Memoria
de la Fundación La Salle de Ciencias Naturales
ISSN: 0037-8518 Versión impresa
ISSN: 2443-4698 Versión electrónica

80 Años
Edición Aniversario

Memoria de la Fundación La Salle de Ciencias Naturales, 2021, 79(187): 63-80

Artículo

The invasive octocoral *Unomia stolonifera* (Alcyonacea, Xeniidae) is dominating the benthos in the Southeastern Caribbean Sea.

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Abstract. The Indo-Pacific octocoral *Xenia* sp. has been reported as a successful invasive species of the Venezuelan coral reefs (Southeastern Caribbean Sea), and the first xeniid octocoral with such invasive properties. This taxon has been recently identified, and assigned to a new genus and combination as *Unomia stolonifera*. Since its first appearance there, it has dispersed along the shallow reefs, overgrowing any hard substrate, including corals and seagrass. Quantitative surveys revealed that *U. stolonifera* dominated all studied sites, featuring an average percentage cover of 30 - 80%, far above that of the native corals or any other benthic taxa. An inverse relationship exists between the loss of diversity and the reduction in coral cover. The spread of *U. stolonifera* in places where it has become established while displacing native benthic species and leads to a decrease in diversity and evenness of the benthic communities. Dispersal of the invasive along the reefs has been intensified by drifting colonies, by colonies settled on detached *Thalassia testudinum* fragments and, additionally, by colonies entangled on fish nets and consequently translocated. The present study explicitly demonstrates that this intensifying invasion is causing severe ecological damage to the Venezuelan reefs. Consequently, *Unomia stolonifera*, should be considered harmful invasive species that requires monitoring and management programs in the vicinity of already invaded reefs. The current study highlights the ecological consequences of this new invasive species.

Key words: Cnidaria; Coral reefs; change in community; reef damage; seagrass; Venezuela

El octocoral invasivo *Unomia stolonifera* (Alcyonacea, Xeniidae) está dominando el bentos en el suroriente del Mar Caribe

Resumen. El octocoral del Indo-Pacífico *Xenia* sp. fue registrado como una especie invasora exitosa en arrecifes de coral de Venezuela (sureste del Mar Caribe), y el primer octocoral de la Familia Xenidae con tales propiedades invasivas. Este taxa ha sido recientemente identificado, e incluido en un nuevo género y combinación como *Unomia stolonifera*. Desde su primera aparición, se ha dispersado rápidamente a lo largo de los arrecifes poco profundos, creciendo agresivamente sobre distintos tipos de sustratos, incluidos corales y pastos marinos. Nuestras evaluaciones determinaron que *U. stolonifera* dominó todos los sitios de estudio presentando porcentajes de cubertura de 30 - 80 %, muy superiores al de los organismos bentónicos nativos. En los lugares donde el invasor se ha establecido, las especies bentónicas nativas han sido desplazadas, lo que conlleva a una disminución de la diversidad y la equidad. La dispersión de *U. stolonifera* se ha intensificado debido al arrastre de fragmentos del coral por el fondo, por colonias asentadas sobre hojas de *Thalassia testudinum* desprendidas a la deriva y por las colonias enredadas en las redes de pesca. El estudio demuestra que esta agresiva especie invasora está causando severos daños ecológicos a los arrecifes en Venezuela. En consecuencia, *Unomia stolonifera* debe ser considerada un invasor perjudicial que requiere la implementación de urgentes programas de monitoreo y manejo en las zonas afectadas.

Palabras clave : Cnidaria; arrecifes de coral; cambios en la comunidad; daños al arrecife; pastos marinos; Venezuela

Introduction

Biological invasions constitute a global environmental threat that may lead to biodiversity loss along with the deterioration of ecosystem function and integrity (Pimentel *et al*. 2001, Mooney and Cleland 2001, Pysek *et al*. 2020). Numerous invasions in marine systems have been recorded, but only a small number of the invasive species and their impact have been studied in depth to date (Delaney *et al*. 2008). The damage caused by some invasive species can be severe and has been studied in various geographical regions (Molnar *et al*. 2008, Rilov and Crooks 2009, Alidoost Salimi *et al*. 2021).

The coral reefs of the Venezuelan northeastern coast, in the Southeastern Caribbean Sea, consist in fringing or patch communities that are poorly developed due to the low temperatures and high turbidity from upwelling and periodic rains (Okuda 1981, Ramírez-Villarroel 2001). These conditions limit the depth distribution of most stony corals there to no more than 15 m (see also Cervigón 1997, Ramírez-Villarroel 2001). The stony coral species diversity in Venezuela's Mochima National Park (MNP) is relatively low compared to the other reefs, such as those of the Los Roques Archipelago National Park, where more than 70 species have been recorded (Villamizar *et al.* 2014). Forty scleractinian species have been recorded in the eastern part of Mochima Bay (Sant 1999) compared to only 17 in the western part (Ramírez-Villarroel 2001). The gorgonian octocoral fauna in the MNP is quite diverse, although it has been little studied; the following species have been recorded: *Erythropodium caribaeorum, Eunicea lanciniata, E. tourneforti, Plexaura flexuosa* and *Pseudoterogorgia* sp. (see Sant 1999). The opportunistic encrusting octocoral *Erythropodium caribaeorum* and the zoanthid *Palythoa caribaeorum* are common there in polluted and eroded reefs. In some deeper areas (> 30 m) the black corals *Cirrhipathes lutkeni*, *Plumapathes* sp. and *Antipathes* sp. inhabit steep underwater canyon walls (J.P.R.A. pers. obs.). During the last two decades coral live cover has declined on many of the Caribbean reefs (Miloslavich *et al*. 2010), including those of the MNP mainly due to coastal development, pollution, indiscriminate artisanal fishing and tourist activity (J.P.R.A. pers. obs.).

There are several studies of introduced and invasive species in Venezuelan marine systems. Perez *et al*. (2007) referred to a total of 22 exotic marine species there, comprising two algae, four mollusks, eight crustaceans, one ascidian and seven fishes. However, in terms of marine fish, only six introduced species have been recorded off the coast of Venezuela, between 1961 and 2020 (Lasso-Alcalá and Posada 2010, Lasso-Alcalá *et al*. 2011, 2019, Cabezas *et al*. 2020).

The most conspicuous species among these invasive species in Venezuela are the algae *Ulva reticulata* (Chlorophyta) and *Kappaphycus alvarezii* (Rhodophyta). The former, being native to the Indian Ocean, accidentally arrived at the Venezuelan coast in the 1980s. Its spread there has displaced several indigenous species and severely affected artisanal fishing and the tourist beaches (Lemus and Balsa 1995). *Kappaphycus* was introduced into Venezuela in 1996 for commercial cultivation and since then has spread to several coral-reef patches (Barrios 2005), affecting coral and sponge diversity (Ruiz-Allais 2012).

Another species of prime environmental concern in regard to the Caribbean Sea is the invasive lionfish *Pterois volitans* (e.g. Albins and Hixon 2013, Ballew *et al*. 2016). It was first recorded in Venezuelan waters in 2009 and since then has rapidly spread, becoming a severe threat to fishes and invertebrates, including those with commercial value (Lasso-Alcalá and Posada 2010).

The marine angiosperm *Halophila stipulacea* (Forsskal 1775), native to the Red Sea and the Indian Ocean (den Hartog, 1970), was first identified in 2002 on Grenada Island (Ruiz and Ballantine, 2004) and it has spread rapidly to 19 islands of the Lesser Caribbean Antilles (Vera *et al*. 2014, Willette *et al*. 2014, Smulders *et al*. 2017, Viana *et al*. 2019, Winters *et al*. 2020). This exotic seagrass, was recorded in the Central Coast of Venezuela from 2012 to 2015 (Vera *et al.* 2014, Rodríguez-Guia *et al*. 2018) So far, there are no studies of the impact of this species on colonized ecosystems.

A well-studied invasion in the Caribbean Sea is that of the ahermatypic Indo-Pacific stony coral *Tubastraea coccinea* Lesson, 1829. This species was first reported in Curacao (Netherlands Antilles) in 1930 to 1940 and since then has further spread to other Caribbean and Gulf of Mexico reef systems and artificial substrata (Sammarco *et al*. 2004, Creed *et al*. 2016, 2020). Although this species is common in Venezuela its ecological impact has not yet been determined (Ramírez-Villarroel 2001). Notably, in Brazilian waters both *T. coccinea* and its congener *T. tagusensis* have been characterized as harmful invasive stony corals (Silva *et al.* 2011, Santos *et al*. 2013, Creed *et al*. 2016, 2020). Similar to *T. coccinea*, the Indo-Pacific azooxanthellate *Tubastraea micranthus* (Ehrenberg 1834), has rapidly invaded artificial substrates (oil/gas platforms) in the northern Gulf of Mexico (Sammarco *et al*. 2010, 2014).

Although not frequently associated with marine invasions, several octocorals have been reported worldwide. The Red Sea *Melithea* (=*Acabaria*) *erythraea* has been introduced into the eastern Mediterranean Sea, probably via ballast water (Fine *et al.* 2005), and has now established there a few sparse populations (Grossowicz *et al*. 2020). *Stragulum bicolor*, a newly-described genus, has been suggested to be a possible invasive in Brazil (Ofwegen and Haddad 2011). An additional invasive species there, *Chromonephthea braziliensis*, was reported earlier by Ofwegen (2005). Both these octocoral species may have been introduced via fouled oil platforms. Recently, the invasive octocorals, *Sansibia* sp. (Xeniidae) and *Clavularia* cf. *viridis* (Clavulariidae), both Indo-Pacific origin and *Erythropodium caribaeorum* (Anthothelidae) of Caribbean origin, were found dominating the Brarzilian Vermelha rocky reef (Mantelatto *et al*. 2018, Carpinelli *et al*. 2020, Creed *et al.* 2020). The Indo-Pacific species *Carijoa riisei* was reported as invasive in Hawaii in 1972 and since then has spread massively even to the deeper reefs (e.g., Kahng and Grigg 2005, Concepcion *et al*. 2010). It has also invaded several tropical East Pacific reefs, including Panama, Colombia and Ecuador, as well as the Indian subcontinent reefs (Quintanilla *et al*. 2017).

The invasive soft coral *Unomia stolonifera* (Gohar, 1938), of the family Xeniidae, which is the subject of the current study, is native to the Celebes island (Sulawesi, Indonesia). Taxonomically, *Unomia stolonifera* is a new identification and combination, with a new Genus (*Unomia*), recently described, to include *Cespitularia* *stolonifera* (Benayahu *et al*. 2021). This taxa, was introduced into northeast Venezuela via the illegal aquarium trade during 2000–2005 and registered at first time as *Xenia* sp. (Ruiz-Allais *et al*. 2014), and it has not been registered in any other location of Venezuela or in the Caribbean Sea, until now. Since its initial discovery it has rapidly spread and now severely affects the benthic communities at northeastern Venezuela. It is therefore clear that the Caribbean reef systems, including the Venezuelan reefs, have been seriously impacted by diverse invasive species.

In this context of biological invasions, the present study aims to 1) assess the distribution of the invasive *Unomia stolonifera* on Venezuelan reefs 2) evaluate its impact on the benthic communities there and 3) also address possible mechanisms that have enhanced its dispersion in the invaded environment. The findings reveal that although only a few octocoral species have been reported to date as invasive, they might already constitute a threat to the indigenous marine life in the invaded environment.

Materials and Methods

During November-December 2013 surveys were conducted in three locations in the northeastern coast of Venezuela (Southeastern Caribbean Sea), totaling 12 sites, all known to be invaded by *Unomia stolonifera*. The surveys encompassed the shallow coast of Bahía de Conoma (BC: 10°14’39’’ N, 64°32’23’’ W, sites 1-8), Isla de Monos (IM: 10°15’42’’ N, 64°32’’48 W, sites 9, 10) and Isla Arapo (IA: 10°15’41’’ N, 64°28’26’ W, sites 11, 12). Isla Arapo and Isla de Mono are within the limits of the Mochima National Park. At each site, the survey was carried out along a 25 m linear transect placed parallel to the coastline at a depth of 2 m. Along each transect twenty 0.5 m^2 photo-quadrats were sampled. The transects were positioned in the portion considered to be most invaded (Figure 1). The photo-quadrats were analyzed, using the ImageJ program, to obtain the percentage cover of the major benthic components: *Unomia stolonifera*, stony corals, octocorals, sea anemones, zoanthids and hydrocorals (see also Coyer and Witman 1990).

In addition, the depth distribution and percentage cover of *Unomia stolonifera* were recorded at site 9 (Figure 1) along four transects, placed parallel to the coast at 2, 5, 10 and 20 m depth. Similarly, in each of these transects 20 quadrats were photographed and analyzed as indicated above. In total 232 photo-quadrats were performed for all sites and depths. The percentage cover of each species was used to calculate the Shannon diversity index, and Pielou's evenness index. In order to compare the results obtained in the quadrates conducted at the different sites and depths, Kruskal–Wallis one way ANOVA and Mann-Whitney test were applied. Variations around mean values are presented as standard deviation. The data do not present normal distribution; therefore non-parametric statistical tests were applied. The program used was Statgraphics Plus 4.1.

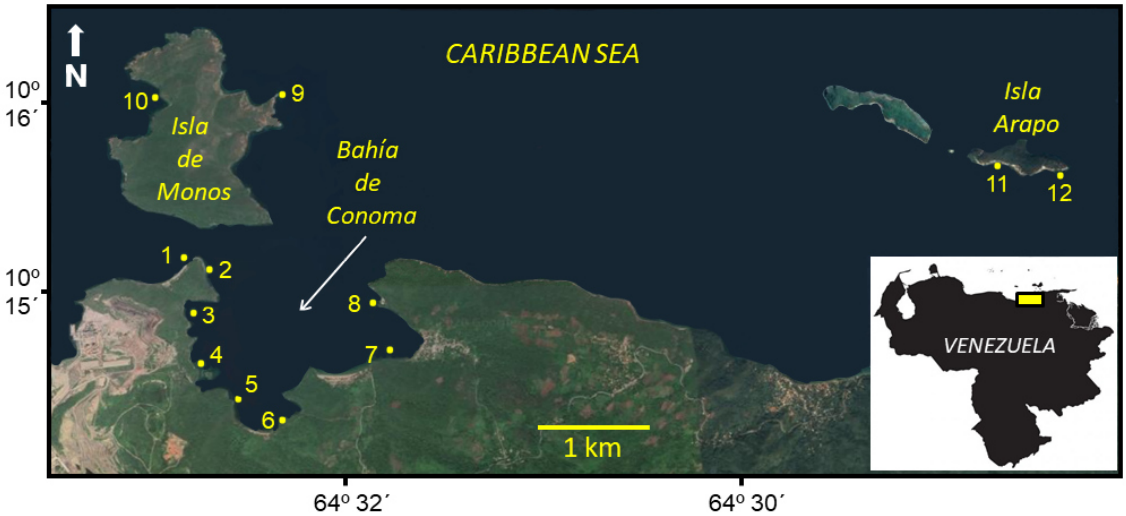

Figure 1. Location of the study sites along the northeastern coast of Venezuela, Southeastern Caribbean Sea: Bahía de Conoma (BC: sites 1-8), Isla de Monos (IM: sites 9, 10) and Isla Arapo (IA: sites 11, 12). Source: Modified from Google Earth 2020 base map. SIO, NOAA, NGA, GEBCO data. Image Landsat / Copernicus.

Results

Table 1 lists the different 14 cnidarian species recorded in the different sites comprising; octocorals (3 species), stony corals (7 species), zoanthid (1 species), sea anemones (2 species) and hydrocoral (1 species), belonging to two classes, three subclasses, five orders and eleven families, respectively. However, a richness of only 3 to 9 species was found per study site. In the quadrats where *Unomia stolonifera* dominated the substrate, a markedly low number of other species was recorded, such as at sites 3, 6, 7, 8 and 9. The encrusting octocoral *Erythropodium caribaeorum* and the zoanthid *Palythoa caribaeorum* co-occurred with *Unomia stolonifera* in areas where a high percentage cover of the invasive species was observed (Table 1). *Unomia stolonifera* was dominant in all three study regions (BC, IM, IA), featuring an average percentage cover far above that of all corals together (Figure 2a). The colonies were found overgrowing the seagrass *Thalassia testudinum* (Figure 2b, c), at sites 6 and 7 (see Figure 1). The average percent cover of *U. stolonifera* per quadrat, considering all the sites, was 52±36% (n=232, range 0-100%), while that of the corals combined was lower, being only 16±21%, (n=232, range 3-34%). At sites 3 and 9 monospecific stands of almost 100% *U. stolonifera* cover were recorded. However, at site 5, where no invasive was found, percentage cover of corals was as high as 80±18% (n = 20, range 35-100%) (Figure 3). There were significant differences in the percentage cover of *Unomia stolonifera* and corals among the different sites (K-W =80.06, p=0.001, and K-W =76.98, p =0.005, respectively. p<0.05), with BC (sites 2, 3) and IM (site 9) featuring the highest percentage cover of *U. stolonifera*. along with the respective lowest coral percentage cover. Sites 5 and 6 featured a significantly higher percentage cover of coral compared to all other sites. Overall, considering all sites combined, a significantly higher percentage cover of *U. stolonifera* was recorded compared with the other coral species combined. Mann–Whitney: W= 39554.0, p-value = 0.00, $p<0.05$) (Figure 4).

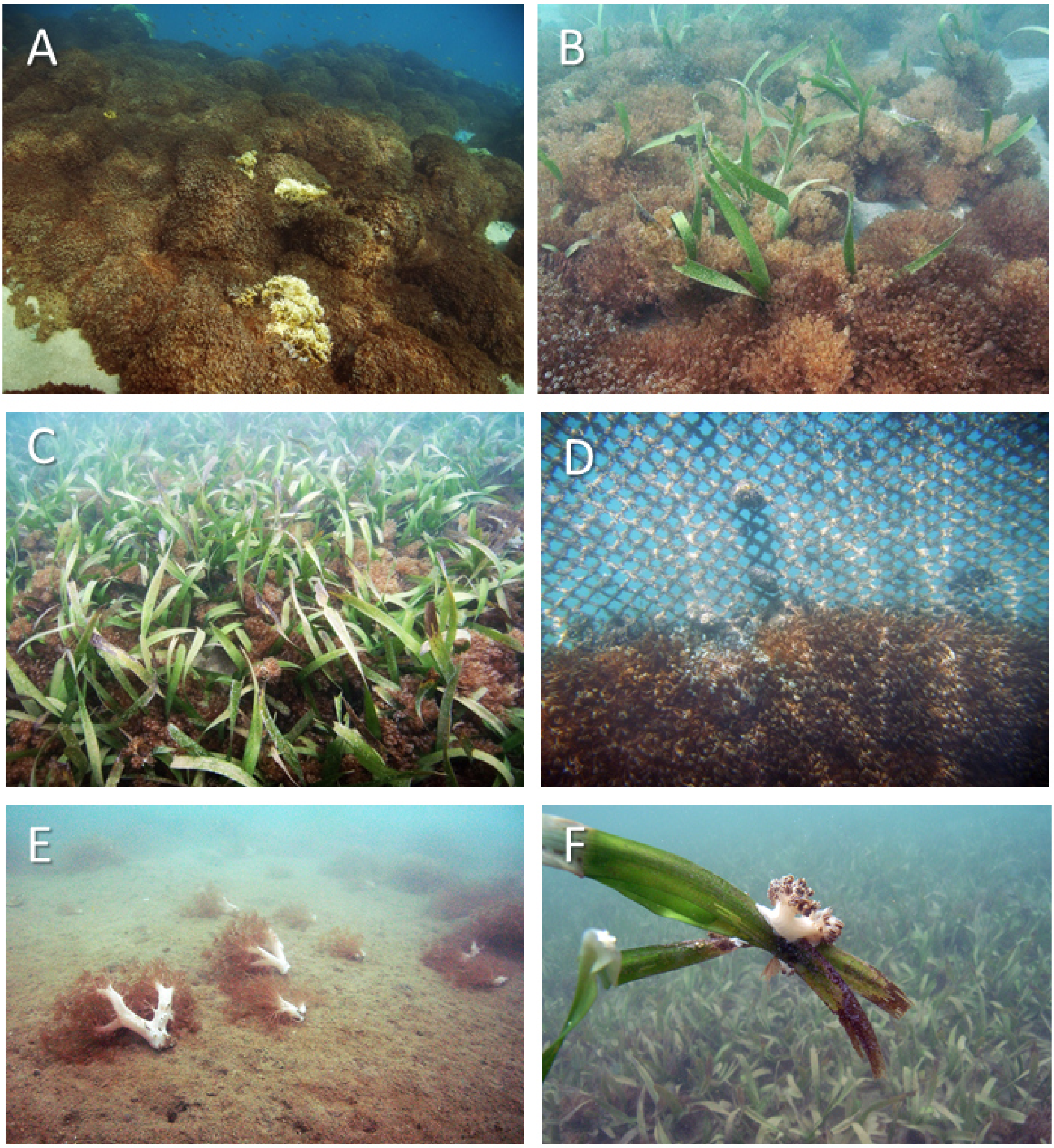

Figure 2. Underwater images of the invasive *Unomia stolonifera* in the study sites along the northeastern coast of Venezuela, Southeastern Caribbean Sea. A. Colonies monopolizing hard reef substrate. B. Colonies overgrowing the seagrass *Thalassia testudinum*. C. Seagrass bed occupied by invasive octocoral. D. Fishing net with colonies. E. Drifted colonies on the bottom. F. Detached *T. testudinum* with colonies floating with currents.

Table 1. Coral species recorded in quadrats at different study sites along the northeastern coast of Venezuela, Southeastern Caribbean Sea. (Bahía de Conoma: sites 1-8, Isla de Monos: sites 9, 10 and Isla Arapo: sites 11, 12), indicated by X and the total number of species per site.

TAXA	SAMPLING SITES											
	BC								IM		IA	
	1	2	3	4	5	6	7	8	9	10	11	12
CLASS ANTHOZOA												
SUBCLASS OCTOCORALLIA												
ORDER ALCYONACEA												
FAMILY ANTHOTHELIDAE												
Erythropodium caribaeorum (Duchassaing & Michelotti, 1860)	X	X	X		X	X	X	X		X	X	X
FAMILY GORGONIIDAE												
Pseudopterogorgia americana (Gmelin, 1791)										X		
FAMILY XENIIDAE												
Unomia stolonifera (Gohar, 1938)	X	X	X	X		X	X	X	X	X	X	X
SUBCLASS HEXACORALLIA												
ORDER SCLERACTINIA												
FAMILY FAVIIDAE												
Colpophyllia natans (Houttuyn, 1772)	X	X			X						X	
Diploria strigosa (Dana, 1846)	X			X	X					X	X	X
Isophyllia sinuosa (Ellis & Solander, 1786)				X							X	
FAMILY MONTASTRAEIDAE												
Montastraea annularis (Ellis & Solander, 1786)					X							X
Montastraea cavernosa (Linnaeus, 1767)					X					X	X	
FAMILY SIDERASTRAEIDAE												
Siderastrea radians (Pallas, 1766)				X							X	
FAMILY PORITIDAE												
Porites astreoides Lamarck, 1816									X	X	X	
ORDER ZOANTHARIA												
FAMILY SPHENOPIDAE												
Palythoa caribaeorum (Duchassaing & Michelotti, 1860)	X	X			X			X	X	X	X	X
ORDER ACTINIARIA												
FAMILY ACTINIIDAE												
Condylactis gigantea (Weinland, 1860)	X			X	X					X		
FAMILY AIPTASIIDAE												
Bartholomea annulata (Le Sueur, 1817)					X							
CLASS HYDROZOA												
SUBCLASS HYDROCORALLIA												
ORDER ANTHOATHECATA												
FAMILY MILLEPORIDAE												
Millepora alcicornis Linnaeus, 1758	X		X	X	X	X	X			X		X
TOTAL	7	4	3	6	9	3	3	3	3	9	9	6

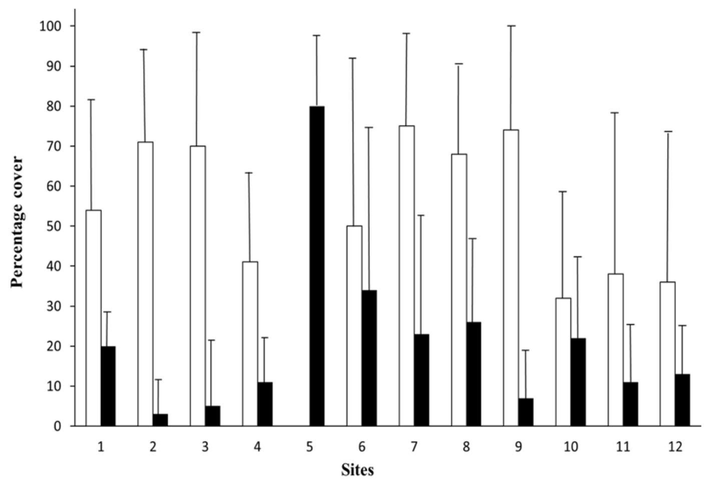

Figure 3. Average percentage cover of *Unomia stolonifera* (white bars) and corals (black bars) per quadrat (±SD) at all study sites (n=20 quadrats per site) . Bahía de Conoma (sites 1-8), Isla de Monos (sites 9, 10) and Isla Arapo (sites 11, 12).

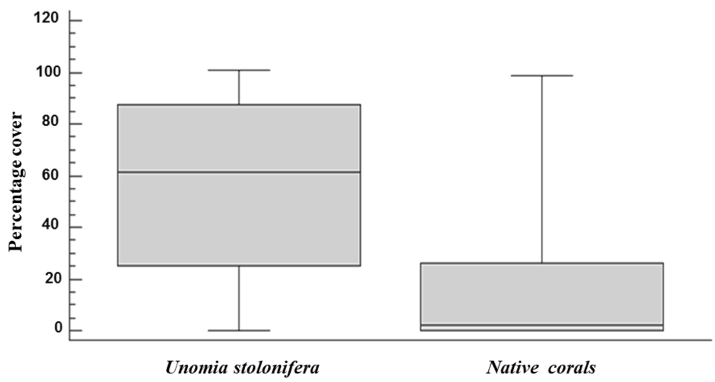

Figure 4. Box plot presenting percentage cover of *Unomia stolonifera* and corals per quadrat based on all sites (Mann-Whitney, $p< 0.05$, n=232 quadrats).

At most sites *Unomia stolonifera* occurred in a wide depth range of 0.5 to 20 m, with lower cover on sandy bottoms below 7 m. An exception was IM (Figure 1: site 10), where some small colonies were found deeper than 40 m, usually on silty substrate. At site 9 the invasive soft coral was found at a depth of 2-20 m, with the highest cover at 2-5 m, occupying almost the entire substrate. *Unomia stolonifera* exhibited at 2 m a variable cover of 68±35% (n=20, range 0-92%) and at 5 m 62±23% (n=20, range 16-86%). The percentage cover of corals (*U. stolonifera* excluded) at the IM (site 9) was as low as 6±10% at 2 m (n=20, range 0-32%) and no corals were recorded at greater depths, similar to what was found at the other 11 sites invaded (Figure 5).

In 35 chosen quadrats with no colonies of *Unomia stolonifera* the average Shannon diversity index was higher (1.36±0.51, range 0.85-2.35, n=35), than that found in a similar number of quadrats in which the invasive dominated the substrate (0.76±0.5, range 0.19-1.8). Similarly, the evenness value in the former quadrats was significantly higher (0.6±0.19, range 0.26-0.84) compared to the latter one (0.28±0.26, range 0.06-0.9). There were significant differences in Shannon diversity index (Mann–Whitney: W= 11.0, p-value = 0.031, $p<0.05$) and evenness (W= 11.0, p-value = 0.023, $p<0.05$), between the quadrats with and without *U. stolonifera* (Figure 6).

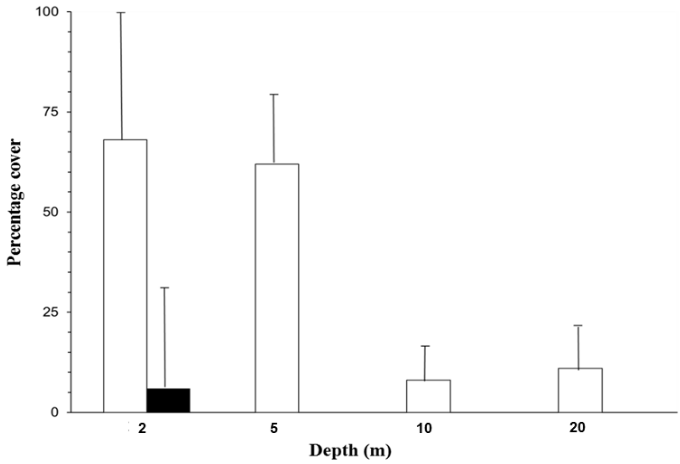

Figure 5. Percentage cover of *Unomia stolonifera* (white bars) and corals (black bar) (±SD) per quadrat along depth at site 9, Isla de Monos (n = 20 quadrats per depth).

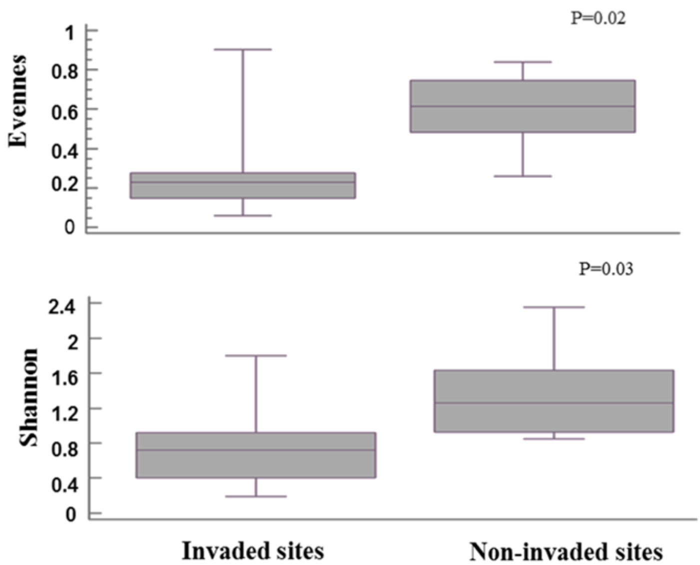

Figure 6. Box plot presenting Shannon diversity index and evenness at sites invaded by *Unomia stolonifera* and devoid of it. (Mann–Whitney, p < 0.05, n=35).

Discussion

The high percentage cover of *Unomia stolonifera* in all the invaded sites significantly reduced the occurrence of stony corals, hydrocorals and other indigenous anthozoans. This invasive octocoral has undoubtedly led to a shift in community structure toward dominance of the invasive species both on the hard reef substrate and on seagrass beds.

The invasive octocoral was found overgrowing *Thalassia testudinum* (site 6, Figure 2 b, c), potentially decreasing its photosynthetic capabilities and thereby causing mortality. It seems that *Unomia stolonifera* is equally capable of successfully colonizing stony reefs, soft substrates (Ruiz-Allais *et al*. 2014) and seagrass beds (Figure 2a,b,c). Stony corals are vital for the survival of a variety of organisms (Komyakova *et al*. 2013); while, similarly, the *T. testudinum* meadows constitute a food source, refuge site, and breeding and nursery grounds for diverse life forms (Zieman and Zieman 1989). Consequently, it is apparent that this invasive octocoral constitutes a source of harm to benthic organisms and fishes, negatively impacting their living space and food sources.

Mantelatto *et al*. (2018) recorded a new biological invasion of non-native soft corals on a rocky reef in southeastern Brazil. The most abundant species, *Sansibia* sp. (Xeniidae), had high coverage in the invaded region, and was dominant in the deeper communities. This invader was positively associated with some macroalgae and negatively with *Palythoa caribaeorum*. Similarly, we observed some prevalence of *P. caribaeorum* and *Millepora alcicornis* in the early stages of the invasion, although eventually, most of the colonies were completely colonized by *Unomia stolonifera*.

It should be noted that most of the sites colonized by the invasive species have also been subjected to prolonged anthropogenic disturbances, such as both land-based and coastal activities as well as overfishing (Burke and Maidens 2004). The invasive soft coral is therefore not the only cause of deterioration in the recipient ecosystem, but it has nonetheless certainly become a determinant factor in weakening this ecosystem's resilience and stability. As Hermoso *et al*. (2011) point out, it is difficult to discern between habitat degradation or biological invasion as potential causes of biodiversity loss since both factors can interact in different ways, however, the proliferation of invasive species represents a strong threat to the persistence of native assemblages in highly fluctuating environments.

Prior to the current study, a preliminary SCUBA survey had indicated that at all sites at a depth of 1-7 m featuring hard substrate, stony corals were dominant (J.P.R.A. pers. obs.). The current findings demonstrate that at all sites the highest abundance of the invasive soft coral is at a depth range at which light intensity is adequate for the symbiotic algae (zooxanthellate). It seems that *Unomia stolonifera* thrives best at this depth, although small colonies have also been noted in deeper water growing on the limited available hard substrate there. Benayahu and Loya (1981) observed in Eilat (northern Red Sea) the highest percentage cover of xeniid soft corals at 4 m, decreasing to a minimum at 29 m and thus resembling the depth distribution of *U. stolonifera* in the Venezuelan waters. It would therefore indicate that the water transparency along with the availability of hard substrate favor the distribution of the invasive *Unomia stolonifera* (Fabricius and Klumpp 1995).

The Bahía de Conoma and Isla de Monos (MNP) were the first regions in Venezuela to be colonized by the invasive alien octocoral, already in 2005 (Ruiz-Allais *et al.* 2014). Since then, it has rapidly spread to other sites, mainly through fishing activity. Artisanal fishing is common near the shallow coastal areas where large assemblages of the invasive species exist. The fishing nets are repeatedly deployed at the same site, providing enough time for them to become colonized, or entangled by *Unomia stolonifera* (Figure 2d). As part of the fishing practice these trawls are rotated among different fishing sites, thus constituting a principal vector by which the colonies are transported from one place to another. Fishing activities (frequent transfer of stationary nets and traps and the use of trawl nets), and dispersion by propagules, have also been pointed out as the causes in the dispersal of the invasive angiosperm *Halophila stipulacea*, in nearby and farther islands of the Caribbean Sea and continental waters of Venezuela (Ruiz and Ballantine 2004, Willette and Ambrose 2009, 2012, Vera *et al*. 2014, Willette *et al*. 2014, Muthukrishnan *et al*. 2020, Winters *et al*. 2020).

Our preliminary results, dealing with sexual reproduction of the Venezuelan *Unomia stolonifera*, suggest that the colonies are fecund and sexually reproductive (Y.B. pers. obs.). Thus, larval dispersal also enhances the spread of the invasive octocoral. Notably, fragments of the colonies can be found on the sea floor (Figure 2e), drifting with the bottom currents and eventually colonizing other sites. Similarly, fragments of *Thalassia testudinum* settled by *U. stolonifera* colonies, occasionally break off, mainly by the mechanical action of the anchor of boats and the dragging of fishing nets, and then float with currents from the surface of the water (Figure 2f), thus similarly enhancing the dispersal capabilities of invasive species. Studies carried out in the Virgin Islands indicate that boat anchors cause losses of more than 1.8% of the *Thalassia testudinum* meadows per year (Williams, 1988). According to Waycott *et al*. (2009), mechanical damage caused by anchors, propellers and fishing gear cause the direct and immediate loss of seagrass. The leaves of *T. testudinum* last longer than the leaves of another more ephemeral species of seagrass and its fruits are estimated to travel up to 3,600 km (Kendrick *et al.* 2012).Therefore, both sexual propagules and asexually produced recruits contribute massively to the dispersal of this invasive species.

A lack of natural predators also favors the success of *Unomia stolonifera*, as has been recorded for other invasive species (Meinesz and Hesse 1991; Piazzi *et al*. 2005). Among the few known predators of xeniid soft corals are aeolid nudibranchs (e.g., Ziegler *et al*. 2014) and butterfly fish (Y.B. personal observations). So far, no nudibranchs have been observed on the Venezuelan *U. stolonifera*. Furthermore, our observations have indicated that at sites highly invaded by this octocoral, fish stocks in general have decreased significantly; an issue that certainly requires further investigation. Therefore, it is highly probable that there is no predator of the invaded octocoral present to control its increased abundance. The enemy release hypothesis in part could explain the dominance of *U. stolonifera* over native species. This hypothesis postulates that, ''the absence of enemies in the exotic range of an exotic species is one of the causes of the success of the invasion". Although, this theory is not totally supported by empirical evidence, due to the enormous variability between organisms, populations, communities and ecosystems (Heger and Jescke, 2014) in this case, it coincides well with what was observed in the pre-investigation surveys and during the current field work.

The findings from the present study indicate a relationship between the loss of diversity and the increasing coral cover associated with the spread of *Unomia stolonifera*. It would seem that in sites where the invasive species has become established, the native corals, and similarly other benthic species, have been displaced, leading to a decrease in diversity and evenness (Valery *et al*. 2009; Shochat and Ovadia 2011). We also found that at most of the sites with low diversity *Erythropodium caribaeorum, Phalythoa caribaeorum* and *Millepora alcicornis* were common. These opportunistic species seem to be dominant in disturbed reef environments (J.P.R.A. pers. obs.), especially the hydrocoral *M. alcicornis* (Herrera-Moreno 1991). Nevertheless, we have seen that even these resistant species are affected by overgrowth of *U. stolonifera*.

Several studies have predicted that species-rich communities should be less susceptible to biological invasion, thus suggesting that there is a positive relationship between biodiversity and resistance to invasion (Inderjit *et al*. 2006). Nevertheless, quantitatively evaluating other factors that limit invasions, such as natural or anthropogenic disturbances, nutrients or consumers, is essential to accurately predicting consequences of species loss for community invasion (Levine and D'antonio 1999). The "intermediate disturbance hypothesis" suggests that species diversity should be highest at moderate levels of disturbance. However, disturbance is known to increase the invasion of natural communities, but frequently it is the interaction between different disturbances that has the largest effect the invasibility of communities (Hobbs and Huenneke 1992). As we have previously pointed out, most of our study area has been subject to prolonged anthropogenic disturbances (e.g. overfishing, anchorage, sewage discharges and coastal sediment runoff) weakening the native ecosystem and probably making it more susceptible to invasion. Nevertheless, a further study is necessary to verify the possible synergistic relationship between these factors and the invasion of *Unomia stolonifera*.

Finally, we consider the importance of being alert to the appearance of *Unomia stolonifera* in other regions of the Caribbean and the tropical Atlantic. Since the invaded sites are adjacent to international trade ports (Guanta and Guaraguao ports) it is likely that the larvae will be transported in ballast water and even small colonies might attach to a ship's hull (biofouling) and become dispersed to other regions. The current study clearly highlights the ecological consequences of this new invasive octocoral, and indicates that this octocorals may have invasive capabilities, causing a shift in the benthic community structure that is far beyond anything considered previously.

Acknowledgements

We would like to thank Maria E. Amaro (Instituto Oceanográfico de Venezuela) for her contribution during the field work, V. Wexler for digital editing .This work was supported by the Fundación La Tortuga. Finally, we thank Joel C. Creed (Universidade do Estado do Rio de Janeiro) and Raul R. Braga (Universidade Federal do Paraná), for the critical review and constructive suggestions to the article, and Donald C. Taphorn (Royal Ontario Museum), for language review.

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Recibido: 21 enero 2021
Aceptado: 21 marzo 2021
Publicado en línea: 24 mayo 2021

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