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The invasion of the azooxanthellate coral *Tubastraea* (Scleractinia: Dendrophylliidae) throughout the world: history, pathways and vectors

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Abstract In this review, we describe the history, pathways and vectors of the biological invasion of the azooxanthellate coral *Tubastraea* (Scleractinia: Dendrophylliidae) throughout the world. In order to do so we consulted previous reports in the literature and also compiled new unpublished information on the distribution of the three species of *Tubastraea* which have been reported as non indigenous species, both within their native and non-native ranges and also on vectors, and where cryptogenic. We combine these data with historical aspects of marine vectors in order to get insights into how *Tubastraea* species have successfully spread around the world, established and invaded and where future studies would be best focused. *T. coccinea* and *T. tagusensis* are recognized as being highly invasive and are causing significant environmental, economic, and social impacts requiring management actions. The third species, *T. micranthus* so far only reported outside its native range on oil platforms, may have similar potential for negative impact. The vectors of introduction of *Tubastraea* may have changed throughout history and the biological invasion of these invasive corals may reflect changing

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practices, demands and legislation in shipping activities over the years. Today it is clear that these corals are fouling organisms strongly associated with oil and gas platforms worldwide which are thus primary vectors for new introductions.

Keywords azooxanthellate Scleractinia · Biological invasion impact · Cryptogenic · Cup coral · Distribution · Non-indigenous species NIS · Oil platforms · Pathway · Range expansion · Review · Sun coral · *Tubastraea coccinea* · *T. tagusensis* · *T. micranthus* · Vector

Introduction

Bax et al. ([2003](#): 313) were correct when they stated that "Invasive alien marine species threaten biodiversity, marine industries (including fishing and tourism), and human health, and unlike oil spills only get worse with time". Biological invasions in the marine environment are prejudicial to both marine biodiversity (Grosholz et al. [2000](#); Carlton [2009](#); Thomsen et al. [2014](#)) and the economies of those countries or regions (Pimentel et al. [2001](#); Bax et al. [2003](#); Williams and Grosholz [2008](#)) that have suffered single or multiple biosecurity breaches.

In order to manage non-indigenous species (NIS) properly it is necessary to identify how they arrived and spread (Hewitt et al. [2009](#)). This is because the invasion process is such that propagules of the NIS enter a transportation pathway (the route NIS take to enter or spread through a non-native ecosystem, Olenin et al. [2011](#)); the vector is the physical means by which the propagule is transferred to or within the non-native ecosystem. Prevention focused on those vectors identified by vector-based risk assessment (Campbell [2009](#)) as the most troublesome is

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considered the most effective pre-border management option (Davidson et al. [2008](#)). It is also essential to identify vectors in order to plan relevant monitoring programs for effective border control. Vectors may also enhance the spread of established NIS through secondary spread, thwarting containment management and facilitating the invasive potential of an established NIS post-border. Finally, vectors remain of concern after successful control or eradication as they have the potential to undo beneficial management actions by reintroducing the NIS (Olenin et al. [2011](#)).

In many instances biological invasion studies are less analytical and predictive because of doubt about vectors involved in the transportation process (Minchin [2007](#); Olenin et al. [2011](#)). It is often difficult to establish a sound link between an invasive marine NIS and the vector that introduced it into the receptor region (Minchin [2007](#); Hewitt et al. [2009](#)). However, using life histories, growth rates, timing, rates of range expansion, analyses of possible points of introduction and their associated activities and vectors, mapping of outbreaks and historical or anecdotal information on vectors preferred by specific NIS or groups it is possible to deduce which vectors are responsible (Ruiz et al. [2000](#); Fofonoff et al. [2003](#); Hewitt et al. [2009](#)). Vectors may be managed to reduce the survival of NIS, thus reducing the propagule pressure, which is the quality, quantity and frequency of invading organisms (Johnston et al. [2009](#); Olenin et al. [2011](#)).

Of all the human-mediated transport pathways of NIS within the marine environment, shipping is considered to be the most important (Carlton and Geller [1993](#); Hewitt et al. [2009](#); Piola and McDonald [2012](#)). After considerable attention was given to ballast water, attention has focused on the importance of biofouling on shipping. According to Otani ([2006](#)), biofouling on shipping is today the most important vector worldwide for marine NIS introductions.

In this review, we describe the history, pathways and vectors for the biological invasion of the azooxanthellate coral *Tubastraea* (Scleractinia: Dendrophylliidae) throughout the world. In order to do so we consulted previous reports in the literature and also compiled new unpublished information on the distribution of the three species of *Tubastraea* which have been reported as NIS, both within their native and non-native ranges and also on vectors. We combine these data with historical aspects of the vectors in order to get insights into how *Tubastraea* species have

successfully spread around the world and where future studies would be best focused.

Materials and methods

We have compiled published current and historical scientific papers from international, Caribbean, Gulf of Mexico and Brazilian journals, unpublished government and NGO reports and university theses, as well as newspaper and magazine articles in English and Portuguese that relate to non-indigenous *Tubastraea* species. We also accessed information available in the online databases [The Global Biodiversity Information Facility (http://www.gbif.org/), Species Link (http://splink.cria.org.br/) and Hexacorallians of the World (http://hercules.kgs.ku.edu/hexacoral/anemone2/index.cfm) as well as the Sun-Coral (*Tubastraea* spp.) records and management database maintained by the *Projeto Coral-Sol*, *Instituto Brasileiro de Biodiversidade*. Geographical records of ranges of the NIS of *Tubastraea* were tabulated (online Appendix) and used to build distributional maps and based on the review of historical records were then classified as native, introduced or cryptogenic (a conservative category of obscure or unknown origin). For Brazil records were used to list all vectors and cumulative records on vectors and natural substrata were compared over time graphically. All available documents were summarized in preparation for this review. We use the term shipping to include all floating vessels, including barges, platforms and floating docks. The review is organized as follows: (1) background information on marine biological invasion; (2) materials and methods; (3) change in vectors through history; (4) distribution and biology of *Tubastraea*; (5) the invasion of the Caribbean; (6) the invasion of the Gulf of Mexico; (7) the invasion of the northwest Atlantic; (8) the invasion of the southwest Atlantic; (9) the Eastern Atlantic and its ambiguities; (10) pathways and vectors; (11) questions arising, future directions, and comments.

Change in vectors through history

Historically, hull fouling was the prominent vector related to shipping. Sailing ships used solid ballast (rocks, sand or metal), which was discharged along the shoreline of most ports and harbors. Solid ballast was replaced by bulk seawater ballast prior to World War I. In the 1960s new and highly effective biocides were used on hulls for antifouling (Qian et al. 2010) and due to their greater efficiency hull fouling was perceived to be a less important vector. At the same time ballast water became recognized as an important vector for unintentional introduction of NIS. During the 1990s the tin based biocides were found to be highly toxic and their use discontinued (e.g., Law et al. 2012). With the uptake of practical measures for ballast water control and management concern focused once again on the challenges of biofouling, especially in the absence of the effective TBT antifoulants (Nehring 2001; Minchin et al. 2009). Since 2003, tin-free technologies have dominated the market of antifouling paints and new technologies such as fluoropolymer-based slime release are emerging. There is a need to improve antifouling paint technologies for structures that remain idle for extended periods (Hopkins 2010).

Longer stationary periods facilitate propagule settlement, recruitment, survivorship and growth of many NIS on submerged surfaces of vectors. The risks are greater for non-trading vessels for which the need for a smooth hull is not critical, such as barges, drilling platforms and some pleasure craft. Stationary periods also constrain the functioning of self-polishing paints, which need movement through the water in order to renew the coating (Floerl and Coutts 2009). Oil platforms, in particular, spend long periods stationary and have been singled out as especially high risk vectors of introduction of fouling organisms (Sammarco et al. 2004; Ferreira et al. 2006; Page et al. 2006; Yeo et al. 2009; Wanless et al. 2010). They usually hold a high fouling biomass and the survivorship on platforms is much higher than on commercial cargo vessels due to the slower speed at which they are towed. This increases the risk of invasion between drilling/production sites or from offshore to onshore (Hopkins 2010). Despite this, modern steel vessels continue to carry fouling species, especially in niche areas such as sea chests, gratings and water intake pipes.

Biofouling associated with commercial and recreational vessels remains largely unmanaged at the international level. The International Maritime Organization (IMO) recently issued non-binding guidelines for the control and management of ships' biofouling to

minimize the transfer of invasive aquatic species (International Maritime Organisation 2011) and also provided guidance for minimizing the transfer of invasive aquatic species through biofouling (hull fouling) on recreational craft (International Maritime Organisation MEPC 2012).

Distribution and biology of *Tubastraea*

Three of the at least six Recent species of *Tubastraea* are considered to have been introduced outside their original ranges (Fig. 1). In these regions, *T. coccinea*

Fig. 1 Three non indigenous *Tubastraea* species: **a** *T. coccinea*, **b** *T. tagusensis*, **c** *T. micranthus*

and *T. tagusensis* are recognized as being highly invasive and causing significant environmental, economic, and social impacts (Creed 2006; Lages et al. 2011; Mantelatto and Creed 2014) requiring management actions. The third species, *T. micranthus* is thus far only found on oil platforms in its introduced range but is established and has similar potential for negative impact (Sammarco et al. 2014b).

Because all Recent species of *Tubastraea* occur in shallow water, some of its species have been described multiple times. For instance, the type species, *T. coccinea* Lesson, 1829 (Fig. 1a), has 14 junior synonyms, as deduced by Boschma (1953), Wells (1982), and finally summarized by Cairns (2001). The tall, arborescent *T. micranthus* (Eherberg, 1834) (Fig. 1c) has three junior synonyms, and a third species *T. diaphana* (Dana, 1846) has one junior synonym. It is somewhat ironic that, in the process of synonymizing almost all the available names for this genus, Wells (1982) described yet another three new species, all from the Galapagos: *T. faulkneri* Wells 1982, *T. tagusensis* Wells 1982 (Fig. 1b) and *T. floreana* Wells 1982. Most extant species were compared by Cairns (1991); another three species are known exclusively as fossils from the Late Eocene of Antarctica, Early Oligocene of Washington, and Late Miocene of France (see Cairns 2001). The living species are usually distinguished by gross morphology, including aspects of their colony form, number and relative size of their septal cycles, and size of their columella (Cairns 1991). Ocaña et al. (2015) recently described a new species, *T. caboverdiana* Ocaña & Brito based on morphological characteristics. Many of these morpho-species have yet to be confirmed by molecular methods although recently Arrigoni et al. (2014) used molecular techniques and recognised seven species of *Tubastraea*.

Tubastraea coccinea Lesson, 1829 (Fig. 1a) is an ahermatypic/azooxanthellate scleractinian coral which was first described from Bora Bora Island with a natural range throughout the Indo-Pacific. The Western Pacific and Eastern Atlantic records appear to be disjunct and here are conservatively considered to be cryptogenic. Its non-native range extends to the Caribbean Sea (1943), the Gulf of Mexico (1977) and Southwestern Atlantic (late 1980s) (Vaughan and Wells 1943; Fenner 1999, 2001; Fenner and Banks 2004; De Paula and Creed 2004; Mantelatto et al. 2011; Silva and Barros 2011; Sampaio et al. 2012). In
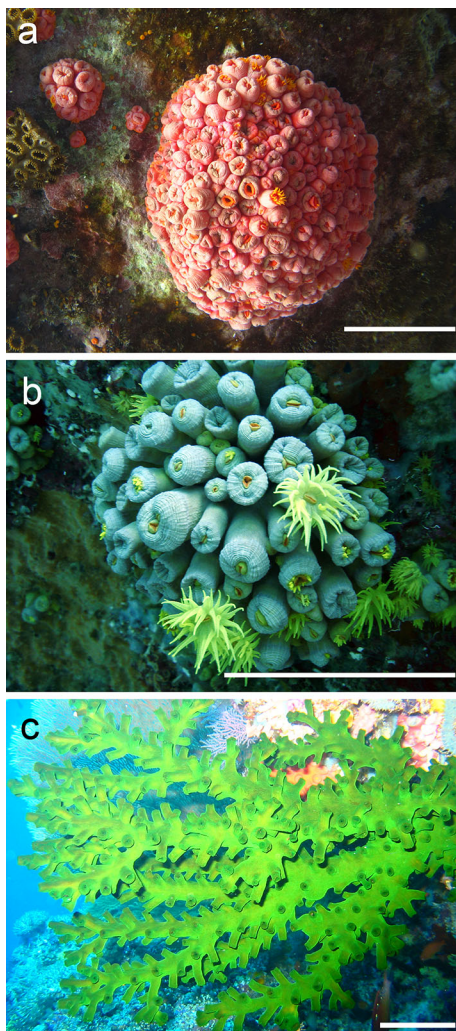
its native range, *T. coccinea* occurs from 1 to 110 m depth (Cairns and Zibrowius 1997). In Brazil *T. coccinea* has been found to at least 12 m depth on rocky shores at Arraial do Cabo, Rio de Janeiro (Mizrahi 2008) and at 16 m at Ilhabela, São Paulo (Mizrahi et al. 2014b) and up to 21 m depth at Todos os Santos Bay, Bahia (Miranda et al. 2016a). However, a single colony was trawled from ≈ 100 m depth off São Paulo state (Mantelatto 2012). On oil and gas platforms in the Gulf of Mexico *T. coccinea* extends down to ≈ 45 m (Sammarco et al. 2013). *Tubastraea coccinea*, at least in the vicinity of the mouth of the Mississippi River, appears to occur in a turbid environment—one with somewhat variable salinities, high sediment, and rich in plankton (Sammarco et al. 2013, 2014b).

Tubastraea coccinea has several modes of reproduction, which is probably one reason why it is effective at dispersal. One mode is sexual reproduction, with internal fertilization and the internal development of planula larvae. The brooder coral can produce planulae both sexually and asexually (Ayre and Resing 1986; Glynn et al. 2008; De Paula et al. 2014). The seasonal reproductive activity is extensive, with multiple reproductive periods during the year—January, February, March, June, July and December on the Pacific coast of Central America (Glynn et al. 2008)–and in November, January and February in the Southeast Atlantic (De Paula et al. 2014). Planulation occurs monthly for several contiguous months during the year. The colonies can be reproductively active with as little as two polyps and produce an average of 15 planulae per polyp that are 0.5–5 mm long (0.5–1.5 mm long, Glynn et al. 2008; 1–3 mm, De Paula et al. 2014; 3–5 mm, Paz-García et al. 2007) and brilliant red to yellow in color.

Paz-García et al. (2007) reported that *T. coccinea* can transport planulae to the substrate using mucus strings that run from the polyp mouth, which may explain the gregarious settlement around mother colonies. Although the larvae begin to metamorphose in 3 days (Glynn et al. 2008), Mizrahi et al. (2014a) kept planulae alive for 4 months in artificial conditions (aquaria). This suggests that *T. coccinea* may be capable of surviving unattached for long periods; during this time they reported a pelagic larva metamorphose into eight-polyp clusters. Pelagic colonies have not, however, been reported in the field yet and may be an artifact of laboratory conditions. Another

recently reported mode of asexual reproduction used by *T. coccinea* is "polyp bail-out" (Sammarco 1982) by which the polyp abandons the skeleton and subsequently settles, secreting a new skeleton (Capel et al. 2014). It should be noted that Vermeij (2005) documented what he considered to be a novel growth strategy as attributed to *T. coccinea*. Colonies were reported to extend runners, which can result in the new growth of corallites. However, we believe that those corals were the genus *Rhizopsammia* Verrill, 1870, which is characterized by forming reptoid colonies by extra-tentacular stoloniferous budding (Cairns 2000).

Recruitment experiments carried out by Creed and De Paula (2007) did not show differences in settlement preference of substratum composition, but *T. coccinea* prefers to settle on the underside of panels (Vermeij 2006) or on vertical surfaces (Mangelli and Creed 2012; Mizrahi et al. 2014b). It also favors artificial substrata (Mangelli and Creed 2012) and often occurs on dock pilings, buoys, cave ceilings, and on the undersides of large rocks (Cairns 2000). *T. coccinea* shows a growth rate of 1.01 cm.yr^{-1} in Brazil (De Paula 2007), 3.02 cm^2 year^{-1} (Vermeij 2005) and 1.35 cm^{2}year^{-1} (Vermeij 2006) in the Caribbean.

***T. tagusensis* Wells** 1982 (Fig. 1b) is an ahermatypic/azooxanthellate scleractinian coral that was first described from Tagus Cove, Isabela Island, Santiago Island and Daphne Minor Island in the Galapagos Archipelago, Ecuador (described in 1983 from material from 1872) and reported as the same species in the Nicobar Islands, India (1975) and Palau (1975); nevertheless these out-of-Galapagos records may be mis-identifications, as discussed further below. The species has also been reported in the Persian Gulf (1988, Carpenter et al. 1997) which is disjunct and here are conservatively considered to be cryptogenic and is invasive in the southwest Atlantic (De Paula and Creed 2004; Mantelatto et al. 2011; Silva and Barros 2011; Sampaio et al. 2012). In the Galapagos *T. tagusensis* has been reported to be locally abundant (Glynn and Wellington 1983) where it formed an important component of the coral fauna (Robinson 1985). It has been reported to occur there at depths between 3 and 43 m and is especially abundant on overhangs (Wells 1982). In Brazil *T. tagusensis* was recorded up to 15 m depth at Ilhabela (Mantelatto et al. 2011) and up to 22 m at Salvador (Sampaio et al. 2012).

This brooding coral can produce planulae through both sexual and asexual reproduction (De Paula et al.

2014). In Brazil this species has two reproductive seasons, one in May and the other in April; male (immature) gonads, however, were found only in March. The planulae, 1.0–2.5 mm diameter, are red to yellow in color (De Paula et al. 2014). In a recruitment experiment, planulae of *T. tagusensis* showed a settlement preference for cement surfaces rather than ceramic or iron (Creed and De Paula 2007). Recruitment on vertical surfaces is preferred (Mangelli and Creed 2012). The growth rate is high for an azooxanthellate scleractinian coral, 0.92 cm year^{-1} (De Paula 2007). *T. tagusensis* favors artificial and natural substrata equally (Mangelli and Creed 2012).

According to Glynn and De Weerdt (1991) *T. tagusensis* must be sensitive to high temperatures as an exceptionally strong El Niño (El Niño - Southern Oscillation) event in 1982/1983 resulted in prolonged high temperature anomalies (2–3 °C above normal), which resulted in a mass mortality of corals in the eastern Pacific, including 100 % mortality of *T. tagusensis*, thought to have become extinct in its native range (Glynn and De Weerdt 1991) but which reappeared 20 years later.

T. micranthus (**Ehrenberg, 1834**) (Fig. 1c) is an hermatypic azooxanthellate scleractinian coral species that naturally occurs through the Indian Ocean to the Comores and Madagascar, and to the Fiji Islands in the Pacific Ocean from 4 to 50 m depth (Schuhmacher 1984). The Red Sea populations (first record 1984) appear to be disjunct and here are conservatively considered to be cryptogenic. On oil and gas platforms in the Gulf of Mexico, *T. micranthus* not only extends down to ≥183 m, but most of its colonies occur at deeper depths when compared to *T. coccinea* (Sammarco et al. 2013). Although it is relatively common in its native range, little is known about its physiology, diet, depth-distribution, reproduction, or other aspects of its life history. According to Schuhmacher (1984), *T. micranthus* had been observed to catch large planktonic organisms such as salps and polychaetes, and can grow laterally at a rate of 4 cm.yr^{-1}. *T. micranthus* is known to occur in light-exposed conditions in its native habitat and has been considered to be a primary reef-builder (Schuhmacher 1984). This is unlike its congener *T. coccinea* which occurs in cryptic environments in its native habitat—in relatively dark crevices, caves, etc. In the Gulf of Mexico, *T. micranthus* appears to grow best in a blue-water environment—one more remote from the river mouth

and possessing less sediment and plankton (Sammarco et al. 2013, 2014b).

The invasion of the Caribbean

Cairns (1994: 93) was the first to suggest that the azooxanthellate coral, *Tubastraea coccinea*, may be an introduced species in the Caribbean, which had spread from the site of its initial introduction (Fig. 2a, 3). He wrote: "Its apparent spread throughout the Caribbean, first noticed in the Netherlands Antilles and progressively in other parts of the Caribbean, would indicate that the western Atlantic was not its original range. Coralla of specimens from the Caribbean, Galapagos, Japan, and the southwest Indian Ocean are indistinguishable."

In 2000: 179–180, Cairns expanded on this, writing:

"The earliest record of the genus in the western Atlantic was that of Vaughan and Wells (1943), who simply listed the locality of 'West Indies' in their generic account, without further documentation. Boschma (1953) ascertained from these authors that this general reference was based on unpublished material collected from Puerto Rico and Curaçao. Although a date was not given, one might assume that the specimens were collected in the late 1930's. The first date-documented specimens were reported by Boschma (1951, 1953) from the Netherlands Antilles between 1948 and 1950, interestingly some of these specimens were attached to a ship's bottom. Later, Roos (1971) remarked that, since the 1950's, the abundance of *T. coccinea* seemed to be increasing both in Curaçao and the northern coast of Jamaica, consistent with the hypothesis that the species was enlarging both its range and abundance….The species was introduced to the Caribbean and Curaçao and/or Puerto Rico in the late 1930's or early 1940's by transport from the Indo-Pacific on a ship's hull, where (Indo-West Pacific) it had been known as early as 1829. From Curaçao this opportunistic species quickly spread". He reported locations where it was known in the eastern and central Caribbean, with the northernmost locations known being Silver Bank and southeast Cuba, and the farthest west being Isla Providencia, while the farthest east in the Leeward Antilles was Saba. He indicated that the species distribution is cosmopolitan in tropical shallow water, and is present in the Eastern Atlantic at Cape
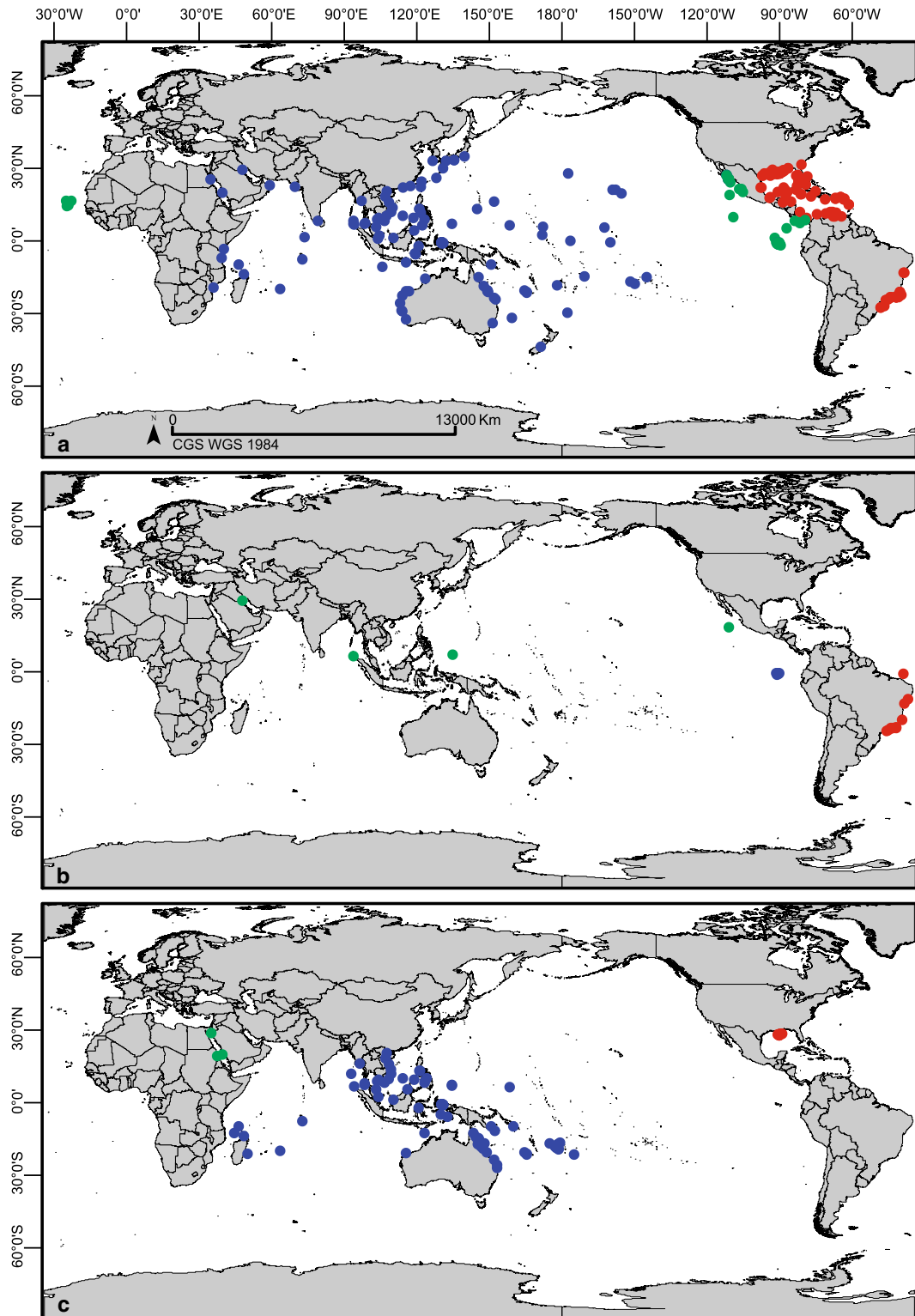
Fig. 2 Maps of the worldwide native (*blue*), cryptogenic (*green*) and introduced (*red*) distributional records of **a** *Tubastraea coccinea*, **b** *T. tagusensis* and **c** *T. micranthus*
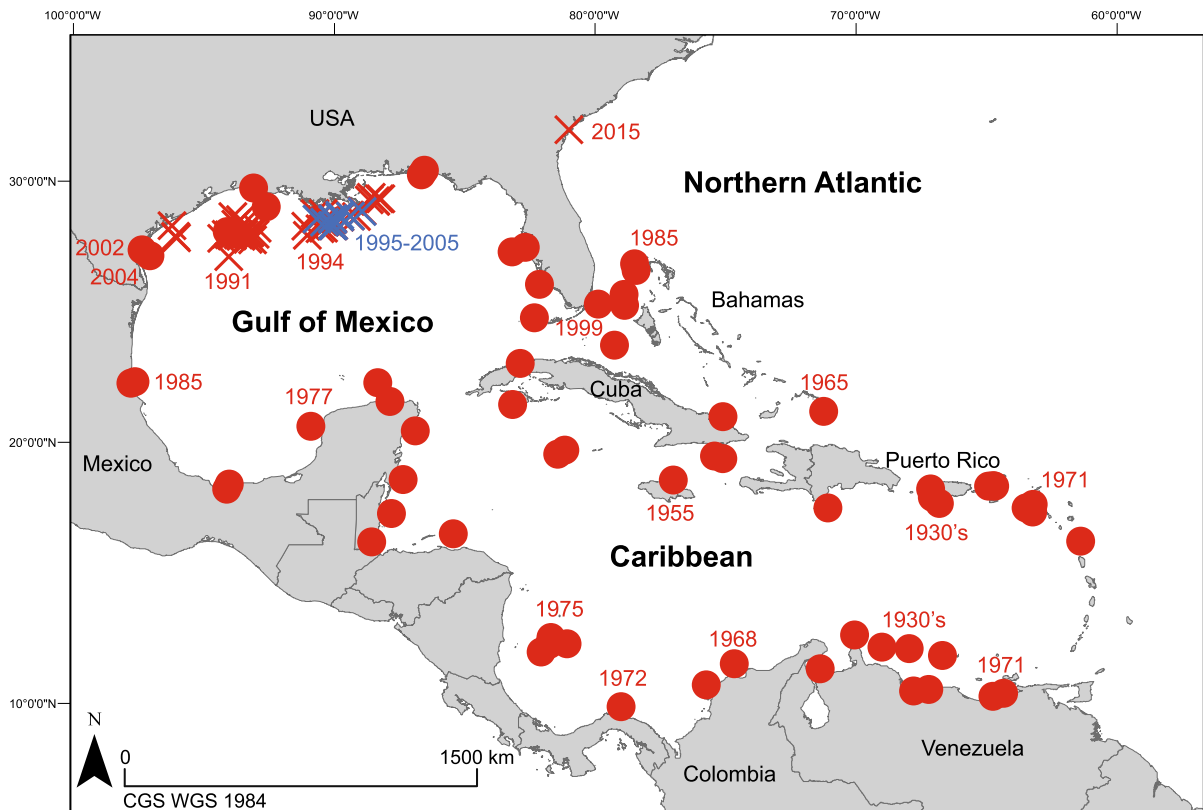
Fig. 3 Map of the historical distributional records of non-indigenous *Tubastraea coccinea* (*red*) and *T. micranthus* (*blue*) on natural substrates (*circles*) and vectors (*crosses*) throughout the Caribbean Sea and Gulf of Mexico

Verde and the Gulf of Guinea. Fenner (2001) followed, further documenting the locations of this species in the Caribbean reported in the literature and additional locations from specimens in museums and sightings reported by researchers, some of which were supported with photographs or specimens (Table 1 Supplementary material; Fig. 3). Fenner (2001) also pointed out that there is no evidence of this species in fossil records in the Caribbean (Vaughan 1919; Cairns 1999), which would be consistent with it having been introduced. Fenner and Banks (2004) reported that most Caribbean corals were described before *T. coccinea* was reported in the Caribbean including all other genera, facts consistent with the view that *T. coccinea* was introduced into the Caribbean.

The invasion of the Gulf of Mexico

In 2001, Fenner documented the locations of *T. coccinea* for the first time, in the Gulf of Mexico

(GOM), in Mexico, Texas and Louisiana, all on oil platforms, but there were no reports from any of the reefs in the GOM. Because the oil platforms were a relatively recent human addition to the GOM, the reports of *T. coccinea* on oil platforms there represented a clear expansion of the range of the species (Fig. 3). In their book Humann and DeLoach (2002: 164) presented a map built on that of Cairns (2000), with an additional site in the northern GOM labeled 1999.

Sammarco et al. (2004) and Fenner and Banks (2004) reported that *T. coccinea* had been found on the Flower Garden Banks (FGB) in the northwestern GOM in 2002, the first report on natural substrate. As the FGB hosts about 20,000 dives per year and *T. coccinea* had not previously been reported it was clearly an expansion onto natural substrate within the GOM. Sammarco et al. (2004) believed that the FGB and the rest of the northern GOM were both being colonized from somewhere else in the Gulf or Caribbean. They also reported that *T. coccinea* was

Table 1 Brazilian shipping and buoys with records of *Tubastraea* spp

Year	Name (Operator)	Type	Location (coordinates)	Species	Source and notes
"Late 1980s"	Unknown	Oil platform	"Campos"	*Tubastraea* sp.	Castro and Pires (2001); alive
1997	SS-6 (= P-65) (Petrobras)	Oil platform—production	Pampo field, Campos Basin (22°54′S, 040°59′W)	*T. coccinea*	Identified by J.C. Creed from photographic register *of* Nicolau (1997); alive.
1999	Unknown	Oil platform—production	Marlin field, Campos Basin (22°27′S, 040°20′W)	*Tubastraea* sp.	C.B. Castro (pers. comm.); De Paula and Creed (2004); alive.
2000	XIV (= P-14) (Petrobras)	Oil platform—production	Caravelas field, Itajaí (26°46′2″S, 046°47′2.15″W)	*T. coccinea*	Identified by J.C. Creed from photografic register of Barreiros et al. (2000); alive.
2002	XIII (Petrobras)	Oil platform	Niterói, (22°52′37.14″S, 043°7′19.91″W)	*T. coccinea*, *T. tagusensis*	Docked in port, De Paula and Creed (2004); skeleton.
2005	Valentin Shashin	Drill ship	Arraial de Cabo (22°58′10″S, 041°59′58″W)	*T. coccinea*	Ferreira et al. (2006), docked in port; alive (C.E.L. Ferreira pers. comm.)
2005	Noble Leo Segerius	Drill ship	Arraial de Cabo (22°58′10″S, 041°59′58″W)	*T. coccinea*	Ferreira et al. (2006), docked in port; alive (C.E.L. Ferreira pers. comm.)
2005	SS-56 (Petrobras)	Drilling plataform	Arraial de Cabo (22°58′10″S, 041°59′58″W)	*T. coccinea*	Ferreira et al. (2006), docked in port; alive (C.E.L. Ferreira pers. comm.)
2005	SS-47 (Petrobras)	Drilling plataform	Arraial de Cabo (22°58′10″S, 041°59′58″W)	*T. coccinea*	Ferreira et al. (2006), docked in port; alive (C.E.L. Ferreira pers. comm.)
2005	Ocean Alliance (9POA) (Diamond Offshore)	Oil platform—production	Arraial de Cabo (22°58′10″S, 041°59′58″W)	*T. coccinea*	Ferreira et al. (2006), docked in port; alive (C.E.L. Ferreira pers. comm.)
2005	PNA-1 (Petrobras)	Oil platform—production	Namorado field, Campos Basin (22°29′21″S, 040°22′42″W)	*T. coccinea*, *T. tagusensis*	Identified by J.C. Creed from photographic register (C.E.L. Ferreira pers. comm.); alive
2006	A Turtle (ex-Petrobras XXI)	Oil platform	Tristan da Cunha (37°08.788′S, 012°14.651′W)	*Tubastraea* sp.	Wanless et al. (2010)—departed Macae, Brazil, 56 days previously bound for Singapore and ran aground on Tristan da Cunha
2007	3 monobuoys, including IMODCO IV and EMH 5411	Monobuoys[a]	Arraial de Cabo (22°58′21.40″S 042°0′49.56″W)	*T. coccinea*, *T. tagusensis*	Mizrahi (2008); alive
2007	P-14 (Petrobras)	Oil platform—production	Angra dos Reis (23°00′53.87″S, 044°18′59.90″W)	*T. coccinea*	In port, J.C. Creed (pers. obs.)
2008	Unknown	Small pleasure boat	Piraquara (23°00′58″S, 044°26′24″W)	*Tubastraea* sp.	On the hull of a small sailboat which was moored and unmaintained; eradicated (Rodrigo Amorim pers. comm.)

Table 1 continued

Year	Name (Operator)	Type	Location (coordinates)	Species	Source and notes
2009	Ocean Winner (= SS-54) (Diamond Offshore/Brasdril Macae)	Drilling plataform	Ilheus (14°47′S, 038°58′W)	*T. coccinea*, *T. tagusensis*	Identified by J.C. Creed from photografic register (Monica Dorigo Correia, pers. comm.); alive. The same platform subsequently moved to Sergipe in December 2009 and Rio de Janeiro in November 2010.
2012	IMODCO-IV (Petrobras)	Monobuoy	São Sebastião (23°48′48.45″S, 045°24′11.78″W)	*T. coccinea*, *T. tagusensis*	In port; J.C. Creed, pers. obs.; alive.
2012	SBM-5 Araça (Petrobras)	Monobuoy	São Sebastião (23°48′48.45″S, 045°24′11.78″W)	*T. coccinea*, *T. tagusensis*	In port; J.C. Creed, pers. obs.; alive
2012	Peroá (= PPER) (Petrobras)	Gas platform—production	Peroá-Cangoá Field, Espírito Santo Basin (19°33′73″S, 039°15′28″W)	*T. tagusensis*	Costa et al. (2014); alive. The plaform was built in Brazil at the Petrobras Enseada do Paraguaçu shipyard.
2013	BSR-Congro (Petrobras)	Riser Support Buoy[b]	Congro field, Campos basin (22°18′S, 040°28 W)	*Tubastraea* sp.	Gustavo Baez Almada (pers comm.); 100 m depth, with 158 colonies (Ana Maria Scofano, pers comm); alive.
2013	P-52 (Petrobras)	Oil platform—production	Roncador Field, Campos basin (21°57′46″S, 039°40′29″W)	*T. coccinea*	Identified by J.C. Creed from photographic register of Gustavo Baez Almada (pers. comm.); alive; the plaform was built in Brazil at Angra dos Reis, the base was built in Singapore and towed to Brazil.
2013	P-27 (Petrobras)	Oil platform—production	Voador Field, Campos Basin (22°22′S, 040°24″W)	*T. coccinea*	Identified by J.C. Creed from photographic register comunicated by Ricardo Guedes dos Santos (pers. comm.).
2013	PCM6 (Petrobras)	Oil platform—production	Off Aracajú (10°58′59″S; 036°55′56″W)	*T. coccinea*, *T. tagusensis*	Identified by J.C. Creed from photographic register in situ comunicated by Giselma Santos do Nascimento (pers. comm.); alive
2013	PDO1 (Petrobras)	Oil platform—production	Off Aracajú (11°05′54″S; 036°57′33″W)	*T. tagusensis*	Identified by J.C. Creed from photographic register in situ comunicated by Giselma Santos do Nascimento (pers. comm.); alive
2014	Unknown	Small pleasure boat	Ilha Grande, Vila do Abraão (23°08′24.42″S, 044°9′54.84″W)	*Tubastraea tagusensis*, *T. coccinea*	On the hull of a small sailboat which was moored and unmaintained; M. Mantelatto pers. obs.
2014	P-27 (Petrobras)	Oil platform—production	Canteiro de São Roque, Paraguaçu (12°51′14″S, 038°50′24″W)	*T. coccinea*	In port, J.C. Creed pers. obs.; alive.
2014	P-14 (Petrobras)	Oil platform—production	Canteiro de São Roque, Paraguaçu (12°51′16.96″S 038°50′17.41″W)	*T. coccinea*, *T. tagusensis*	In port, J.C. Creed pers. obs.; alive.

[a] Monobuoy is a floating platform anchored offshore in deep water and equipped with pipelines leading to storage tanks, to which large, deep-draft tankers moor to load or unload

[b] Riser Support Buoy is a rectangular-shaped buoy structure weighing around 2000 metric tons, installed 250 m subsea and anchored to the seabed by eight tethers. The buoys will support a total of 27, 3.9-km long steel catenary risers (SCRs) suspended in parallel vertically to the seafloor, and connected to the FPSO via non-bonded, flexible jumpers

one of the three most abundant coral species on Gulf oil platforms. Fenner and Banks (2004) also reported it for the first time in Florida, on 10 sunken ships, one set of oil rig jackets, a floating dock and limestone boulders making up the Port of Miami Mitigation Reef. Florida reefs have been intensively studied and yet *T. coccinea* had never been reported there before.

In the GOM Hickerson et al. (2008) reported *T. coccinea* on the East Flower Garden Bank (EFGB), on the Geyer Bank (>100 colonies) located 52 km east-southeast of the EFGB and the Sonnier Bank, so *T. coccinea* is colonizing additional banks and the number of colonies is increasing. Shearer (2009) documented colonies on sunken ships in Florida. The number of colonies on wrecks in Broward County, Florida increased until all but one wreck was covered with them (K. Banks, personal comm.). Precht et al. (2014) report that although *T. coccinea* occurs on artificial substrates like buoys in Jamaica, it has not yet colonized native reef habitats. It has also been reported on the *Aquarius* underwater habitat and nearby natural hard-bottom at Conch Key, Florida. There are, however, at least 33 other named topographic features (banks) throughout the GOM that support a lower cover of scleractinian corals (Rezak et al. 1985) and could serve as sites for recruitment and establishment of this species.

Little is known about the supposed migratory path of *T. micranthus*. All we know is that it is Indo-Pacific in origin. The specific country of origin is unknown. Judging by sightings, in the northern GOM in 2008 and beyond near the mouth of the Mississippi River, and the size of the populations in this region, it most likely arrived between 1995 and 2005 (Sammarco et al. 2010) (Fig. 3).

The invasion of the northwest Atlantic

Tubastraea coccinea has also been reported in the Northwest Atlantic. In Humann and DeLoach's book (2002: 164) an additional site is shown in the northern Bahamas and labeled 1985. In 2014 it was also sighted on the bottom of a weather buoy in Greys Reef National Marine Sanctuary in Georgia, USA (S. Fangman, pers. comm.) (Fig. 3), but has not been seen on natural substrates yet. This appears to be the most northerly sighting for this species to date. Now that this coral is abundant on wrecks in Florida, the

volume of larvae released may be sufficient to start colonizing artificial structures occurring to the north—being carried by the Gulf Stream, in the same way that the lionfish invaded that area (Whitfield et al. 2002; Schofield 2010). The limit of spread will likely be set by the thermal tolerance of the coral and availability of suitable substrate.

The invasion of the southwest Atlantic

Tubastraea is the only scleractinian coral to have been introduced into Brazilian waters (De Paula and Creed 2005) (Fig. 4). Castro and Pires (2001) and De Paula and Creed (2004) make the first report of the genus as *Tubastraea* from an offshore oil platform in the Campos Basin, north of Rio de Janeiro in the late 1980s (Table 1; Fig. 4b). The first register that allowed the identification of species was Nicolau (1997) who photographed *T. coccinea* on an oil platform in the Pampo oil field, Campos Basin, Brazil (Table 1). It was erroneously reported as a species endemic to the platforms of the Campos Basin (Nicolau 1997). At that time the occurrence of the coral was interpreted as contributing to the richness of the region, but today demonstrates the role that the industry has played in the introduction and range expansion of *Tubastraea* around the world. By the late 1990s, the genus was first reported on tropical rocky shores at Ilha Grande Bay, Rio de Janeiro (P.S. Young and F.B. Pitombo, pers. comm.) (Fig. 4a); the first published record of the genus on rocky shores in Brazil was Castro and Pires (2001) and thereafter on several oil platforms mainly off Rio de Janeiro in the Campos Basin (Table 1). In 1999 a few colonies of *T. coccinea* were found on rocky shores at Arraial do Cabo, Rio de Janeiro state (23°44′S–42°W) (Ferreira 2003). In 2000, two species, *T. coccinea* and *T. tagusensis*, were identified occurring at 32 from the 37 sites studied at Ilha Grande, Rio de Janeiro state, where they expanded their range rapidly and dominated the coastline (> 200 colonies m^{-2}; De Paula and Creed 2005; Creed et al. 2008) (Fig. 4a).

According to Lages et al. (2011) the abundance of *Tubastraea* spp. increased by up to 76 % in just 1 year at Ilha Grande. By 2003, *T. coccinea* and *T. tagusensis* were widely distributed in Ilha Grande Bay but still concentrated around Ilha Grande - *T. coccinea* and *T. tagusensis* were found at 50 % and 56 % of the 66 studied sites, respectively (Creed et al. 2008). The

range expansion continued and both species invaded the Tamoios Marine Protected Area (Silva et al. 2011) and beyond (Silva et al. 2014). Both species had reached the neighboring Sepetiba Bay by 2011 (unpublished data). *T. tagusensis* was also recorded and removed from the Cagarras Archipelago (Mantelatto 2012) in 2004 and recorded again in 2011. Further north *Tubastraea* spp. expanded their range from Arraial do Cabo to Armação dos Búzios (registered in 2011) and Cabo Frio (2013) (Fig. 4a).

Until 2008, *Tubastraea* species were restricted to the shores of Rio de Janeiro State (Fig. 5a) or on oil platforms (Fig. 5c). Subsequent new occurrences began to be recorded at other locations along the Brazilian coast (Mantelatto et al. 2011; Sampaio et al. 2012). Between 2008 and 2010, both species were observed for the first time on two islands at Ilhabela, São Paulo State (130 km south of Ilha Grande Bay; Mantelatto et al. 2011). In 2011, *T. tagusensis* was also

found at the Alcatrazes Archipelago, inside the Tupinambás Marine Protected Area, São Paulo State (Mantelatto 2012). In 2012 *T. coccinea* was observed at the Laje de Santos Marine State Park (Alexandre Costa, pers. comm.) and in 2014 in the Alcatrazes Archipelago, São Paulo State (Kátia Capel, pers. obs.). *T. coccinea* was also observed further south at Arvoredo (Santa Catarina state) in 2012 (Mantelatto 2012) nearby the Arvoredo Marine Protected Area, where a few colonies have also recently been found (Ana Flora Sarti Oliveira, pers. comm.). In 2015 *Tubastraea* expanded to four sites on Ilha de Arvoredo and one site at Ilha da Galé (Alberto Lindner, pers. comm.) (Fig. 4a).

In Espírito Santo State, north of Rio de Janeiro, *T. coccinea* was registered on the rocky shores of Ilha Escalvada at Guarapari in 2011 (Ivan Caldas, pers. comm.). Nearby lies a shipwreck, the *Victory 8B* which has also been reported to have *T. coccinea* (Ivan
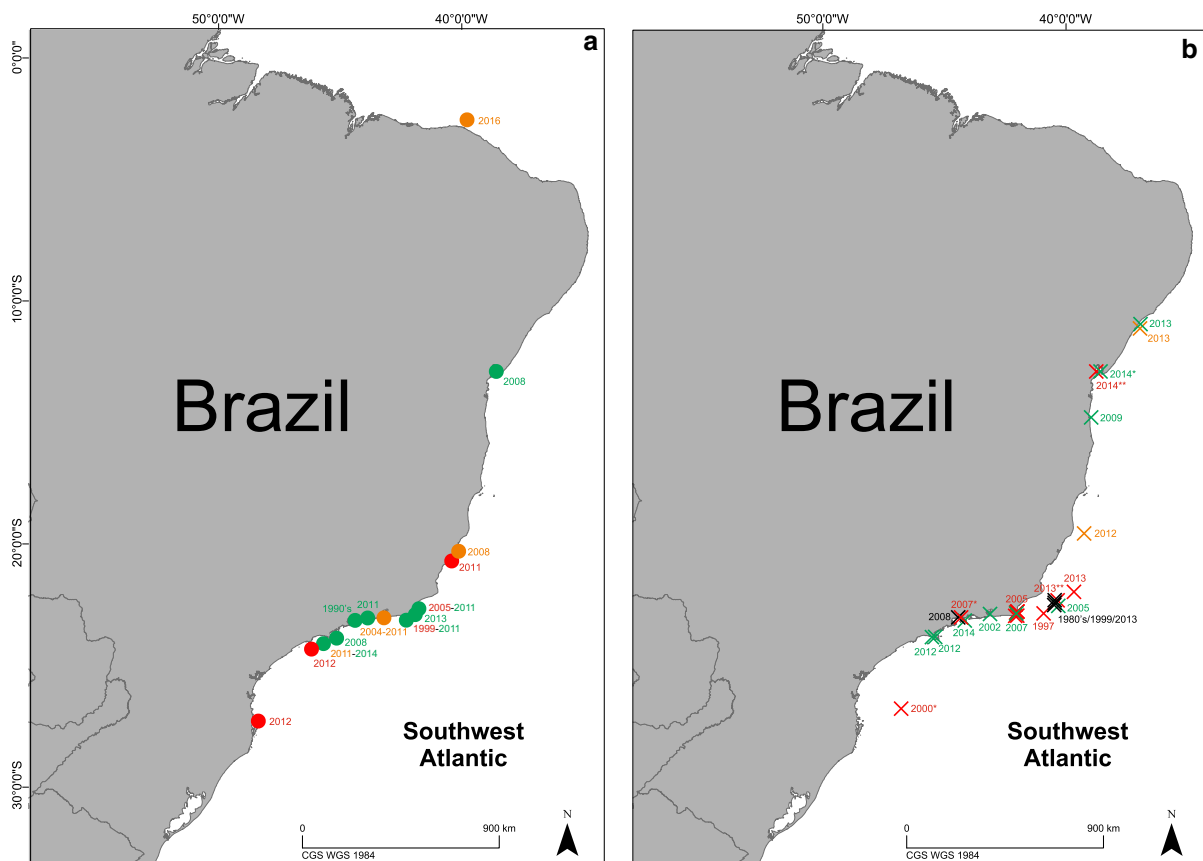

Fig. 4 Map of the historical distributional records of non-indigenous *Tubastraea coccinea* (*red*), *T. tagusensis* (*orange*), both species (*green*) and unidentified *Tubastraea* (*black*) on

a natural substrates and wrecks and **b** on vectors, throughout southwest Atlantic. * = platform P-14 and ** = platform P-27

Caldas, pers. comm.). Costa et al. (2014) recently registered *Tubastraea* sp. at Vitoria harbor on port structures in 2008; thus it is probable that the *Victory 8B* was sunk with *Tubastraea* already having colonized during its 7-year stay in the harbor pre-sinking (it was sunk as a diving amenity). *T. tagusensis* was also registered in 2012 on a gas production platform in northern Espírito Santo on the Abrolhos Bank, the most extensive reef complex in the south Atlantic (Costa et al. 2014; Table 1; Fig. 5e).

Tubastraea coccinea and *T. tagusensis* were first recorded in Bahia State in 2008 on the *Cavo Artemidi* shipwreck off Salvador, then in 2010 at Itaparica Marina in the Todos-os-Santos Bay. In 2011, *T. tagusensis* was reported for the first time on a coral reef at Cascos (Sampaio et al. 2012) (Fig. 5b) where its cover reached approximately 9 % of the reef substrate (Miranda et al. 2016b). At this coral reef site *T. tagusensis* was dominant on reef walls and likely altered native coral assemblage structure by direct competition (Miranda et al. 2016b). This region is known to harbor a rich coral fauna (Castro and Pires 2001; Leão et al. 2003; Cruz et al. 2009) and is also characterized by extensive shipping traffic (Sampaio et al. 2012). *T. tagusensis* and *T. coccinea* have been recorded at 18 sites in the reef and estuarine complex around Todos-os-Santos Bay, Bahia (Miranda et al. 2016a). In 2013, this species was also registered further north on oil platforms operating off Aracajú, Sergipe State (Giselma Santos do Nascimento pers. comm.; Table 1). In 2016 *Tubastraea* (apparently *T. tagusensis*) was registered on the wreck of an oil tanker, the Eugene V R Thayer (*Petroleiro do Acaraú*), 27 km off the coast of Ceará State (Marcus Davis pers. comm.).

Currently *Tubastraea* species are found discontinuously along more than 3000 km of the Brazilian southwest Atlantic coastline on rocky shores and on reefs from Bahia (Sampaio et al. 2012) to Santa Catarina state (Mantelatto 2012). They have also been found within at least seven Marine Protected Areas (Tamoios Ecological Station, Anchieta Island State Park, Tupinambás Ecological Station, Laje de Santos Marine State Park, Arvoredo Marine Biological Reserve, and the Baía de Iguape and Arraial de Cabo Marine Extractive Reserves), and on 23 oil or gas platforms, drill ships, monobuoys, riser support buoys and small pleasure craft (Table 1; Fig. 4). Figure 6 presents the cumulative reports of *Tubastraea* spp. in the southwest Atlantic, both on shipping (drill ships and platforms) and buoys and on the natural coastline. Recent studies, using species distribution modeling, demonstrated that suitable habitat is available for *Tubastraea* along almost the entire length of the Brazilian coast and some oceanic islands. These models have been successfully predicting range expansion along the Brazilian coastline (Riul et al. 2013; Carlos-Júnior et al. 2015).

The Eastern Atlantic and its ambiguities

As far as is known, the records of *Tubastraea* in the Eastern Atlantic only go back to the 1950s, when Chevalier (1966) reported it as *Enallopsammia micranthus*, based on Recent specimens collected off Cape Verde in 1950 (Laborel 1974). It is surprising that such a conspicuous, shallow and often highly abundant coral was not reported before. Laborel (1974) described two forms of *Tubastraea* in West Africa (Gabon, Sierra Leone) and the Gulf of Guinea islands as "a sulphur yellow form with long, elevated, sometimes branching calices united at their base by feebly developed exotheca, with columella feeble or absent and thin septa" in contrast to "an orange form with short, low, wide corallites, united tightly, sometimes in a subplocoid manner, by a well developed exotheca, and possessing a wide shallow columella". The later description seems compatible with *T. coccinea*.

Laborel (1974) states that the two forms do not intergrade but in the Cape Verde Archipelago, on the contrary, two color forms have similar skeletons which are bushy and brittle and resemble the yellow form described above (Fig. 7). Boekschoten and Best (1988) describe *T. coccinea* as Pleistocene and Recent in Cape Verde; Baarli et al. (2013) also briefly mention *Tubastraea* sp. on Cape Verde but do not provide figures or discussion to support a Pleistocene presence. Ocaña et al. (2015) described the Cape Verde *Tubastraea* as a new species *Tubastrea caboverdiana* Ocaña & Brito new species, mainly based on its differences from *T. coccinea*.

It seems rather surprising that another species of *Tubastraea* would be found in the eastern Atlantic, far from the Indo-West Pacific centre of *Tubastraea* diversity. Considering the biogeographical context of the coral fauna of West Africa Laborel (1974)
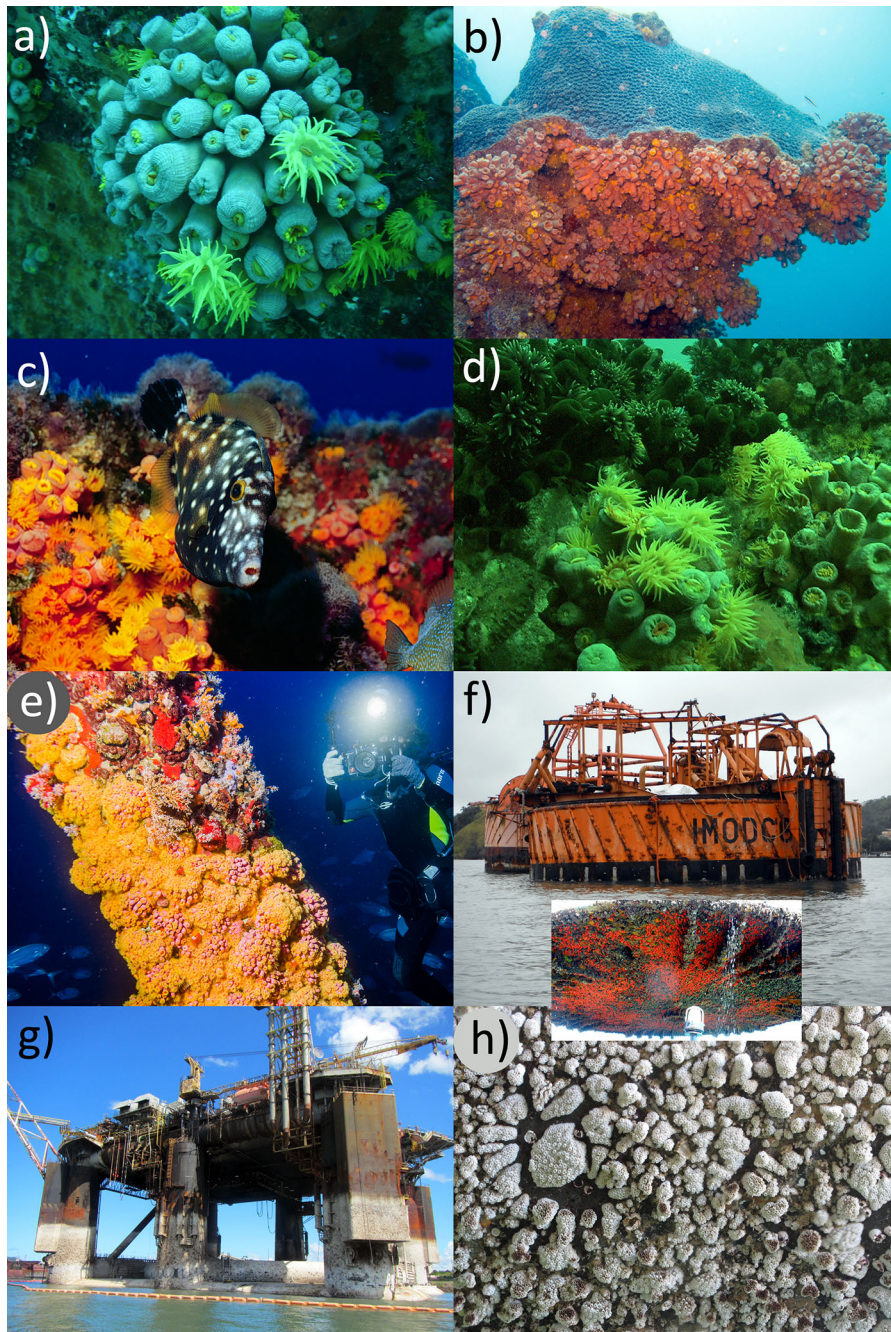
Fig. 5 *Tubastraea* on natural substrate and on vectors: *T. tagusensis* on **a** tropical rocky shore and **b** a coral reef in Brazil; *T. coccinea* fouling **c** the oil platform P-14, Brazil (2000) **d** together with *T. micranthus* (*darker*) on a platform in the Gulf of Mexico, **e** on a gas platform on the Abrolhos Bank, Brazil; known vectors: **f** Monobuoys at São Paulo (*inset*: base of monobuoy with *T. coccinea*) and **g** oil platform P-27 at Paraguaçu, Brazil, with the lighter lower portion showing dead biofouling by *T. coccinea* and **h** detail of the density of *Tubastraea* dead due to exposed to air during transit. Photos of the authors, except **c** by Jorge Miguel Rodrigues Fontes, **d** by Scott A. Porter, **e** by Leonardo Schlögel Bueno and **f** (*not inset*) Gilberto Morão/Projeto Coral-Sol, used with permission

concluded that *Tubastraea* "must be a relatively recent invader, maybe coming from the Indo Pacific". Friedlander et al. (2014) reported *Tubastraea* sp. on 100 % of oil rigs investigated off Gabon, where it was the most abundant taxon. They also considered it likely a relatively recent invader to the Gulf of Guinea. These observations, the absence of older records of this highly conspicuous genus and the current doubts regarding identification lead us to conservatively categorize the African *Tubastraea* records as cryptogenic *T. coccinea* (Fig. 2).

Pathways and vectors

Although all three invasive *Tubastraea* species are traded and used by hobby aquarists, it is most probable that the pathway for introduction of *Tubastraea* into the southern Caribbean and southwest Atlantic has been shipping (a term used here to include all floating vessels). It is difficult to identify any other pathways that could be responsible for these introductions. Regarding shipping, the two most common vectors are hull fouling and ballast water (Hewitt et al. 2009). As far as we are aware, coral larvae have not yet been documented in the literature as derived from ballast water or tanks, but may be difficult to identify in preserved material, although anemones have been been found (J. Carlton, pers. com.). Furthermore

characteristics such as the delicate nature of the larvae, slow range expansion of *Tubastraea* compared to other invasive invertebrates, the patchy distribution of colonies and the fact that larvae quickly settle near parental colonies (De Paula and Creed 2005; Glynn et al. 2008; de Paula et al. 2014) make ballast water an unlikely vector. Thus, although there is strong evidence for the transport of these organisms by hull fouling on slow moving vessels, there is no evidence supporting the concept of larval dispersal of *Tubastraea* spp. via ballast water.

Considering the timeline of spread through the Caribbean and GOM (Fig. 3), the probable points of initial introduction were Curaçao or Puerto Rico, probably in the early 1940's. Puerto Rico was a major coaling station and shipping port. *T. coccinea* might have been brought there first by a ship and carried on to Curaçao before subsequent dispersal by currents (Fenner and Banks 2004). Ceiba, Puerto Rico was also the home of the U.S. Naval Operations Base at Roosevelt Roads where substantial expansion of the base occurring between 1941–1943 (Department of the Navy Bureau of Yards and Docks 1947; Lindsay-Poland 2009) brought an influx not only of ships, but also of floating docks and platforms from other theaters, all potential vectors for introduction of *T. coccinea* through fouling. Roosevelt Roads, commissioned in 1943, was so enlarged that it became known as the "Pearl Harbor of the Caribbean" and was a

Fig. 6 Cumulative reports of *Tubastraea* spp. on vectors and on natural substrates (by municipality) in Brazil from 1990–2015

$y = 0.0603x^2 - 240.36x + 239542; R^2 = 0.98$
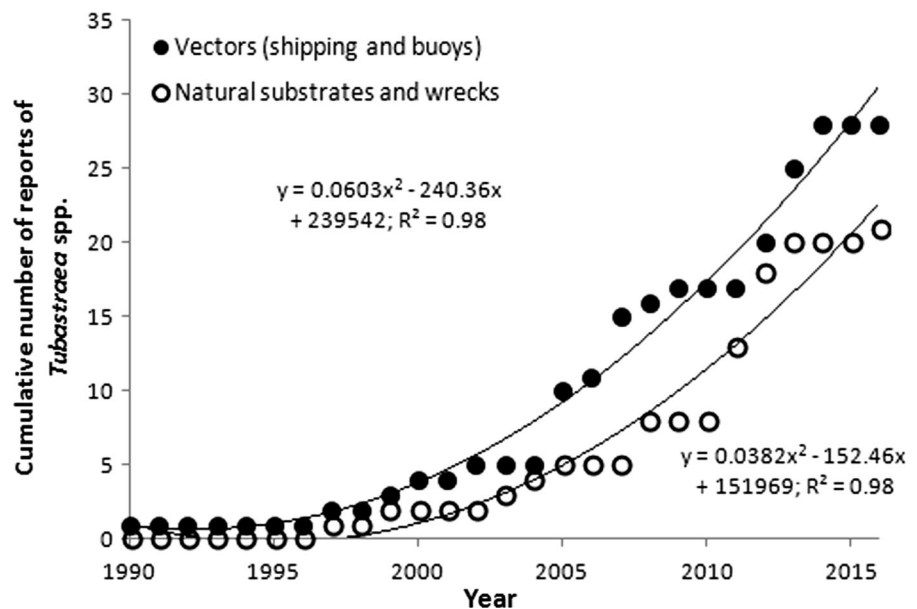
$y = 0.0382x^2 - 152.46x + 151969; R^2 = 0.98$

Fig. 7 Two intermingled color forms of what is considered to be *Tubastraea* sp. at Santiago Island, Cape Verde, Eastern Atlantic Ocean. *T. coccinea*, *T. caboverdiana* or some other species? Photo Joel Creed

central point for the Caribbean Defense System (Department of the Navy Bureau of Yards and Docks 1947). Cairns (2000) suggested that *T. coccinea* was carried from the Indo-Pacific to the Caribbean on a boat hull and may have spread through the Caribbean by transport on ship hulls (Cairns 1994). Humann and DeLoach (2002) also believed that this species was transported into the Caribbean on a ship's bottom from either the eastern Pacific or tropical Indo-Pacific. This would logically be via the Cape of Good Hope, Straits of Magellan or from the west African coast, as the Panama Canal would subject hull fouling to immersion in rapidly moving fresh water for several hours, which kills *Tubastraea* spp. colonies (Moreira et al. 2014). Boschma (1951) reported *T. coccinea* on a ship's bottom in the Caribbean (Cairns 2000). Boschma (1953) reported *T. coccinea* at Aruba fouling a ship that had been cleaned 2 years previously at dock nearby in Curaçao, which suggest local shipping vectors. The appearance of the coral at both Puerto Rico and Curaçao nearly simultaneously would be consistent with this shipping vector (Fig. 3).

From Puerto Rico and/or Curaçao, *T. coccinea* undoubtedly spread through the Caribbean and into the GOM. Humann and DeLoach (2002: 164) wrote

that "it is easy to theorize that the species…has dispersed by following typical current patterns throughout the region". There are three lines of evidence that suggest most dispersal of *T. coccinea* through the Caribbean was passive: (1) The historical records match known current patterns (Cairns 2000; Fenner 2001; Humann and DeLoach 2002; Fenner and Banks 2004 and Fig. 3); (2) similar patterns have been seen in other invasive species with very different life cycles; (3) the timeline of range expansion does not follow the major shipping routes.

Fenner and Banks (2004) drew parallels between the spread of *T. coccinea* in the Western Atlantic and the pattern of spread of the urchin (*Diadema antillarum*) die-off. The urchin die-off began in Caribbean Panama, and spread rapidly with the currents to the north and into the GOM and to Florida and eastward from Panama and Florida through the eastern Caribbean (Lessios et al. 1984; Fenner and Banks 2004). Lessios et al. (1984) reported that it was carried by an eastward-flowing current along the northern shore of South America. The die-off was induced by a microscopic planktonic pathogen easily transported and viable for long periods spread throughout the Caribbean, GOM, and to Florida and Bermuda within 1 year (Lessios et al. 1984; Lessios 1988).

Similarly the dispersal of the lionfish (*Pterois volitans* [Linnaeus, 1758] and *P. miles* [Bennett, 1828]) from Florida provides another model for natural dispersal along the US east coast and in the Caribbean and GOM (http://www.reef.org/lionfish). Lionfish were first reported off the coast of Southeast Florida in 1985, dispersed north to Bermuda in 2000 and the Bahamas around 2004, to the southern Caribbean in 2009 and the windward Antilles including Barbados in 2011 and Tobago in 2012. They also passed west into the eastern Gulf of Mexico in 2008 and then spread westward in the Gulf of Mexico. The expansion of lionfish required nearly 30 years to reach almost all of the U.S. east coast, Bermuda, and all of the Bahamas, the Caribbean and the Gulf of Mexico. Dispersal to the north up the U.S. east coast and to Bermuda fits the flow of the Florida Current and subsequently the Gulf Stream to Bermuda. The lionfish swim and produce large numbers of eggs; in contrast *T. coccinea* has required about 60 years to spread throughout the Caribbean, Gulf of Mexico and Florida and has not yet reached Bermuda.

The timing of the appearance of *T. coccinea* at different locations in the Caribbean, Gulf of Mexico and Florida is not easily consistent with shipping, since it would have appeared first along shipping routes (Fig. 3). Although planulae have been observed to swim and may remain competent to settle for up to 18 days (De Paula et al. 2014) or 100 days [R. Richmond, pers. comm. in Fenner (2001)] in aquaria without provision of natural substrata, studies indicate where natural substratum is available settlement and metamorphosis occur quickly [R. Richmond, pers. comm.; after 1–3 days (Glynn et al. 2008), overnight (J.C. Creed pers. obs., settling onto the base of mother colonies in preference to aquaria surfaces)]. These observations together with strong coupling between adults and nearby local recruitment (Creed and De Paula 2007; Paz-García et al. 2007) indicate that slow dispersal by many short steps, not a few long-distance dispersal events, is the norm.

According to Fenner (2001) there are several possible modes of dispersal of *T. coccinea* into the Gulf of Mexico. Attached adult colonies may have been carried on oil platforms from the Caribbean (Venezuela) or Indo-Pacific redeployed into the Gulf of Mexico, similarly to what occurred in Brazil and Gabon (see below and Friedlander et al. 2014). Ships may have carried it from the Caribbean but are currently not allowed to tie up at Texas or Louisiana oil rigs (S. Gittings, pers. comm.). Alternatively it could have been carried on floating rafts or planula could have been carried from the Caribbean directly to Texas on the loop current (Gittings 1992; Lugo-Fernández et al. 2001) or along the continental shelf using the approximately 3800 oil platforms (Dokken 1993) as 'stepping stones' (Sammarco et al. 2004). A recent study of the genetics of *T. coccinea* on oil platforms in the northern Gulf of Mexico demonstrated two separate sources which imply two discrete introduction events (Sammarco et al. 2012a, b; Sammarco 2014).

The vectors affecting *Tubastraea micranthus* transit to the Gulf of Mexico are no different than those affecting other parts of the world, outlined earlier. According to Sammarco et al. (2013) it is quite possible that the vector for this introduction to platforms in the GOM was a vessel traveling from the Indo-Pacific due to its relatively close proximity to two major fairways servicing the mouth of the Mississippi River (near New Orleans, Louisiana) and

Port Fourchon, a major deep-water port for the northern GOM. From an initial introduction probably on one platform from a colony on a ship's hull, larvae may have dispersed to other platforms (Sammarco et al. 2014b).

In summary most parsimonious explanation of the vectors for the dispersal of *T. coccinea* throughout the Caribbean, GOM, Bahamas, Georgia and Florida, USA, is a combination of introduction by hull fouling on shipping (ship or floating platforms) and then passive dispersal of larvae throughout the Caribbean, GOM and Florida by currents (see Sammarco et al. 2012a, b, 2014a, b) with at least two discrete introductions onto oil platforms and subsequent range expansion between them.

In the southwest Atlantic, there is no longer any reasonable doubt that *T. coccinea* and *T. tagusensis* were introduced through biofouling on oil platforms and/or drill ships, probably redeployed from Africa, the GOM or Indo-Pacific via the Straits of Magellan or the Cape of Good Hope. Large oil platforms cannot transit the Panama Canal. Four lines of evidence support biofouling on oil platforms and/or drill ships as the pathway into Brazil: (1) all the earliest records of *Tubastraea* in Brazil are on oil platforms (Table 1); (2) records of oil and gas associated shipping are mirrored by records of invasions into natural communities (Fig. 6); (3) the primary coastal introduction points are always coupled with associated, nearby coastal port facilities, used by oil and gas industry associated shipping (compare Fig. 4a, b) and (4) the estimated ages of colonies on at least one platform were 15 years older than the arrival of the platform in Brazil.

For example, using population characteristics and their spatial variation, Silva et al. (2014) determined the first introduction in Brazil as at an anchorage site for oil platforms in transit or repair at Ilha Grande, Rio de Janeiro (Fig. 4). The second introduction, at Arraial de Cabo, Rio de Janeiro, has also received a number of oil platforms, drill ships, and monobuoys biofouled with *Tubastraea* spp. (Table 1; Fig. 4). In fact, taking into account the timelines and movements, it is possible to pinpoint the platform P-27 (Fig. 5g) as being responsible for this introduction. *Tubastraea* was reported on a rocky shore at Arraial de Cabo in 1999, and P-27 had arrived there from Singapore in 1998. There it remained anchored for 6 months before being moved offshore to start production in the

Campos Basin. Taking into account growth rates of *T. coccinea* in Brazilian waters (De Paula 2007), and the size of samples taken from P-27 in 2014 (Fig. 5g, h), larger colonies were estimated to be >30 years old, pre-dating the arrival of the platform in Brazil by at least 15 years. It is not clear whether the platform was towed or carried on a heavy lift vessel but it had niche areas at crossbeam points which retain seawater pools even when emerged from the water.

The same geographical coupling between vector reports and primary invasion points could be observed with: the P-14 oil platform, which operated in Itajaí from 2000 to 2007 (Table 1; Fig. 4) and the invasion of Santa Catarina State (Arvoredo), monobuoys at São Sebastião and the invasion of São Paulo (Ilhabela, Alcatrazes, Laje de Santos); the platforms at São Roque do Paraguaçu (Fig. 5g) and the invasion of Bahia State (Todos-os-Santos Bay). Another example is the shipyard at São Roque do Paraguaçu which built the Peroá (PPER) platform in 2004. It was positioned in Espirito Santo State in 2005 for production; in 2012, *T. tagusensis* was reported to occur on 40 % of its submerged area (Costa et al. 2014; Fig. 4b, 5e). This was therefore a secondary introduction from Bahia State. Following this pattern, we would predict there will soon be reports of *Tubastraea* spp. on natural substrates at Aracajú, Sergipe State, and nearby the Peroá (PPER) on the Abrolhos Bank (compare Fig. 4a, b).

In Brazil *Tubastraea* spp. have been reported on 19 platforms, two drill ships, five monobuoys and one Riser Support Buoy associated with oil and gas exploration and production (Table 1; Fig. 6). Two small pleasure boats have also been reported to have *Tubastraea* species as hull fouling (Table 1)—both of which had effectively been abandoned in the water in small harbors within the range of occurrence at Ilha Grande Bay without maintenance or cleaning. Small pleasure craft therefore have the potential to be vectors for secondary introduction. Despite this, corals are highly sensitive to rapid water movement associated with modern ships and boats and are usually absent when compared to other fouling organisms. In contrast, *Tubastraea* spp. have been observed to survive well on slow moving drill ships and objects, such as the oil platforms P-27 and P-14 (see Fig. 4b), which were towed 1280 and 1440 km, respectively, to port where they remained living and subsequently reproductive (Creed et al. 2014; Fig. 5).

Questions arising, future directions, and comments

Given the demonstrated propensity of no fewer than three species of *Tubastraea* to be introduced into the Western Atlantic, it would seem logical to consider whether the ranges of these invasive *Tubastraea* species elsewhere truly reflect the original range or have been extended through human shipping in the past. For lack of information we conservatively categorized some records for *T. coccinea* and *T. tagusensis* as cryptogenic, but it seems very possible that both the West African and the Eastern Tropical Pacific populations of *T. coccinea* are introduced, given that *Tubastraea* is a hull fouling species, the long history of shipping around the world and the disjunct distributions. The same may be true of *T. micranthus* in the Red Sea given its isolation there and the presence of the shipping route through the Suez canal. Carlton (2009) hypothesized that a vast number of historical invasions have been overlooked and it may even be the case that some records of *Tubastraea* are what he termed pseudoindigenous (introduced species that are mistakenly considered as native). Hull fouling has historically been considered important (see section Change in vectors through history); the non-indigenous *Tubastraea* spp. are known to be hull fouling organisms and the history of shipping around the world is ancient. Darwin collected *T. coccinea* in the Galapagos in 1835—by which time long-distance (transoceanic) foreign vessels had been visiting the Islands for 300 years.

During the present review the authors came across a number of discrepancies regarding the current taxonomy and identification of different species as well as apparent range mismatches, so a revision of the genus using both traditional and molecular techniques is necessary. For example as well as issues previously discussed for *Tubastraea* in the Eastern Atlantic (ex. Fig. 7); (Arrigoni et al. 2014) presented molecular evidence for at least seven *Tubastraea* species, two of which are undescribed, as well as separating some species synonymised by Wells (Wells 1982). In the case of *T. tagusensis* it seems possible that the few records outside the Galapagos Islands are misidentifications. For example the records of Carpenter et al. (1997) illustrate and state in the Persian Gulf that both *T. coccinea* and *T. tagusensis* have a strong Pourtalès arrangement, a feature which is absence for the genus (Cairns 2000).

Further genetic studies are also required to better understand pathways of introduction, for example to shed light on the question of whether *T. coccinea* in the Caribbean was introduced from the Pacific or the eastern Atlantic, and possibly where from within those areas (Sammarco et al. 2012a, b). With respect to genetic studies, comparisons of populations of *T. coccinea* from the Northwestern Atlantic with populations from Brazil in the Southwestern Atlantic would help to determine whether the two are related. It might also lend insight into the question as to whether the two sets of populations were derived from different introductions, which is likely the case. The relationships between populations in the Gulf of Mexico are already known (Sammarco et al. 2012a, b).

With respect to genetic studies of the populations of *Tubastraea micranthus* in the GOM, studies of populations in the western Indo-Pacific would have a low probability of identifying the source population. Firstly, the source population could have been derived from any continent or island within its natural range (Fig. 1c). Secondly, there would be genetic variation from different points on that potential source country.

Tubastraea coccinea, T. tagusensis and *T. micranthus* have proven themselves to be formidable competitors for space, excellent at sexual reproduction, larval dispersal, and recruitment as well as asexual reproduction via polyp bail-out. This has allowed them to invade, so far, four regions of the planet where they are causing environmental, economic, and social problems. There is therefore an urgent need to prioritize holistic policies with legal and institutional frameworks to enable the affected nations to manage *Tubastraea* species in order to conserve marine biological diversity at national, regional and global levels (IUCN 2000). We recommend ensuring appropriate legislation in order to provide for the necessary administrative powers to be ready to respond with multiple management measures to act pre-border, at border and post border.

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