via shipping. However, biofouling-mediated transport does not depend on commercial traffic alone—fishing boats, recreational yachts, and other small vessels can also act as vectors (Davidson et al. 2010, Murray et al. 2011, Ulman et al. 2019, Ashton et al. 2022). A scenario involving independent introductions associated with maritime infrastructure (e.g., in ballast water or on fouled hulls or fishing gear) also appears plausible. This is supported by the proximity of the two Cuban soft coral sites (Fig. 1A) to the port of Havana: approximately 12 km from Bacuranao Inlet and 27 km from Boca de Calderas, both located east of the port. Similarly, the first documented patches of *X. umbellata* in Puerto Rico were discovered near the port of Ponce, a busy hub of international maritime traffic (Toledo-Rodriguez et al. 2025a).

Sessile marine organisms such as soft corals disperse naturally through larval propagation. Based on near-surface buoy drifter data, there is a persistent westward surface flow across the Venezuelan Basin extending as far as the Jamaican Ridge, followed by a northwestward flow toward the Yucatán Channel (Centurioni and Niiler 2003). This circulation pattern suggests that propagules would be transported from east to west—that is, from Puerto Rico toward Cuba—rather than in the opposite direction. Though the invasion sites detected in Puerto Rico are located on the south side of the island, in Cuba they have been encountered exclusively on the north side, and the "Bojeo a Cuba 2023" expedition found none off Cuba's southern coast between 2023 and 2025 (P González-Díaz, University of Havana, pers comm). This is inconsistent with the east-to-west propagule scenario, and together with the near-simultaneous discovery of *X. umbellata* on both islands, natural dispersal seems unlikely.

Although the precise route of *X. umbellata* introduction into Cuba remains uncertain, several pathways are plausible, such as the marine aquarium trade (Ruiz-Allais et al. 2014, Mantelatto et al. 2018, Menezes et al. 2021, Bolick and Lee 2023), hull fouling (Samimi-Namin et al. 2022, Hoeksema et al. 2023a,b), ballast water transport (Bailey 2015), floating debris (Soares et al. 2023), macroplastics (García-Gómez et al. 2021), and rafting on *Sargassum* (Fine 1970) or man-made flotsam (e.g., Hoeksema et al. 2012). Local propagation may be aided by wild farming practices (Carpinelli et al. 2020), as three new soft-coral aggregations have been observed

in Boca de Calderas (Espinosa Sáez, Estrada Estrada, Martínez Pérez, and Luguera González, pers comm).

Our study does not rule out the presence of *U. stolonifera* in Cuba; rather, it provides evidence that a sample from the second documented octocoral aggregation in Boca de Calderas—initially thought to be *U. stolonifera*—was unequivocally identified as *X. umbellata* through molecular barcoding. The sample was randomly collected by divers as representative of the observed octocoral aggregations. Therefore, unless new data indicate otherwise, we assume that all other sightings in the area correspond to *X. umbellata*. This assumption, however, does not rule out other potential introductions, as marine vessel traffic between Venezuela and Cuba continued uninterrupted through at least mid-2020, providing a potential route for accidental transport of *U. stolonifera* propagules or other species in ballast water or on contaminated gear (Ruiz-Allais et al. 2021). Hull fouling from commercial and noncommercial marine vessel traffic may also serve as an introduction pathway (e.g., the octocoral *Stragulum bicolor*; Samimi-Namin et al. 2022, Hoeksema et al. 2023a). Accordingly, marine resource managers in Cuba should remain vigilant for the possible introduction of *U. stolonifera* or other marine invaders into the country's coastal ecosystems.

Early detection and aggressive intervention efforts may still reduce the expansion of these invasive xeniids. Eradication efforts in Cuba have been successful in managing recurrences at a particular site through contact surveillance and action (Espinosa et al. 2023); however, given the regenerative capabilities of *X. umbellata* (Nadir et al. 2023), management must continue. Reports for other areas of Cuba could not be confirmed due to limited resources. In Puerto Rico, the distribution is confirmed to be widespread along the southwest coast, with large colony sizes (NV Schizas, University of Puerto Rico, Mayagüez, unpubl data). Coordinated eradication was implemented but was limited due to a lack of funds. As expected, the areas were repopulated by presumably untreated nearby aggregations (unpubl data). Xeniids are spreading across the Caribbean. With adequate funding, perseverance, and collaboration, these soft corals could be eradicated—or at least controlled—if early detection is achieved. A coordinated monitoring approach that integrates wide-area autonomous underwater vehicle (AUV) surveys, remotely operated vehicles (ROVs), environmental DNA (eDNA) sampling, and diver-based ground-truthing through direct observations and specimen collections would establish their current distribution and early detection of outbreaks in areas where they have not been reported, helping safeguard Caribbean coastal ecosystems.

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## Literature Cited

Ashton GV, Zabin CJ, Davidson IC, Ruiz GM. 2022. Recreational boats routinely transfer organisms and promote marine bioinvasions. Biol Invasions. 24:1083–1096. https://doi.org/10.1007/s10530-021-02699-x

Bailey SA. 2015. An overview of thirty years of research on ballast water as a vector for aquatic invasive species to freshwater and marine environments. Aquat Ecosyst Health Manag. 18(3):261–268. https://doi.org/10.1080/14634988.2015.1027129

Benayahu Y, van Ofwegen LP, Ruiz-Allais JP, McFadden CS. 2021. Revisiting the type of *Cespitularia stolonifera* Gohar, 1938 leads to the description of a new genus and a species of the family Xeniidae (Octocorallia, Alcyonacea). Zootaxa. 4964(2):330–344. https://doi.org/10.11646/zootaxa.4964.2.5

Bolick H, Lee K. 2023. Two new occurrence records for the Hawaiian Islands of invasive octocorals (Cnidaria: Anthozoa: Octocorallia: Malacalcyonacea) reported in Pearl Harbor: *Unomia stolonifera* (Gohar, 1938) and *Capnella* cf. *spicata* (May, 1899). Bish Mus Occas Pap. 155:181–184.

Carpinelli AN, Cordeiro RTS, Neves LM, de Moura RL, Kitahara MV. 2020. *Erythropodium caribaeorum* (Duchassaing and Michelotti, 1860) (Cnidaria: Alcyonacea), an additional alien coral in the Southwestern Atlantic. Zootaxa. 4822(2):175–190. https://doi.org/10.11646/zootaxa.4822.2.2

Centurioni LR, Niiler PP. 2003. On the surface currents of the Caribbean Sea. Geophys Res Lett. 30:1279. https://doi.org/10.1029/2002GL016231

Darriba D, Posada D, Kozlov AM, Stamatakis A, Morel B, Flouri T. 2020. ModelTest-NG: a new and scalable tool for the selection of DNA and protein evolutionary models. Mol Biol Evol. 37:291–294. https://doi.org/10.1093/molbev/msz189

Davidson IC, Zabin CJ, Chang AL, Brown CW, Sytsma MD, Ruiz GM. 2010. Recreational boats as potential vectors of marine organisms at an invasion hotspot. Aquat Biol. 11:179–191. https://doi.org/10.3354/ab00302

Edler D, Klein J, Antonelli A, Silvestro D. 2021. raxmlGUI 2.0: a graphical interface and toolkit for phylogenetic analyses using RAxML. Methods Ecol Evol. 12:373–377. https://doi.org/10.1111/2041-210X.13512

Espinosa J, Estrada R, Ruiz-Allais JP. 2023. Presencia en Cuba de la especie marina invasora *Unomia stolonifera* (Gohar, 1938) (Octocorallia, Alcyonacea). Acciones para su control y eliminación. Rev Invest Mar. 43(1):140–146. https://doi.org/10.5281/zenodo.8018890

Felsenstein J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution. 39(4):783–791. https://doi.org/10.1111/j.1558-5646.1985.tb00420.x

Fine ML. 1970. Faunal variation on pelagic *Sargassum*. Mar Biol. 7:112–122. https://doi.org/10.1007/BF00354914

García-Gómez JC, Garrigós M, Garrigós J. 2021. Plastic as a vector of dispersion for marine species with invasive potential: a review. Front Ecol Evol. 9:629756. https://doi.org/10.3389/fevo.2021.629756

Halász A, McFadden CS, Toonen R, Benayahu Y. 2019. Re-description of type material of *Xenia* Lamarck, 1816 (Octocorallia: Xeniidae). Zootaxa. 4652(2):201–239. https://doi.org/10.11646/zootaxa.4652.2.1

Hoeksema BW, Meijer zu Schlochtern MP, Samimi-Namin K, McFadden CS. 2023a. In the aftermath of Hurricane Irma: colonization of a 4-year-old shipwreck by native and non-native corals, including a new cryptogenic species for the Caribbean. Mar Pollut Bull. 188:114649. https://doi.org/10.1016/j.marpolbul.2023.114649

Hoeksema BW, Roos PJ, Cadée GC. 2012. Trans-Atlantic rafting by the brooding reef coral *Favia fragum* on man-made flotsam. Mar Ecol Prog Ser. 445:209–218. https://doi.org/10.3354/meps09460

Hoeksema BW, Samimi-Namin K, McFadden CS, van Ofwegen LP, Rocha RM, Hiemstra A-F, Vermeij MJA. 2023b. Non-native coral species dominate the fouling community on

a semi-submersible platform in the southern Caribbean. Mar Pollut Bull. 194:115354. https://doi.org/10.1016/j.marpolbul.2023.115354

Katoh K, Standley DM. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Mol Biol Evol. 30:772–780. https://doi.org/10.1093/molbev/mst010

Koido T, Imahara Y, Fukami H. 2022. *Xenia konohana* sp. nov. (Cnidaria, Octocorallia, Alcyonacea), a new soft coral species in the family Xeniidae from Miyazaki, Japan. ZooKeys. 1085:29–49. https://doi.org/10.3897/zookeys.1085.77924

Kozlov AM, Darriba D, Flouri T, Morel B, Stamatakis A. 2019. RAxML-NG: a fast, scalable and user-friendly tool for maximum likelihood phylogenetic inference. Bioinformatics. 35(21):4453–4455. https://doi.org/10.1093/bioinformatics/btz305

Mantelatto MC, da Silva AG, dos Santos Louzada T, McFadden CS, Creed JC. 2018. Invasion of aquarium origin soft corals on a tropical rocky reef in the southwest Atlantic, Brazil. Mar Pollut Bull. 130:84–94. https://doi.org/10.1016/j.marpolbul.2018.03.014

McFadden CS, Gonzalez A, Imada R, Shi SS, Hong P, Ekins M, Benayahu Y. 2019. Molecular operational taxonomic units reveal restricted geographic ranges and regional endemism in the Indo-Pacific octocoral family Xeniidae. J Biogeogr. 46:992–1006. https://doi.org/10.1111/jbi.13543

McFadden CS, Haverkort-Yeh R, Reynolds AM, Halasz A, Quattrini AM, Forsman ZH, Benayahu Y, Toonen RJ. 2017. Species boundaries in the absence of morphological, ecological or geographical differentiation in the Red Sea octocoral genus *Ovabunda* (Alcyonacea: Xeniidae). Mol Phylogenet Evol. 112:174–184. https://doi.org/10.1016/j.ympev.2017.04.025

Menezes NM, McFadden CS, Miranda RJ, Nunes JACC, Lolis L, Barros F, Sampaio CLS, Pinto TK. 2021. New non-native ornamental octocorals threatening a South-west Atlantic reef. J Mar Biol Assoc UK. 101(6):911–917. https://doi.org/10.1017/S0025315421000849

Murray CC, Pakhomov EA, Therriault TW. 2011. Recreational boating: a large unregulated vector transporting marine invasive species. Divers Distrib. 17(6):1161–1172. https://doi.org/10.1111/j.1472-4642.2011.00798.x

Nadir E, Lotan T, Benayahu Y. 2023. *Xenia umbellat*a (Octocorallia): a novel model organism for studying octocoral regeneration ability. Front Mar Sci. 10:1021679. https://doi.org/10.3389/fmars.2023.1021679

Ruiz-Allais JP, Amaro ME, McFadden CS, Halász A, Benayahu Y. 2014. The first incidence of an alien soft coral of the family Xeniidae in the Caribbean, an invasion in eastern Venezuelan coral communities. Coral Reefs. 33(2):287. https://doi.org/10.1007/s00338-013-1122-1

Ruiz-Allais JP, Benayahu Y, Lasso-Alcalá OM. 2021. The invasive octocoral *Unomia stolonifera* (Alcyonacea, Xeniidae) is dominating the benthos in the Southeastern Caribbean Sea. Mem Fund La Salle Cienc Nat. 79(187):63–80. https://doi.org/10.5281/zenodo.4784709

Samimi-Namin K, van Ofwegen LP, Hoeksema BW, Woodall LC, Meijer zu Schlochtern M, McFadden CS. 2022. New records of the cryptogenic soft coral genus *Stragulum* (Tubiporidae) from the Eastern Caribbean and the Persian Gulf. Diversity. 14:909. https://doi.org/10.3390/d14110909

Soares MO, Garcia TM, Giarrizzo T, Filho JEM, Tavares TCL, Ziveri P, Smith TB, Bejarano S, Teixeira CEP. 2023. Marine debris provide long-distance pathways for spreading invasive corals. Sci Total Environ. 900:165637. https://doi.org/10.1016/j.scitotenv.2023.165637

Stamatakis A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30(9): 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Toledo-Rodriguez DA, McFadden CS, Jimenez Marrero NM, Muñoz-Maravilla JD, Veglia AJ, Weil E, Schizas NV. 2025b. Discovery of *Latissimia ningalooensis*: a new invasive soft coral species in Puerto Rico. Biol Invasions. 27:246. https://doi.org/10.1007/s10530-025-03702-5

Toledo-Rodriguez DA, Veglia AJ, Jimenez-Marrero NM, Gomez-Samot JM, McFadden CS, Weil E, Schizas NV. 2025a. Shadows over Caribbean reefs: identification of a new invasive

soft coral species, *Xenia umbellata*, in southwest Puerto Rico. Coral Reefs. 44:1439–1444. https://doi.org/10.1007/s00338-025-02670-5

Ulman A, Ferrario J, Forcada A, Seebens H, Arvanitidis C, Occhipinti-Ambrogi A, Marchini A. 2019. Alien species spreading via biofouling on recreational vessels in the Mediterranean Sea. J Appl Ecol. 56:2620–2629. https://doi.org/10.1111/1365-2664.13502

Veglia AJ, Toledo-Rodriguez DA, Watkins JA, Schizas NV. 2025. Early invasion genomic resources for *Xenia umbellata* (native to the Red Sea) and its associated dinoflagellate symbionts in Puerto Rico. Biodivers Genomes. November. Available from: https://doi.org/10.56179/001c.147130