

Research Article

Depth distribution of a new invasive coral (Gulf of Mexico) –*Tubastraea micranthus*, comparisons with *T. coccinea*, and implications for control

Paul W. Sammarco^{1,2*}, Scott A. Porter^{1,3}, James Sinclair⁴ and Melissa Genazzio^{1,5}

¹ Louisiana Universities Marine Consortium (LUMCON), 8124 Hwy. 56, Chauvin, LA 70344 USA

² Department of Oceanography and Coastal Sciences, Louisiana State University, Baton Rouge, LA 70803 USA

³ Ecologic Environmental, Inc., PO 886, Houma, LA 70361 USA

⁴ US Department of the Interior, Bureau of Safety and Environmental Enforcement (BSEE), 1201 Elmwood Park Blvd., New Orleans, LA 70123-2394 USA

⁵ Center for Marine Science, University of North Carolina at Wilmington, 601 S. College Rd., Wilmington, NC 28403-5928 USA

E-mail: psammarco@lumcon.edu (PS), Ecologic2020@aol.com (SAP), James.sinclair@bsee.gov (JS), mgenazzio@gmail.com (MG)

*Corresponding author

Received: 14 August 2013 / Accepted: 24 October 2013 / Published online: 25 November 2013

Handling editor: Alisha Dahlstrom

Abstract

The Indo-Pacific coral *Tubastraea micranthus* recently invaded a region near the Mississippi River mouth, Gulf of Mexico, and its populations have been expanding. Its congener, *Tubastraea coccinea*, invaded during the 1940s and is now common in the western Atlantic. Accessibility is important in determining whether an invasive species can be controlled/eradicated. In the marine environment, depth limits accessibility. We assessed the depth distribution of *T. micranthus* and *T. coccinea* on 15 oil/gas platforms using remotely operated vehicles (ROVs). Pooled data indicated that *T. micranthus* extends to 138 m and probably deeper, while *T. coccinea* is generally limited to ≤ 78 m. Average depths for *T. micranthus* were shallower west of the Mississippi River, in its plume, and deeper towards the east. *Tubastraea coccinea* exhibited a similar geographic depth-distribution pattern, but shallower and subtler. Broad geographic patterns were similar whether using density or percent-cover data for analysis. When considering individual platforms, *T. micranthus* often reached the bottom and sometimes occurred at depths ≥ 138 m. *Tubastraea coccinea* were limited to shallow waters on all platforms. Detailed depth distribution patterns varied significantly between analyses using density and percent-cover data, with density probably indicating colonization rates, and percent-cover colony growth. Depth limitation by *T. coccinea* may be associated with food availability rather than light since it is azooxanthellate. The occurrence of *T. micranthus* in deep water will most likely make any control or eradication efforts difficult, due to cost and a rapid rate of population expansion.

Key words: coral; *Tubastraea micranthus*; depth; eradication; control; Gulf of Mexico; oil platforms

Introduction

A new invasive species of coral was discovered in the Gulf of Mexico - *Tubastraea micranthus* (Ehrenberg, 1834) (Cairns and Zibrowius 1997). It is an ahermatypic coral native to the Indo-Pacific, occurring in the Philippines (Schuhmacher and Zibrowius 1985), the Maldives (Scheer and Obrist 1986), The Red Sea (Kleemann 1992), Australia (Veron et al. 1980), and elsewhere. This scleractinian coral is a member of the Dendrophyllidae and is azooxanthellate (Schuhmacher and Zibrowius 1985). It was first discovered on a single oil platform (GI-93C), SW of the mouth of the Mississippi River, which occurs near the

juncture of two safety fareways (Sammarco et al. 2010). These fareways are major shipping channels for the Port of New Orleans and the nearby Port Fourchon. It was estimated to have colonized around 2005 or earlier. It was first reported in 2010, and has since been expanding its populations to other oil platforms in that region (Sammarco et al., in press).

As an invasive coral species, *T. micranthus* is preceded by its sister congeneric species – *T. coccinea* Lesson, 1829. This species was introduced during the early 1940s to Puerto Rico (Cairns 2000; Humann and DeLoach 2002) and from that point spread in all directions as far south as Brazil (Figueira de Paula and Creed

2004) and as far north as the Flower Garden Banks (Fenner 1999; Fenner and Banks 2004; Sammarco et al. 2004; two coral reefs in the northern Gulf of Mexico), and the Florida Keys (Shearer 2008). The discovery of *T. micranthus* has raised the question of whether this species may have the same capabilities as its congener to spread throughout the western Atlantic. At this point, its populations are confined to an area with a radius of ~50 km, just south of the mouth of the Mississippi River (Sammarco et al., in press).

The question arises as to whether it is necessary or possible to eradicate this new invasive species (Clout and Veitch 2002a). This becomes important if the species is potentially harmful to native species and can disrupt native populations and community structure. Eradication is generally difficult, because it requires that certain conditions be met (Clout and Veitch 2002b). Firstly, this is a marine invasion, and many marine species are difficult to eradicate or control because they possess swimming larvae dispersed by currents and often spend varying periods of time in the water column prior to settling (e.g., Ackerman et al. 1994; Osman and Shirley 2007). This can be confounded by the species having multiple breeding seasons per year, or breeding continuously (Sakai et al. 2001), as is suspected to be the case with the lionfish (*Pterois volitans*), recently introduced into the western Atlantic Ocean (Albins and Hixon 2008).

Attempts to eradicate invasive species have met with substantial challenges. Examples of successful eradications or control efforts do exist, though. One such case is that of the *Terabrasabella heterouncinata*, an ectocommensal sabellid polychaete which invaded via the importation of South African abalone to a mariculture unit in central California, USA (Fitzhugh and Rouse 1999). This worm was successfully controlled by removing all turban snails – the preferred hosts – from the unit. The population was small, however, and isolated, and the mitigation response was rapid. Using this same approach was also successful in the eradication of the invasive black striped mussel (*Mytilopsis sallei*) in Australia (Bax et al. 2002), a species similar to the species which invaded the US (*Dreissena polymorpha*). Factors that can thwart attempts at invasion control or eradication include rapid reproduction on the part of the invasive species, broad dispersal capabilities of the invaders' planktonic larvae, ready access to the colonizing and expanding populations, and slow response

by the responsible party to a marine invasion of the adults (Clout and Veitch 2002a). For example, *Tubastraea coccinea* is highly fecund and is known to reproduce year-round (Glynn et al. 2008a,b). All of these factors are important, but accessibility to the reproducing members of the population is critical, because without accessibility, there will always be reproducing members of the population remaining.

In the marine environment, accessibility is partially defined by depth and the new depth range of the target organism (Bax et al. 2003). Different depths may be reached by different techniques, and these techniques grow rapidly more expensive (and risky) with increasing depth. Thus, the depth distribution of a new invasive species is important for determining the viability of any eradication efforts targeting it.

Here, we assessed the depth-distribution of *T. micranthus* on a set of oil/gas platforms in the northern Gulf of Mexico, near the mouth of the Mississippi River. The objectives of the study were: 1) To determine the depth distribution on the platform of presumed initial colonization; 2) To determine the same for a number of platforms in the same region; and 3) To compare these depth distributions with those of its congener, *T. coccinea*. This was done with the assistance of a remotely operated vehicle (ROV). We then considered these results in light of probability of control or eradication.

Materials and methods

Study site

Platform GI-93-C served as a control platform of the study, since it was the location of first sighting possessed the highest abundances of this species (Sammarco et al. 2010). Fourteen additional platforms surrounding it within a 20 km radius were also surveyed for *T. micranthus* (Figure 1; Table 1; see Sammarco et al. unpubl. data). Some of these possessed this species. A subset of that group yielded population data sufficient in sample size to analyze for depth distribution and were used in this study (Table 1). The M/V *Fling* (33 m, Fling Charters, Inc., Freeport, Texas) supported our operations while at sea, along with the R/V *Acadiana* (18 m, Louisiana Universities Marine Consortium - LUMCON). The study was conducted over a two-year period, utilizing 12 days of ship-time. Each platform required approximately two-thirds of one day to complete ROV surveys.

Figure 1. Map of the study area, depicting all offshore oil and gas platforms surveyed for *Tubastraea micranthus* and *T. coccinea* by ROV. Geospatial information (latitude and longitude) given along with position of various landmarks to assist in orientation of three-dimensional graphs shown below.

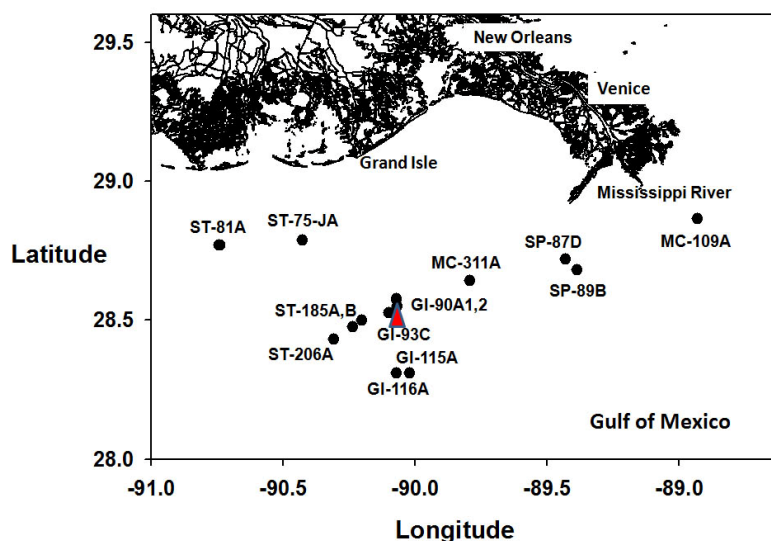


Table 1. A list of all platforms surveyed by ROV during this study. Platform code, oil or gas company owner, and geospatial position via latitude and longitude are given. Asterisks represent those platforms for which sufficient data were available for detailed analysis regarding comparative depth distributions.

Platform		Analyzed in		
Code	Owner	Latitude	Longitude	This Study
GI-90A-1	Apache Corp.	28.575144	-90.072429	
GI-90A-2	Apache Corp.	28.575144	-90.072429	
GI-93C	Apache Corp.	28.548886	-90.068677	*
GI-94B	Apache Corp.	28.540000	-90.275000	*
GI-115A	Walter Oil & Gas Corporation	28.3076123	-90.0219665	
GI-116A	Apache Corp.	28.30928306	-90.07054334	*
MC-109A	Stone Energy Corporation	28.86467752	-88.93079054	*
MC-311A	Apache Corp.	28.642636	-89.794241	*
SP-87D	Apache Corp.	28.72001853	-89.43078669	
SP-89B	Apache Corp.	28.680464	-89.387596	
ST-75-JA(B)	Stone Energy Corporation	28.76955709	-90.74085664	
ST-81A	Stone Energy Corporation	28.78656092	-90.42747823	
ST-185A	Black Elk Energy Offshore Operations, LLC	28.495501	-90.203098	*
ST-185B	Black Elk Energy Offshore Operations, LLC	28.47493	-90.235942	*
ST-206A	Apache Corp.	28.45372522	-90.38341283	*

Survey technique

LUMCON’s Deep Ocean Engineering Phantom S2 ROV was used to conduct the surveys. This unit has 333 m of umbilical and is capable of working to 170 m depth. We used techniques previously employed for similar surveys (Sammarco et al. 2010, 2012a). The Alliance for Robot-Assisted Crisis Assessment and Response (ARACAR) also provided assistance by making a SeaBotix LBV-300 available for the study. The US Department of the Interior Minerals Management Service (MMS)/Bureau of Ocean Energy Management (BOEM) also had a similar

ROV, which was used as a back-up when the primary ROVs needed maintenance. All units had vertical and horizontal propulsion units, site-to-surface color video transmission, a monitor, forward lights, laser beams of a known inter-beam distance (reference for spatial scale), and a fixed grab for sample retrieval.

Surveys were run from the surface to the bottom of the platforms, to a maximum of 138 m depth. For safety purposes, the down-current side of the platform was always surveyed. This was done in order to keep the ROV and its umbilical outside of the structure, avoiding having the

umbilical drawn inside the jacket of the platform and possibly snagging or becoming entangled there. (It is unlikely that there would be any difference in coral settlement on upcurrent vs. downcurrent sides of the platforms, because most settlement would have been influenced by microcurrents associated with pilings on either side. Obstruction of the far-field flow was minimal.) Vertical pilings were surveyed along with two sets of horizontal struts, usually at depths of 13–17 m, and 21–27 m. Two to four vertical pilings were surveyed and processed for each platform, depending upon the number of pilings available for survey and wind and sea conditions.

A Dell Precision 340, a T3400 desktop computer, and a Dell Precision M4300 Workstation were used to process the video images, using MicroSoft video imaging software. Nero 7.0, VideoLAN, and MicroSoft Windows Media Player, capable of zoom and still-image capture, were also used. Within each video transect, images were frozen and analyzed at 2 m intervals. On vertical pilings, one quadrat was analyzed for every 2 m of depth per transect. Up to four replicates per depth (derived from up to four pilings) per platform were captured. These were analyzed for the presence of both *Tubastraea* species. Counts of these species were taken for each quadrat to provide density data (see Sammarco 2012a) standardized to no./10 m². The total for both taxa was tallied for each quadrat. Horizontal struts afforded many more quadrats per depth, of course, than vertical pilings; therefore, horizontal strut area was estimated and standardized for, prior to calculating densities of either species.

In order to compare depth distributions, data were collected for both *T. micranthus* and *T. coccinea*. *Tubastraea coccinea* population densities were extraordinarily high; thus, visual counts were estimated using a log₅ code system (0=1, 1=5, 2=25, 3=125, etc.). This system was developed for use in the field by Williams (1982) for making reef fish counts and has been utilized successfully in related studies (e.g., Halford et al. 2004). Two laser lights of known inter-beam distance fell within the video field of view were used to standardize for coral density (no. corals per unit area). To assist in sampling and taking measurements in the laboratory, a transparent 10 x 10 2.54 cm grid was placed over the computer screen and used as a reference guide. Percent-cover data were also collected. Mean densities along with percent-cover were calculated for each depth bin on each platform.

Data handling and analysis

All quantitative data were logged in EXCEL files, stored on the primary workstation, and backed-up on a 250G Western Digital G-Book external hard-drive.

Basic statistics (g_1 – skewness, and g_2 – kurtosis; see Sokal and Rohlf 1981) were calculated for colony size frequency distributions. In addition, distributions were tested against normal and Poisson distributions using Lilliefors Tests and Goodness of Fit Tests, respectively. Analyses were performed using BiomStat 3.2 and 3.3 (Rohlf and Slice 1996). Where necessary, data were transformed by square root of (Y+ 0.5) for normalization purposes (see Sokal and Rohlf 1981).

Two-dimensional graphs were drawn using SigmaPlot 10.0. Data presented in a geographic context are presented in three dimensions constructed with the assistance of SURFER 8.0 (Golden Software 2002). In those cases, data consisted of latitudes, longitudes, and the variate in question as X, Y, and Z variables, respectively. Kriging was used to calculate averages - a geostatistical gridding method designed for irregularly spaced data, incorporating a smoothing interpolator. Point kriging was used, which estimates interpolated values of points at grid nodes and a default linear variogram (without a nugget effect). See Golden Software (2002) for additional details.

Results

Results from data based on density vs. percent-cover were tested against each other and found to be highly significantly different from each other. This was despite apparent visual similarities in the depth distributions. Thus, results are shown for both of these variables.

When depth distribution data based on coral density from all platforms were pooled, it became evident that *T. micranthus* can occur at all depths, from near the surface to the deepest encountered in this study – 138 m (Figure 2a). This was evident whether one measured abundance by colony density or percent-cover (Figure 2b). The overall pattern of depth distribution was bimodal, with a peak in shallow water (12–18 m) and another set of peaks in deep-water (108–138 m), and the pooled depth distribution data based on density and percent-cover of *T. micranthus* yielded visually similar (although significantly different) patterns (Figure 2b).

Tubastraea coccinea occurred in much higher numbers than *T. micranthus* on all platforms, and

Depth distribution of *Tubastraea micranthus*

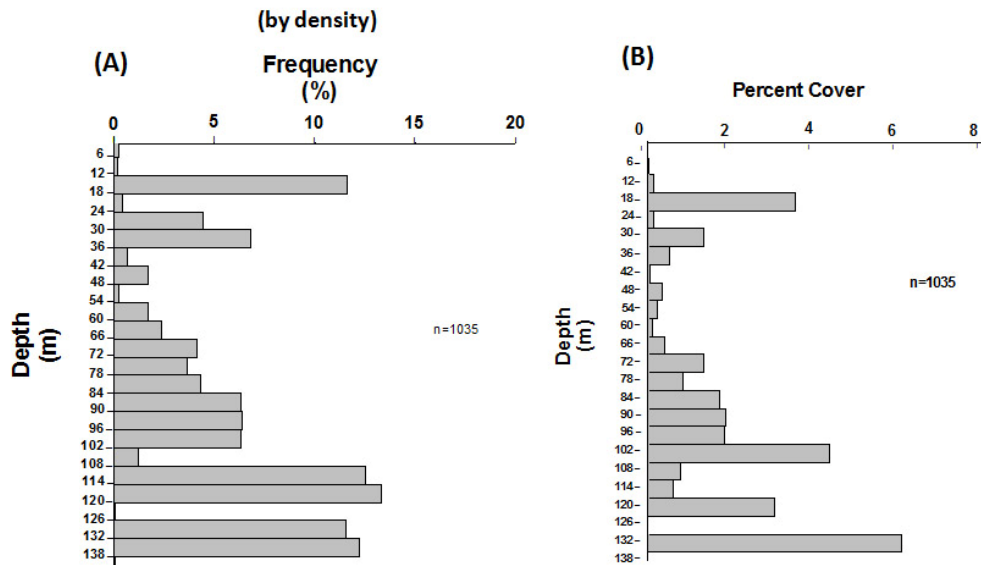


Figure 2. Depth distribution of *Tubastraea micranthus* in the northern Gulf of Mexico. Data pooled from three oil/gas production platforms – GI-93C, GI-116A, and MC-109A. (A) Distribution based upon colony density in no./10 m² and provided in frequency (%). Significantly different than a normal distribution ($p < 0.001$, Lilliefors test) and Poisson distribution ($p < 0.001$, Goodness of Fit test). $g_1 = 8.583$, $g_2 = 94.761$. (B) Same, but data derived from percent-cover instead of colony density. Significantly different than a normal distribution ($p < 0.001$, Lilliefors test) and Poisson distribution ($p < 0.001$, Goodness of Fit test). $g_1 = 9.597$, $g_2 = 113.657$. Significant difference between *T. micranthus* distributions measured by density vs. percent-cover ($p < 0.001$, R x C Goodness of Fit test).

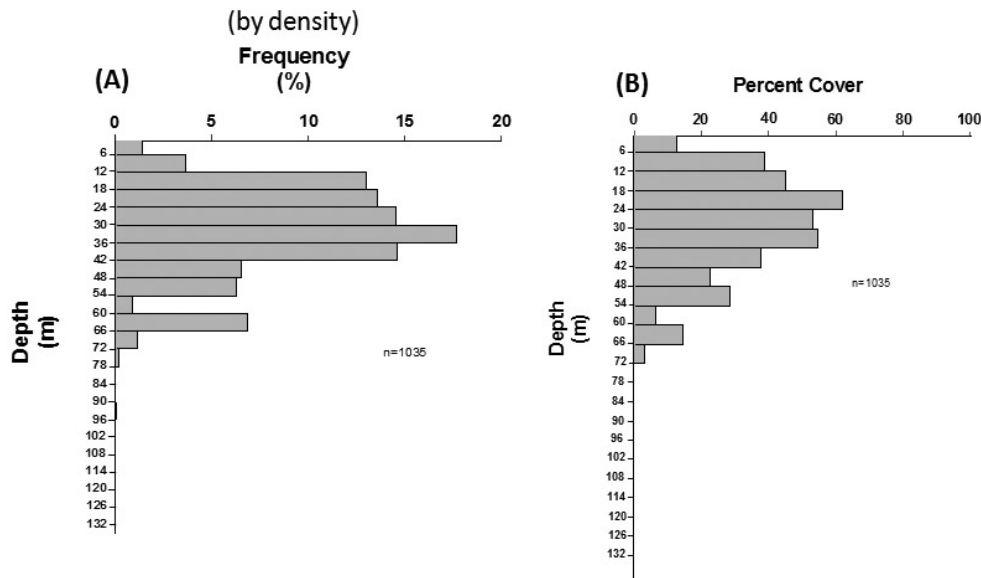


Figure 3. Depth distribution of *Tubastraea coccinea* in the northern Gulf of Mexico. Data pooled from six oil/gas production platforms – GI-94B, GI-116A, MC-311A, ST-185A, ST-185B, and ST-206A. (A) Distribution based upon colony density in no./10 m² and provided in frequency (%). Significantly different than a normal distribution ($p < 0.001$, Lilliefors test) and Poisson distribution ($p < 0.001$, Goodness of Fit test). $g_1 = 4.001$, $g_2 = 33.264$. (B) Same, but data are derived from percent-cover instead of colony density. Significantly different than a normal distribution ($p < 0.001$, Lilliefors test) and Poisson distribution ($p < 0.001$, Goodness of Fit test). $g_1 = 0.553$, $g_2 = -1.123$. Significant difference between *T. coccinea* distributions measured via density vs. percent-cover ($p < 0.001$, R x C Goodness of Fit test). Significant difference between distributions of *T. micranthus* vs. *T. coccinea* whether measured by density or percent-cover ($p < 0.001$, R x C Goodness of Fit Test, in both cases).

Figure 4. Geographic distribution of average depth of distribution for *Tubastraea micranthus* in the northern Gulf of Mexico. (A) Data based on colony density in no./10 m². (B) Data based on percent-cover.

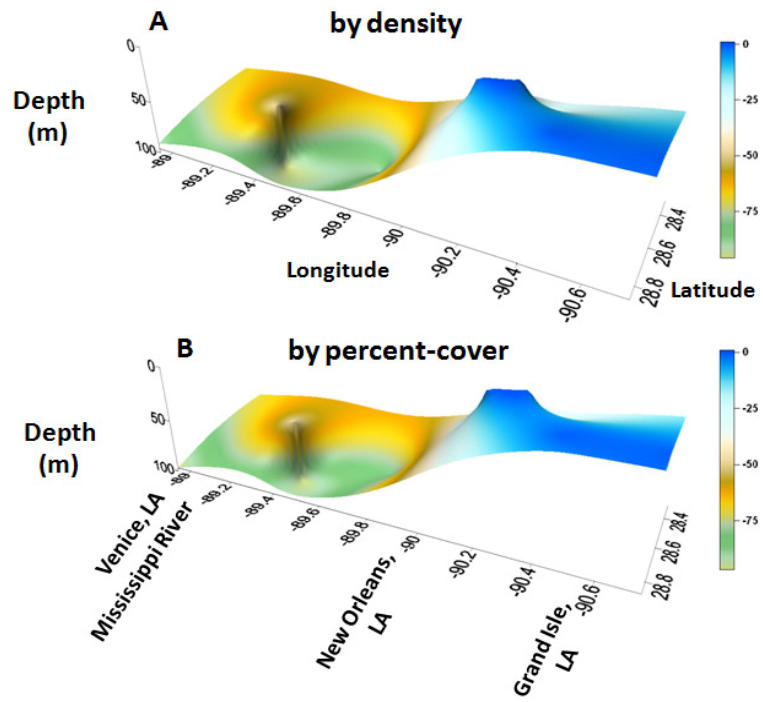
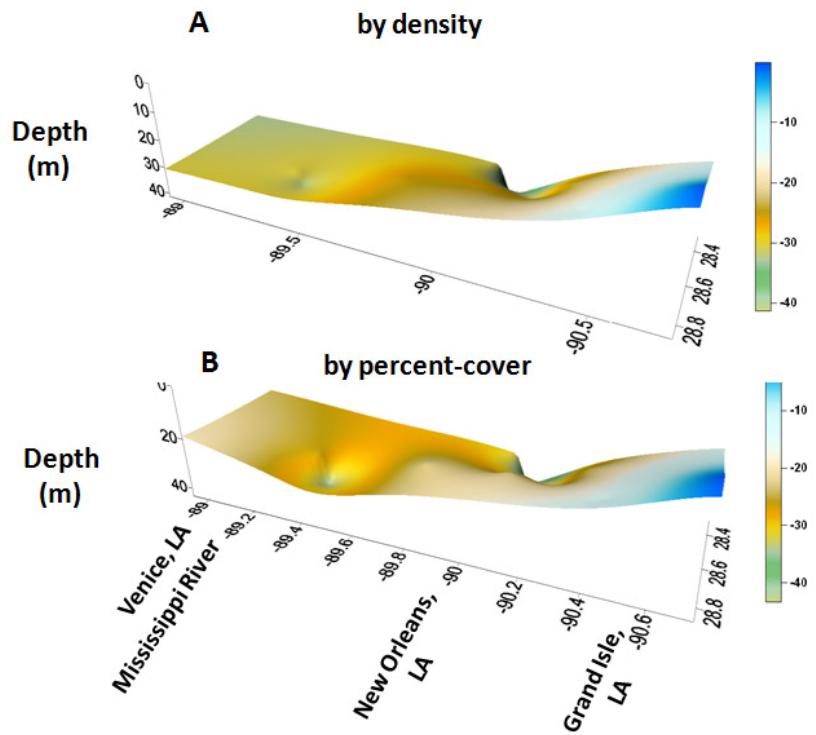


Figure 5. Geographic distribution of average depth of distribution for *Tubastraea coccinea* in the northern Gulf of Mexico. (A) Data based on colony density in no./10 m². (B) Data based on percent-cover.



for this reason afforded higher sample sizes and more sites for analysis. When all coral density data were pooled for *T. coccinea* over all platforms, this species exhibited quite a different pattern in depth distribution than *T. micranthus*, whether measured by colony density or percent-cover (Figure 2). Overall, effective maximum depth of *T. coccinea* on all of the study sites was 72–78 m, although a small number of colonies were observed at 90–96 m depth at one site (Figure 2). The general distribution was unimodal, with peak average colony density occurring at 30–36 m depth when measured by colony density and 18–24 m when measured by percent-cover. It should be noted that *T. coccinea* percent-cover reached levels of ~60% on this platform, clearly dominating the benthic community.

When one considers the overall geographic pattern of this distribution, it is clear that the shallowest average depths of distribution based upon colony density are found west of the Mississippi River mouth (Figure 3a). The deeper distributions are towards the east, south of the Mississippi River mouth, at the head of the Mississippi River Canyon. The pattern of average depths with respect to geographic position using percent-cover as the variable is almost identical to that calculated using coral density (Figure 3b).

When one examines the geographic pattern of these average depths based on average colony density in *Tubastraea coccinea*, it varies greatly from that of *T. micranthus*. Firstly it is relatively uniform across the study area (Figure 4a). Secondly, on the average (as might be expected from the previous analysis), it is much shallower than *T. micranthus*. There is a general trend for average depth of *T. coccinea* to be shallower in the west than in the east, in a manner similar to that of *T. micranthus*; but, by comparison, this trend is much more subtle. The trends, once again, are almost identical between patterns generated *via* colony density and percent-cover (Figure 4b).

Examining patterns of depth distribution on individual platforms based on coral density provides additional insight into the overall patterns. Platform No. GI-93C is believed to be the original platform of colonization of *T. micranthus*, as inferred from initial observations by SAP and earlier analyses of distribution and abundance (Sammarco et al. 2010). On this platform, the coral extended in distribution all the way to the bottom of the platform – 66 m (Figure 5a). It also exhibited a clear peak average density in relatively shallow water at 18–24 m depth. By comparison, on Platform No. MC-109A, this species

not only extended all the way to the bottom of the platform at 138 m depth, it was not observed until a depth of 66–72 m (Figure 5b). On this platform, the distribution was relatively uniform. On Platform GI-116A, *T. micranthus*' depth distribution was limited to mid-depths of 30–48 m (Figure 5c). GI-116A lies in close proximity to GI-93C, to the south.

When one considers the same platforms as above, but using percent-cover instead of colony density data for *T. micranthus*, once again, similar patterns are revealed. With respect to GI-93C, average percent-cover peaks at 18–24 m depth, but extends down to 54–60 m (Figure 6a). On MC-109A, the range of occurrence was once again 66–138 m depth, although percent-cover peaked at 102–108 m depth (Figure 6b). On GI-116A, the pattern of average percent-cover closely mimicked that generated by density data, concentrating at mid-depths, ranging from 30–48 m depth (Figure 6c), but being absent from both very shallow and very deep waters.

Tubastraea coccinea's depth distribution patterns on individual platforms was variable, but always remained within the shallower depths. On Platform G-116A, *T. coccinea* exhibited its highest average densities at relatively shallow depths - 12–18 m (Figure 7a). Another peak set of densities was observed at 36–42 m. This platform occurred in 78 m of water, and *T. coccinea*'s deepest colonies occurred at 60–66 m. Platform ST-185B occurred in waters only 48 m deep, and *T. coccinea*'s depth distribution extended all the way to the bottom there (Figure 7b). Its peak colony densities were found, however, to occur at 30–36 m depth. On nearby Platform ST-185A, the pattern of depth distribution and maximum depth of occurrence was similar in range and peak depth to ST-185B (Figure 7c).

The pattern of depth distribution of *T. coccinea* on Platform GI-116A based on percent-cover was broken. It was tri-modal in character, with percent-cover peaking at 12–18 m depth, 30–36 m, and 60–66 m (Figure 8a). In addition, colonies were observed down to the maximum depth of the platform at 72–28 m. On Platforms ST-185A&B, the patterns of depth distribution were similar with respect to peak percent cover (30–76 m), but the depth of this region was only 48–54 m (Figure 8b&c). *Tubastraea coccinea* again extended all the way to the bottom.

Tubastraea coccinea invaded the western Atlantic Ocean approximately 70 yrs ago (Cairns 2000). For this reason, its range extension has been broad, and its abundances have reached

Figure 6. Depth distribution of *Tubastraea micranthus* observed on individual platforms in the northern Gulf of Mexico. Data based on colony density in no./10 m². Heavy horizontal line represents depth of bottom. (A) *T. micranthus* depth distribution on Platform GI-93C. n = 125. Significantly different than a normal distribution ($p < 0.001$, Lilliefors test) and Poisson distribution ($p < 0.001$, Goodness of Fit test). $g_1 = 4.000$, $g_2 = 20.646$. (B) *T. micranthus* depth distribution on MC-109A. Significantly different than a normal distribution ($p < 0.001$, Lilliefors test) and Poisson distribution ($p < 0.001$, Goodness of Fit test). $g_1 = 2.358$, $g_2 = 5.095$. (C) Depth distribution of *T. micranthus* on GI-116A. Significantly different than a normal distribution ($p < 0.001$, Lilliefors test) and Poisson distribution ($p < 0.001$, Goodness of Fit test). $g_1 = 4.659$, $g_2 = 23.771$

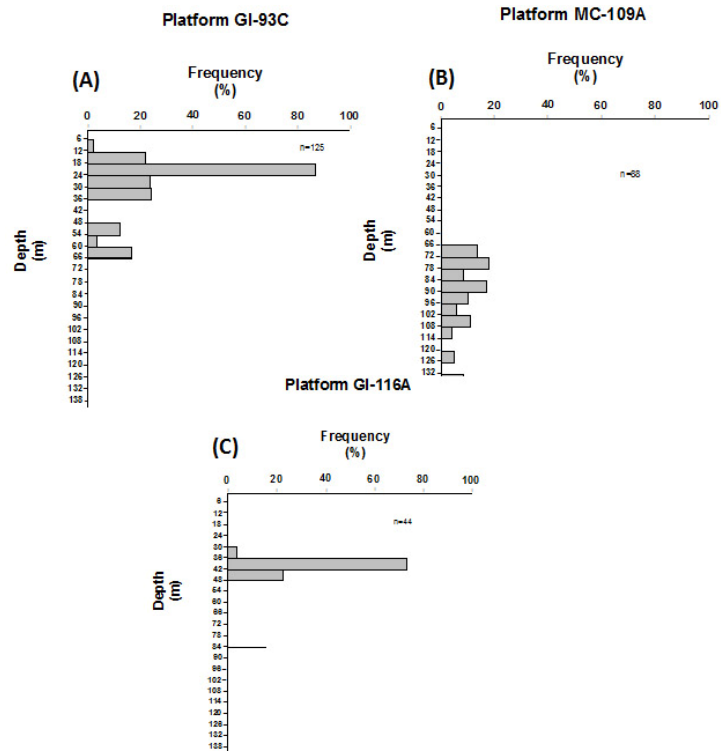


Figure 7. Depth distribution of *Tubastraea micranthus* observed on individual platforms in the northern Gulf of Mexico. Data based on percent-cover. Heavy horizontal line represents depth of bottom. (A) *T. micranthus* depth distribution on Platform GI-93C. n = 125. Significantly different than a normal distribution ($p < 0.001$, Lilliefors test) and Poisson distribution ($p < 0.001$, Goodness of Fit test). $g_1 = 3.973$, $g_2 = 16.836$. (B) *T. micranthus* depth distribution on MC-109A. Significantly different than a normal distribution ($p < 0.001$, Lilliefors test) and Poisson distribution ($p < 0.001$, Goodness of Fit test). $g_1 = 2.310$, $g_2 = 5.311$. (C) Depth distribution of *T. micranthus* on GI-116A. Significantly different than a normal distribution ($p < 0.001$, Lilliefors test) and Poisson distribution ($p < 0.001$, Goodness of Fit test). $g_1 = 4.403$, $g_2 = 19.336$.

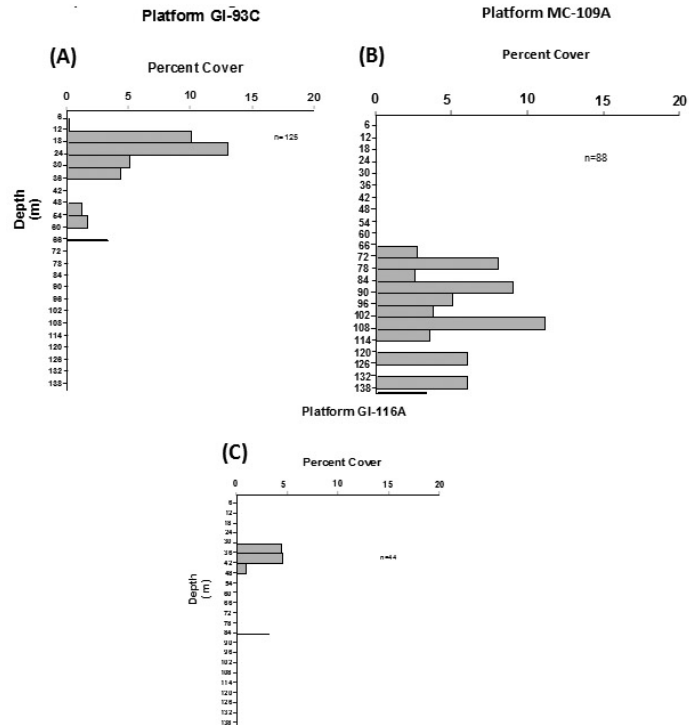


Figure 8. Depth distribution of *Tubastraea coccinea* observed on individual platforms in the northern Gulf of Mexico. Data based on colony density in no./10 m². Heavy horizontal line represents depth of bottom. (A) Depth distribution of *T. micranthus* on GI-116A. Significantly different than a normal distribution ($p < 0.001$, Lilliefors test) and Poisson distribution ($p < 0.001$, Goodness of Fit test). $g_1 = 4.659$, $g_2 = 23.771$. (B) *T. coccinea* depth distribution on Platform ST-185B. $n = 20$. Significantly different than a normal distribution ($p < 0.001$, Lilliefors test) but not significantly different from a Poisson distribution ($p > 0.05$, Goodness of Fit test). $g_1 = 3.639$, $g_2 = 14.634$. (C) *T. coccinea* depth distribution on ST-185A. Significantly different than a normal distribution ($p < 0.001$, Lilliefors test) and Poisson distribution ($p < 0.001$, Goodness of Fit test). $g_1 = 2.358$, $g_2 = 5.095$.

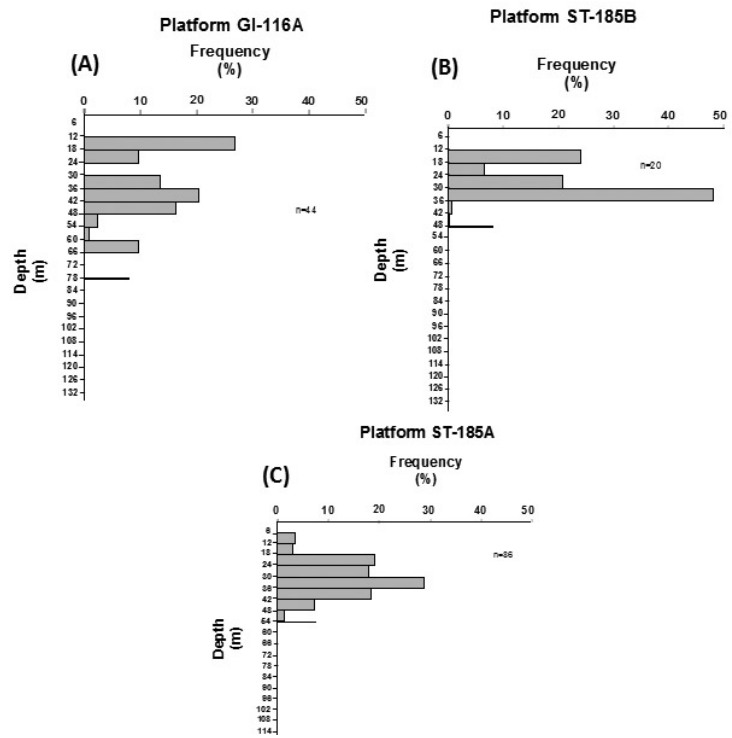


Figure 9. Depth distribution of *Tubastraea coccinea* observed on individual platforms in the northern Gulf of Mexico. Data based on percent-cover. Heavy horizontal line represents depth of bottom. (A) *T. coccinea* depth distribution on Platform GI-116A. $n = 44$. Not significantly different than a normal distribution ($p > 0.05$, Lilliefors test) but significantly different from a Poisson distribution ($p > 0.001$, Goodness of Fit test). $g_1 = 0.539$, $g_2 = -0.460$. (B) *T. micranthus* depth distribution on ST-185B. Significantly different than a normal distribution ($p < 0.01$, Lilliefors test) but not from a Poisson distribution ($p > 0.05$, Goodness of Fit test). $g_1 = 0.489$, $g_2 = -1.296$. (C) Depth distribution of *T. micranthus* on ST-185A. Significantly different than a normal distribution ($p < 0.001$, Lilliefors test) and Poisson distribution ($p < 0.001$, Goodness of Fit test). $g_1 = 0.827$, $g_2 = -0.750$.

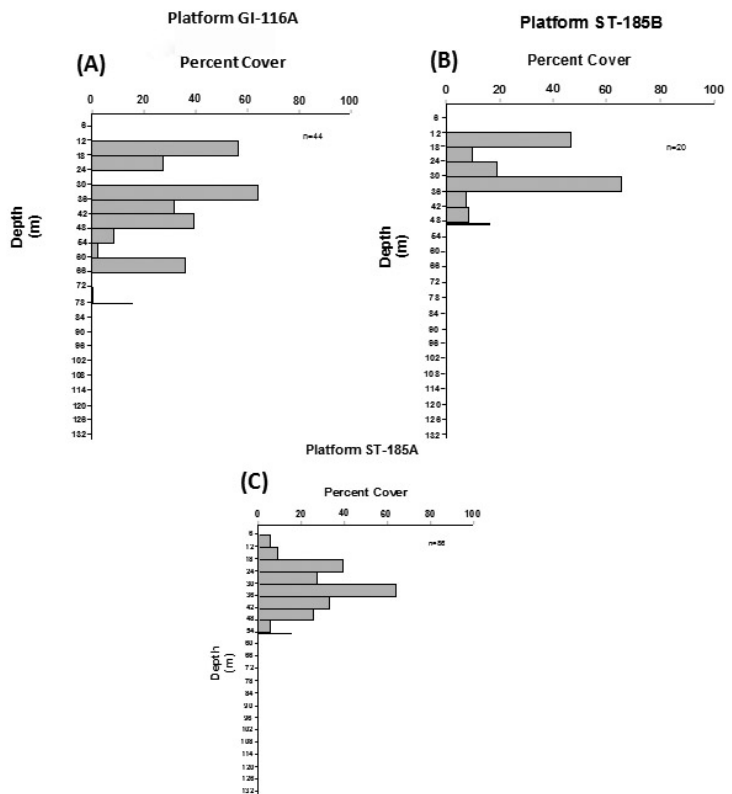
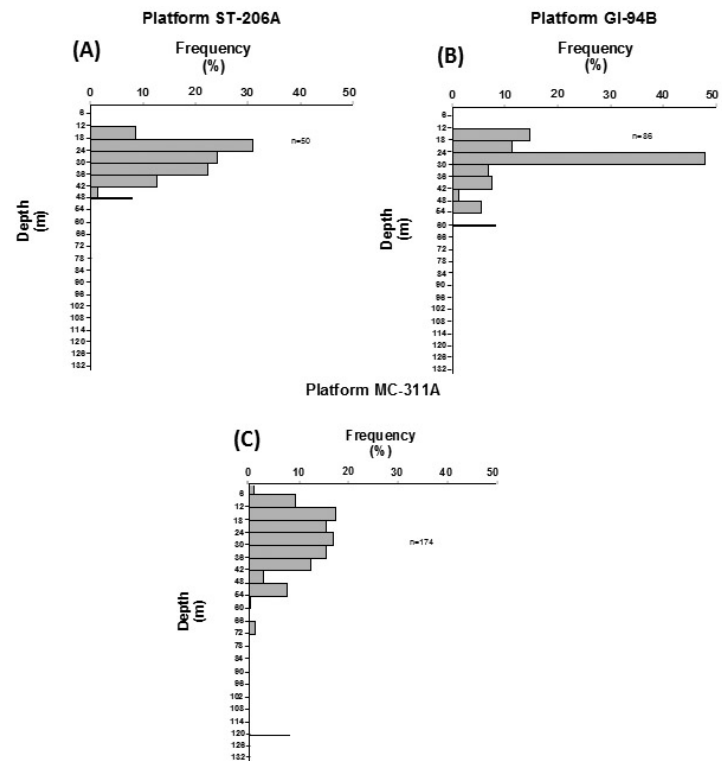


Figure 10. Depth distribution of *Tubastraea coccinea* observed on individual platforms in the northern Gulf of Mexico. Data based on density in no./10 m². Heavy horizontal line represents depth of bottom. (A) *T. coccinea* depth distribution on Platform ST-206A. n = 50. significantly different than a normal distribution ($p < 0.05$, Lilliefors test) and a Poisson distribution ($p < 0.01$, Goodness of Fit test). $g_1 = 0.591$, $g_2 = -0.254$. (B) Depth distribution of *T. coccinea* on GI-94B. Significantly different than a normal distribution ($p < 0.001$, Lilliefors test) and a Poisson distribution ($p < 0.001$, Goodness of Fit test). $g_1 = 2.837$, $g_2 = 14.899$. (C) *T. coccinea* depth distribution on MC-311A. Significantly different than a normal distribution ($p < 0.001$, Lilliefors test) and from a Poisson distribution ($p < 0.001$, Goodness of Fit test). $g_1 = 1.092$, $g_2 = 0.521$.



high levels, particularly on artificial reefs such as the platforms being surveyed here. These high densities of *T. coccinea* allowed us to analyze more platforms for depth distribution trends for the newer invasive *T. micranthus*.

On Platform ST-206A, an overall trend very similar to that observed on ST-185A&B was observed, except peak colony densities occurred at 18–24 m depth instead of 30–36 m (Figure 9a). The pattern was similar on GI-94B, with a higher peak in colony density at 24–30 m depth (Figure 9b). The pattern on Platform MC-311A was somewhat different. Firstly, the maximum depth of the platform was 120 m. The maximum depth of colonization and growth in *T. coccinea* was 66–72 m (Figure 9c). This underlines the fact that *T. coccinea* was distributed in relatively shallow water. Secondly, its depth distribution pattern was unimodal, almost following a normal distribution, with higher colony densities occurring over a wide depth range, covering 12–54 m.

Discussion

Perhaps one of the first, most important results to emerge from this study is the finding that

T. micranthus has the ability to readily reach a depth in its new environment of at least 138 m. This is more than three times deeper than its reported depth range in its native Indo-Pacific habitat - 40 m (Anon. 2013) to 50 m (Cairns 2013) depth, most likely surveyed via SCUBA. In addition, this species appears to survive and grow equally well in both shallow and deep water, but with an apparent preference for deeper water. *Tubastraea coccinea*, on the other hand, appeared to be restricted to shallower depths. It primarily ranged from 0–78 m depth, although one or two colonies were found at a maximum depth of 96–102 m. Even so, ~99% of the colonies were found in shallower depths. Thus, *T. coccinea* seems to have a narrower and shallower depth range than *T. micranthus*. With respect to *T. micranthus*, 138 m was only the depth of the deepest platform considered here. It is likely that *T. micranthus* is capable of colonizing substrate at deeper depths.

In addition, the geographic patterns of depth distribution for the two species varied greatly from each other. Firstly, *T. micranthus* exhibited its shallower depth distributions towards the west of the study area – in the primary plume of the Mississippi River. Its deepest distributions

were found at the head of the Mississippi Canyon. This region does receive meanders of the Mississippi River plume, but generally receives blue water from the Gulf of Mexico (Sturges and Lugo-Fernandez 2005). *Tubastraea coccinea*, on the other hand, was much shallower in its overall depth throughout the study region, but also tended to display a shallower average depth distribution in the west, like *T. micranthus*. This implies that *T. micranthus* may be limited in its depth distribution by hyposalinity, turbidity, sedimentation, or other river-associated discharge characteristics. It is unlikely that either species is limited by light, since both are azooxanthellate (Creed 2006; Cairns 2013). Temperature does not appear to play a role in limiting depth in *T. micranthus*, because a temperature differential may be expected to occur at these depths. One anomaly that emerged in both species was that the shallowest depth of distribution for *T. micranthus* occurred in the vicinity of GI-93C, while the deepest depth for *T. coccinea* was found in the same region. It is unlikely that *T. micranthus* tended to colonize deeper habitats because of lack of space availability in shallower water due to dominance by *T. coccinea*. Firstly, it was found in shallow water. Secondly, preliminary evidence suggests that *T. micranthus* is dominant over *T. coccinea* when involved with it in active competition for space (Sammarco et al. 2012b,c). The reason for this depth anomaly remains to be explained.

Analyses of Platforms GI-93C and MC-109A confirmed that *T. micranthus* will colonize substrate available to the deepest depth available, at least to a depth of 138 m, which was the maximum depth encountered in this study. MC-109A occurs within the Mississippi Canyon and receives blue water from the Gulf of Mexico. GI-93C, on the other hand, occurs in the western plume of the Mississippi River and receives turbid, sediment-laden, lower salinity water regularly as the plume meanders regularly over the site (Sturges and Lugo-Fernandez 2005). GI-116A's restriction of *T. micranthus* to intermediate depths, despite the availability of substratum in deeper waters, may be an artifact of small sample size.

An analysis of *T. coccinea* on six individual platforms, however, covering both shallow and deep sites, indicated that its depth distribution is clearly more limited than that of *T. micranthus*. *Tubastraea coccinea* occurred down to the maximum depth of the platforms while in shallow water, but it did not approach the maximum depth

of platforms in deeper water, as indicated by the distribution found on MC-311A. The details of these individual depth distributions once again illustrate that *T. micranthus* occupies a wider spatial niche than *T. coccinea* and can accommodate a broader set of environmental conditions, most likely temperature.

The fact that percent-cover data track the coral density data so closely in generating geographic patterns indicates that, for these two species, either variable may be used in quantitative calculations to estimate broad-scale patterns. On the other hand, there are significant differences in specific depth distribution patterns generated by these two variables. This is because density data primarily provide an estimate of colony counts and recruitment while percent-cover provides an estimate of asexual budding, colony growth, and success (or lack of such) in competition for space. The object of the sampling should be considered and matched with the technique prior to choosing one variable or the other as the basis for estimating depth distribution.

Implications of depth distributions for control or eradication

Whenever considering eradication of a new invasive species, one of the major factors which must be taken into consideration when assessing the potential efficacy of any such attempts is population accessibility (Clout and Veitch 2002b). Even if the primary spatial distribution of an organism is accessible to eradication efforts, if there is a reasonable portion of that distribution which is not accessible to such attempts to control or mitigate, the population could possibly still rebound from a mass mortality. It is possible to eradicate a population, particularly if small, from all parts of its new domain, but the probability of success decreases with decreasing accessibility.

In addition, in the marine environment, the cost of access increases greatly with increased depth. For example, the cost of eliminating an intertidal species is associated primarily with man-hours, not technology. The same would apply to snorkeling in shallow depths, although ease of access would decrease from the intertidal and the amount of man-hours required for the task would increase. In deeper waters, SCUBA would be required, dive time would be highly limited, and the expense of using divers would increase greatly over snorkeling. In still deeper waters, surface-supplied commercial divers

would have to be used, which are quite expensive. After that, ROVs and manned submersibles would have to be used to eliminate the organisms, being prohibitively expensive, not to mention highly limited in scope and effectiveness. Unfortunately, the situation faced here with *T. micranthus* is one where accessibility is highly limited. This is similar to the current situation of an excessively deep distribution of the lionfish *Pterois volitans* in the Gulf of Mexico (Hickerson, Nuttall, and Schmahl, unpubl. data; PWS, pers. obs.). The probability of being able to eliminate all colonies down to a depth of 138 m (and possibly beyond) on these platforms and other hard substratum is low, even over the relatively small geographic area where their populations currently reside.

A second major factor influencing attempts to control or eradicate an invasive marine species is multiple invasions through time. Such would thwart even the most effective eradication, for the exercise would have to be repeated through time to keep the population under control. As an example, it is believed that the Asian Tiger Mosquito, *Aedes japonicus japonicus*, known to be a disease vector, invaded the northeastern US multiple times via a variety of transport mechanisms (Fonseca 2001). *Tubastraea micranthus* is likely being transported via ballast water or ship's hulls from the Indo-Pacific, and if infected ships are continually frequenting the harbors of New Orleans or Port Fourchon, then this region could be repeatedly exposed to the planulae of this species. In this case, it would be better to attempt to control the carrier of the invasive than the invasive itself.

Another point to consider is whether control or eradication is called for. There has been debate as to whether invasion by *T. coccinea* has actually caused any damage or loss of native species in the western Atlantic. Unfortunately, no data are available on its impact, except for extensive cover and potential monopolization of benthic space; thus, this question remains open. Preliminary evidence, both field and laboratory, suggests, however, that *T. micranthus* is highly aggressive and capable of outcompeting local sessile epifauna for space (Sammarco et al. 2012b,c).

At this point, unless a concerted effort is made to eliminate *T. micranthus* from this area of the Gulf of Mexico in the near future, it is possible that the window for eradication may close and this new species could become common in the western Atlantic in decades to come.

Acknowledgements

We express our thanks to the many folks who assisted us in this study: LUMCON - C. Sevin, T. Widgeon, M. Wike (ROV pilot); ARACAR – J. Blitz & A. Campbell (ROV pilots); M/V Fling – B. Allen, K. Bush, K. Dies, M. McReynold, B. Oldham, M. Spurgeon, J. Tyler; National Aeronautics and Space Administration (NASA)/US Air Force – D. Perrenod; Others – M. Gaskill. We also extend our thanks to MMS/BOEM, US Department of Interior (Grant #M10AC20006) through the Louisiana State University Coastal Marine Institute (CMI) program for their financial support of the project. Thanks to L. Rouse and S. Welsh who directed that program. Our thanks also extends to the anonymous reviewers who offered valuable comments on the manuscript.

References

- Ackerman JD, Sim B, Nichols, SJ, Claudi R (1994) A review of the early life history of zebra mussels (*Dreissena polymorpha*): Comparisons with marine bivalves. *Canadian Journal of Zoology* 72: 1169–1179, <http://dx.doi.org/10.1139/z94-157>
- Albins MA, Hixon MA (2008) Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. *Marine Ecology Progress Series* 367: 233–238, <http://dx.doi.org/10.3354/meps07620>
- Anonymous (2013) Black sun coral – *Tubastraea micranthus*. Florent's guide to the tropical reefs. <http://reefguide.org/tubastraeamicranthus.html> (Accessed 2 August 2013)
- Bax N, Hayes K, Marshall A, Parry D, Thresher R (2002) Man-made marinas as sheltered islands for alien marine organisms: Establishment and eradication of an alien invasive marine species. In: Clout CR, Veitch MN (eds), Turning the tide: The eradication of invasive species, Proceedings of the International Conference on the Eradication of Island Invasives. International Union of the Conservation of Nature, Gland, Switzerland, Occasional Paper IUCN Species Survival Committee No. 27, p. 26–39
- Bax N, Williamson A, Aguero M, Gonzalez E, Geeves W (2003) Marine invasive alien species: A threat to global biodiversity. *Marine Policy* 27: 313–323, [http://dx.doi.org/10.1016/S0308-597X\(03\)00041-1](http://dx.doi.org/10.1016/S0308-597X(03)00041-1)
- Cairns SD (2000) Revision of the shallow-water azooxanthellate Scerlactinia of the western Atlantic. *Studies of the Natural History of the Caribbean Region* 75: 1–240
- Cairns S (2013) *Tubastraea micranthus* (Ehrenberg 1834). Accessed through: World Register of Marine Species (WoRMS) at <http://www.marinespecies.org/aphia.php?p=taxdetails&id=291255> (Accessed 2 August 2013)
- Cairns SD, Zibrowius H (1997) Cnidaria Anthozoa: Azooxanthellate Scleractinia from the Philippine and Indonesian regions. *Memoires du Museum National d'Histoire Naturelle* 172: 27–243
- Clout CR, Veitch MN (eds) (2002a) Turning the tide: The eradication of invasive species. Proc. Int. Conf. Eradication of Island Invasives. International Union of the Conservation of Nature, Gland, Switzerland, Occasional Paper IUCN Species Survival Committee No. 27, 414 pp
- Clout CR, Veitch MN (2002b) Turning the tide: The eradication of invasive species (article), In: Clout CR, Veitch MN (eds), Turning the tide: The eradication of invasive species, Proc. Int. Conf. Eradication of Island Invasives. International Union of the Conservation of Nature, Gland, Switzerland, Occas. Paper IUCN Species Survival Committee No. 27, p. 1–3

- Creed J (2006) Two invasive alien azooxanthellate corals, *Tubastraea coccinea* and *Tubastraea tagusensis*, dominate the native zooxanthellate *Mussismilia hispida* in Brazil. *Coral Reefs* 25: 350, <http://dx.doi.org/10.1007/s00338-006-0105-x>
- de Paula AF, Creed JC (2004) Two species of the coral *Tubastraea* (Cnidaria, Scleractinia) in Brazil: A case of accidental introduction. *Bulletin of Marine Science* 74: 175–183
- Fenner D (1999) New observations on the stony coral (Scleractinia, Milleporidae, and Stylasteridae) species of Belize (Central America) and Cozumel (Mexico). *Bulletin of Marine Science* 64: 143–154
- Fenner D, Banks K (2004) Orange cup coral *Tubastraea coccinea* invades Florida and the Flower Garden Banks, northwestern Gulf of Mexico. *Coral Reefs* 23: 505–507
- Fitzhugh K, Rouse GW (1999) A remarkable new genus and species of fan worm (Polychaeta: Sabellidae: Sabellinae) associated with marine gastropods. *Invertebrate Biology* 118: 357–390, <http://dx.doi.org/10.2307/3227007>
- Fonseca DM, Campbell S, Crans WJ, Mogi M, Miyagi I, Toma T, Bullians M, Andreadis TG, Berry RL, Pagac B, Saradelis MR, Wilkinson RC (2001) *Aedes (Finlaya) japonicas* (Diptera: Culicidae), a newly recognized mosquito in the United States: Analysis of genetic variation in the United States and putative source populations. *Journal of Medical Entomology* 38: 135–146, <http://dx.doi.org/10.1603/0022-2585-38.2.135>
- Glynn PW, Colley SB, Mate JL, Cortes J, Guzman HM, Bailey RL, Feingold JS, Enochs IC (2008a) Reproductive ecology of the azooxanthellate coral *Tubastraea coccinea* in the equatorial eastern Pacific: Part V. Dendrophylliidae. *Marine Biology* 153: 529–544, <http://dx.doi.org/10.1007/s00227-007-0827-5>
- Glynn PW, Colley SB, Mate JL, Cortes J, Guzman HM, Bailey RL, Feingold JS, Enochs IC (2008b) Reproductive ecology of the azooxanthellate coral *Tubastraea coccinea* in the equatorial eastern Pacific: Part V. Dendrophylliidae (erratum). *Marine Biology* 154: 199, <http://dx.doi.org/10.1007/s00227-008-0926-y>
- Golden Software (2002) Surfer 8 Users Guide, Contouring and 3D surface mapping for scientists and engineers. Golden Software, Inc., Golden, CO, USA, 640 pp
- Halford A, Cheal AJ, Ryan D, Williams DMcB (2004) Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef. *Ecology* 85: 1892–1905, <http://dx.doi.org/10.1890/03-4017>
- Humann P, DeLoach N (2002) Reef coral identification: Florida, Caribbean, Bahamas, including marine plants. New World Publs., Jacksonville, Florida, USA, 278+ pp
- Kleeman K (1992) Coral communities and coral-bivalve associations in the northern Red Sea at Safaga, Egypt. *Facies* 26: 1–10, <http://dx.doi.org/10.1007/BF02539790>
- Osman R, Shirley T (eds) (2007) The gulf of Mexico and Caribbean marine invasive species workshop: Proceedings and final report. Harte Res Inst, Texas A&M University – Corpus Christi, Texas, USA, 47 pp
- Rohlf FJ, Slice DE (1996) BIOMStat for Windows: Statistical software for biologists. V. 3.2. Exeter Software, Setauket, New York, USA, 62 pp
- Sakai AK, Allendorf FW, Holt JD, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neill P, Parker IM, Thompson JN, Weller SG (2001) The population biology of invasive species. *Annual Review of Ecology and Systematics* 32: 305–332, <http://dx.doi.org/10.1146/annurev.ecolsys.32.081501.114037>
- Sammarco PW, Atchison AD, Boland GS (2004) Expansion of coral communities within the northern Gulf of Mexico via offshore oil and gas platforms. *Marine Ecology Progress Series* 280: 129–143, <http://dx.doi.org/10.3354/meps280129>
- Sammarco PW, Porter SA, Cairns SD (2010) New invasive coral species for the Atlantic Ocean: *Tubastraea micranthus* (Cairns and Zibrowius 1997) (Colenterata, Anthozoa, Scleractinia): A potential major threat? *Aquatic Invasions* 5: 131–140, <http://dx.doi.org/10.3391/ai.2010.5.2.02>
- Sammarco PW, Atchison AD, Boland GS, Sinclair J, Lirette A (2012a) Geographic expansion of hermatypic and ahermatypic corals in the Gulf of Mexico, and implications for dispersal and recruitment. *Journal of Experimental Marine Biology and Ecology* 436–437: 36–49, <http://dx.doi.org/10.1016/j.jembe.2012.08.009>
- Sammarco PW, Porter SA, Genazzio M, Sinclair J (2012b) A new invasive coral – *Tubastraea micranthus* – in the Western Atlantic: A potential threat. Australian Marine Science Association – New Zealand Marine Science Society Joint Conference, Hobart, Tasmania, Australia, Abstract, p 169
- Sammarco PW, Porter SA, Genazzio M, Sinclair J (2012c) Successful invasion of *Tubastraea micranthus* into the western Atlantic. Abstracts of the International Coral Reef Symposium, Cairns, Qld., Australia, July 2012, Abstract
- Sammarco PW, Porter SA, Sinclair J, Genazzio M (in press) Population expansion of a new invasive coral species – *Tubastraea micranthus* – in the northern Gulf of Mexico. *Marine Ecology Progress Series*
- Shearer TL (2008) Range expansion of an introduced coral: Investigating the source and ecological impact of the invasion. 2008 Ocean Sciences Meeting: From the watershed to the global ocean, Orlando, Florida, USA, 2–7 Mar 2008 (Abstract)
- Silva AG, Lima RP, Gomes AN, Fleury BG, Creed JC (2011) Expansion of the invasive corals *Tubastraea coccinea* and *Tubastraea tagusensis* into the Tamoios Ecological Station Marine Protected Area, Brazil. *Aquatic Invasions* 6: S105–S110, <http://dx.doi.org/10.3391/ai.2011.6.S1.024>
- Scheer G, Obrist K (1986) *Distichida nitida* Verrill (Cnidaria, Hydrozoa) from the Maldives, a new record from the Indian Ocean. *Coral Reefs* 5: 151–154, <http://dx.doi.org/10.1007/BF00298181>
- Schuhmacher H, Zibrowius H (1985) What is hermatypic? A re-definition of ecological groups in corals and other organisms. *Coral Reefs* 4: 1–9, <http://dx.doi.org/10.1007/BF00302198>
- Sokal RR, Rohlf FJ (1981) Biometry – The principles and practice of statistics in biological Research. WH Freeman and Co, San Francisco, California, USA, 859 pp
- Sturges W, Lugo-Fernandez A (eds) (2005) Circulation in the Gulf of Mexico: Observations and models. American Geophysical Union, Monograph No 161, 360 pp + CD Appendix, <http://dx.doi.org/10.1029/GM161>
- Veron JEN, Pichon M (1980) Scleractinia of Eastern Australia Part III. Families - Fungiidae, Oculinidae, Memlinidae, Mussidae, Pectinidae, Caryophylliidae, Dendrophylliidae. Australian Institute of Marine Science, Townsville, Qld, Australia, Monogr Ser
- Williams DMcB (1982) Patterns in the distribution of fish communities across the central Great Barrier Reef. *Coral Reefs* 1: 35–43, <http://dx.doi.org/10.1007/BF00286538>