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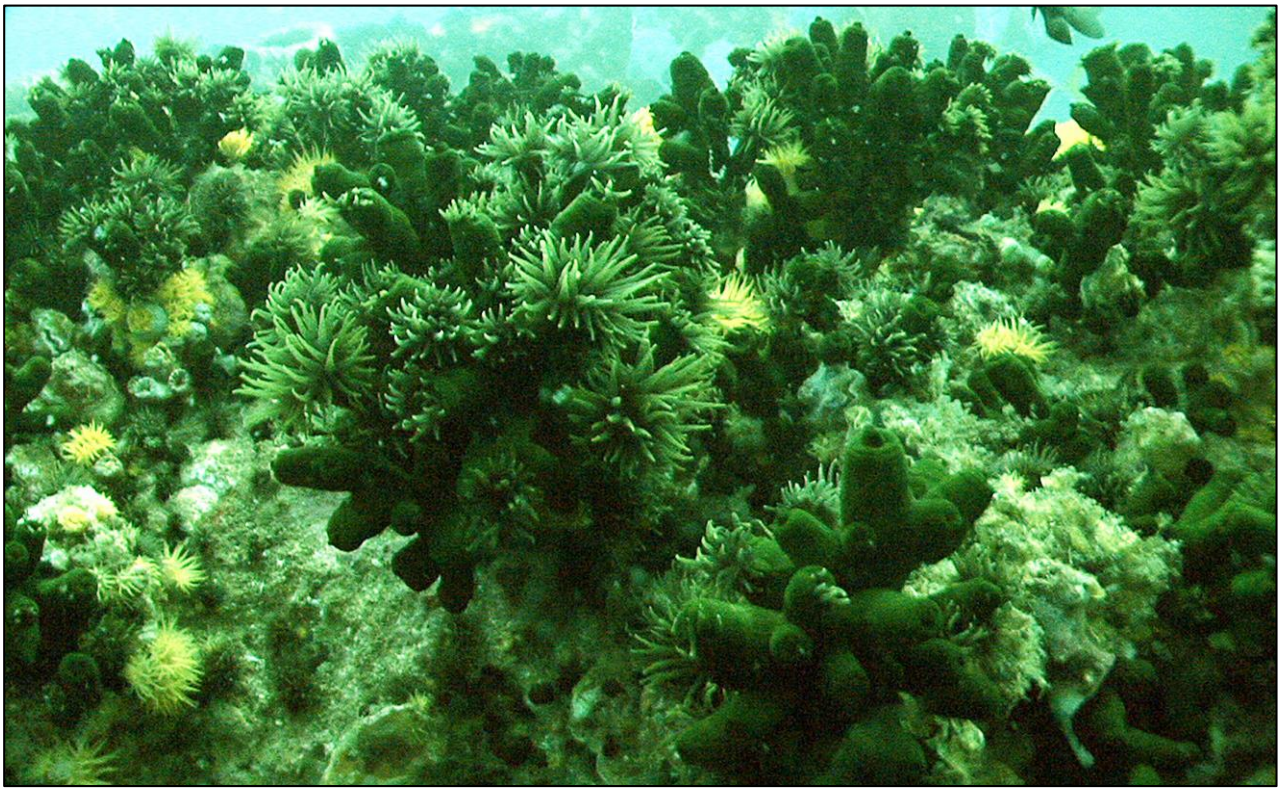
# New Invasive Species Colonizing Energy Platforms in the Northern Gulf of Mexico



**U.S. Department of the Interior**
**Bureau of Ocean Energy Management**
**Gulf of Mexico OCS Region**

**Cooperative Agreement**
**Coastal Marine Institute**
**Louisiana State University**

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# New Invasive Species Colonizing Energy Platforms in the Northern Gulf of Mexico

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## ABOUT THE COVER

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# EXECUTIVE SUMMARY

## POPULATION EXPANSION

A new Indo-Pacific scleractinian coral has invaded the northern Gulf of Mexico (GOM): *Tubastraea micranthus*. Initially, it was observed on one energy platform (GI-93C) near the Mississippi River. We determined whether its populations were spreading throughout the region and whether there was evidence of rapid population expansion. We also compared population density data with that of *Tubastraea coccinea*, a congeneric species that had successfully invaded the western Atlantic Ocean 70 years earlier. Fourteen energy platforms were assessed down to 138 m depth (max.) by a remotely operated vehicle (ROV) using digital video. Colony densities in no./$m^2$ were determined for both species, and colony size for *T. micranthus*. Data were analyzed by platform and also with respect to geographic distribution. *T. micranthus* densities were highest on GI-93C and on GI-116A, southwest (SW) of the mouth of the Mississippi River, and were significantly higher than those on most other platforms. Densities declined radially from there. Mean colony size was highest on MC-311A, at the head of the Mississippi Canyon, suggesting this to be the epicenter of colonization. This site is characterized by blue water instead of the turbid, lower salinity water of other sites. This suggests that *T. micranthus* may grow best under blue-water conditions. Size frequency distributions of colonies for *T. micranthus* were skewed towards the bin size of 1–200 $cm^2$, sometimes reaching >90% of the population, which indicates that populations are in an explosive growth phase. *T. coccinea* densities were high (range: ~50–300/$m^2$). Its populations were also centered SW of the Mississippi River.

## DEPTH DISTRIBUTION

In the marine environment, depth limits accessibility. We assessed the depth distribution of two Indo-Pacific invasive coral species–*T. micranthus* and *T. coccinea*–on 14 energy platforms using ROVs. Pooled data indicated that *T. micranthus* extends to 138 m and probably deeper and *T. coccinea* is generally limited to $\leq$ 78 m. Average depths for *T. micranthus* were shallower west of the Mississippi River, in its plume, and deeper towards the east. *T. coccinea* exhibited a similar geographic depth-distribution pattern, but shallower and more subtle. Broad geographic patterns were similar, whether using density or percent-cover data as the variable for analysis. When considering individual platforms, we found that *T. micranthus* often reached the bottom and sometimes occurred at depths $\geq$66 m. *T. coccinea* were limited to shallow water on all platforms. Detailed depth distribution patterns varied significantly between analyses using density and percent-cover as the variable for analysis; density probably indicated colonization rates, and percent-cover colony growth. Depth limitation by *T. coccinea* may be associated with food availability, rather than light, because it is azooxanthellate.

## COMPETITION FOR SPACE

Invasion success by an alien species into a new environment depends not only on the rate of reproduction, growth rates, mortality rates, or the physical characteristics of the environment; it also depends on the ability to successfully compete with native species for resources. For sessile, epibenthic marine species, one critical resource is space. We examined the competitive abilities of two invasive Indo-Pacific coral species, *T. micranthus* and *T. coccinea*, on 14 artificial reefs (offshore energy platforms) in the northern Gulf of Mexico, south of the Mississippi River. Both species were involved widely in competition for space. Underwater videos were taken using an ROV down to 183 m depth on the platforms, and still-capture photos were analyzed from them. *T. micranthus* was competitively superior ($\leq$90%) to all competitor species pooled, although frequency of competitive wins varied significantly between platforms. Success was highest in the NE part of the study area, characterized by blue water, and lowest in the SW area near the river plume, indicating that it may be better adapted to blue-water conditions. *T. coccinea* was also competitively superior to all competitors pooled, with little variability between platform populations and little spatial variation. The two congeneric coral species, when in competition with each other, were equal in their abilities for competitive success, although *T. coccinea* had a slight competitive advantage. *T. coccinea*'s abilities appeared to peak in the SW part of the study area, suggesting that it may be better adapted to surviving in a more turbid, nutrient-rich environment. *T. coccinea* was found to be competitively superior to almost all its competitors, including the encrusting sponge *Xestospongia* sp. (with the commensal *Parazoanthus catenularis*), the light grey encrusting sponge *Dictyonella finicularis*, the black encrusting sponge *Xestopongia carbonaria*, the brown encrusting sponge *Mycale carmigropila*, and the red encrusting sponge *Phorbas amaranthus*. Both *T. micranthus* and *T. coccinea* are formidable competitors for space in the northern Gulf of Mexico.

# 1. INTRODUCTION

## 1.1. POPULATION EXPANSION

### 1.1.1. Species invasions in the marine environment

Species introductions can have major impacts on ecosystems (Roberts and Pullin, 2008). This is particularly so in the marine environment because of the ease with which reproductive propagules can disperse and colonize nearby habitats once they have established a new population (Griffiths, 1991; Johnson and Carlton, 1996; Wonham et al., 2000). Examples include marine algae (Chapman et al., 2006), such as *Codium fragile*, a Japanese cholorophyte apparently introduced through the ballast water of ships (Trowbridge, 1998; Pederson, 2000; Williams, 2007). This species is now common throughout much of the western Atlantic (Chapman, 1999). Another more recent example is the Indo-Pacific volitan lionfish (*Pterois volitans*). This species was apparently released into western the waters of Florida ~20 years ago (Whitfield et al., 2002; Hamner et al., 2007) and is now distributed in US Atlantic waters off the state of New York and south through the Caribbean and South America (Albins and Hixon, 2011).

Vectors for transport of invasive marine or freshwater species (Kerr et al., 2005) include the ballast water of barges or ships (Chesapeake Bay Commission, 1995; ICES, 2002), the hulls of the same (Minchin and Gollasch, 2003), transfer through towing of energy platforms to new sites (Hicks and Tunnell, 1993), the accidental release of exotic species from mariculture operations (Sapota, 2004), and the deliberate release of exotics by aquarium hobbyists (Weidema, 2000; Christmas et al., 2001; Hindar et al., 2006).

Recently, there has been concern about species occurring that have invaded the Gulf of Mexico (GOM; Osman and Shirley, 2007). This includes the Australian scyphozoan *Phyllorhiza*, which colonized the region within the past 15 years (Perry and Graham, 2000) and has the ability to suppress seasonal zooplankton populations (Graham et al., 2003; Graham and Bayha, 2008) important for commercial fisheries. Another is the zebra mussel, *Dreissena polymorpha*, which was originally introduced to the Great Lakes in the mid-1980s and has since spread south through North American waterways (Baker et al., 2006; Dextrase and Mandrak, 2006; Ram and Pallazola, 2008) all the way to the mouth of the Mississippi River (Anon., 1997; Liffman, 1997).

### 1.1.2. Coral species invasions in the Atlantic

There have been very few successful invasions of corals to the Atlantic. *Fungia scutaria* was accidentally introduced to Discovery Bay, Jamaica, W.I. (Judith C. Lang, pers. comm., 1972; Paul W. Sammarco, pers. obs., 1973; Lajeunesse et al., 2005). The Indo-Pacific *T. coccinea* (Cairns and Zibrowius, 1997) species was first introduced into Puerto Rico in 1943 and by 1948 had spread to Curacao, Netherlands Antilles (Cairns, 2000). By the late 1990s and mid 2000s, the species had spread to Belize and Mexico (Fenner, 1999), Venezuela, northern Gulf of Mexico, and the Florida Keys (Fenner, 2001; Fenner and Banks, 2004; Sammarco et al., 2004; Shearer, 2008), Brazil (Figueira de Paula and Creed, 2004), Colombia, Panama, the Bahamas,

and throughout the Lesser and Greater Antilles (Cairns, 2000; Humann and Deloach, 2002). *T. coccinea* is also abundant in the Gulf of Mexico on artificial substrata (Sammarco et al. 2004, 2007a, b, 2012a). It is present on energy platforms in abundances of hundreds of thousands of colonies per platform, with average colony densities reaching from $28/m^2$ to $300/m^2$. It also occurs on deep banks in the northern Gulf of Mexico but in lower abundances (Schmahl, 2003; Hickerson et al., 2006; Schmahl and Hickerson, 2006). It may also be found as a cryptic species on the coral reefs of the Flower Garden Banks (Fenner and Banks, 2004; Hickerson et al., 2008).

From 2000 to 2010, Sammarco et al. (2004, 2007a,b, 2008, 2012a) and S.A. Porter conducted independent surveys using SCUBA and a remotely operated vehicle (ROV) on the distribution and abundance of scleractinian corals on 81 platforms; in both shallow and deep water throughout the northern Gulf of Mexico. Surveys stretched from the waters off Corpus Christi, Texas to those off Mobile, Alabama. In his surveys, Porter found a new invasive species for the Gulf of Mexico, the Indo-Pacific species *T. micranthus*; (Cairns and Zibrowius 1997) a congener of *T. coccinea* (Sammarco et al., 2010). It was observed on a single platform; GI-93-C (28º32.96'N, 90º40.11'W; Fig. 1). This was near the crossing of two major safety fairways or shipping channels southwest of the Port of New Orleans, Louisiana, near the mouth of the Mississippi River and Port Fourchon, Louisiana.

After a population of a new invasive species becomes established, its spread can be rapid and broad, greatly confounding any attempt to control or eradicate it (Elton, 2000). Examples include the invasion of the fire ant (*Solenopsis invicta*) into the US (Buhs, 2004). It was accidentally introduced into Mobile, Alabama during the 1940s and is now distributed around the margins of the 48 continental states in the US from the state of Washington to New Jersey, extending approximately 800 km inland. Another example is the nutria (*Myocastor coypus*), a South American coastal herbivore, 20 individuals of which were introduced into Avery Island, Louisiana during the 1930s. Its populations are now distributed from Delaware to Texas and reach to inland mid-eastern and northwest states.

*T. coccinea* exhibited a similar broad range extension since it was introduced in the 1940s. It is not yet known whether *T. micranthus* exhibits the same population growth characteristics as its congener. *T. coccinea* exhibits asexual reproduction using budding, simple colony growth, and asexual planula production (Ayre and Resing, 1986; Shearer, 2008) and runner production (Pagad, 2007). It also uses sexual reproduction, producing gametes all year-round, even in the smallest colonies (2–10 polyps; Glynn et al., 2008a,b). The planular development period is six weeks, and the planulae settle and metamorphose within three days. Planular release occurs from March through July and it is considered to be highly fecund (Glynn et al., 2008a, b). Its larval dispersal capabilities are formidable (Sammarco, 2012b). If the reproductive and dispersal capabilities of *T. micranthus* are similar to those of *T. coccinea*, the former could reach similarly high abundances in the western Atlantic (Sammarco et al., 2004; Shearer, 2008).

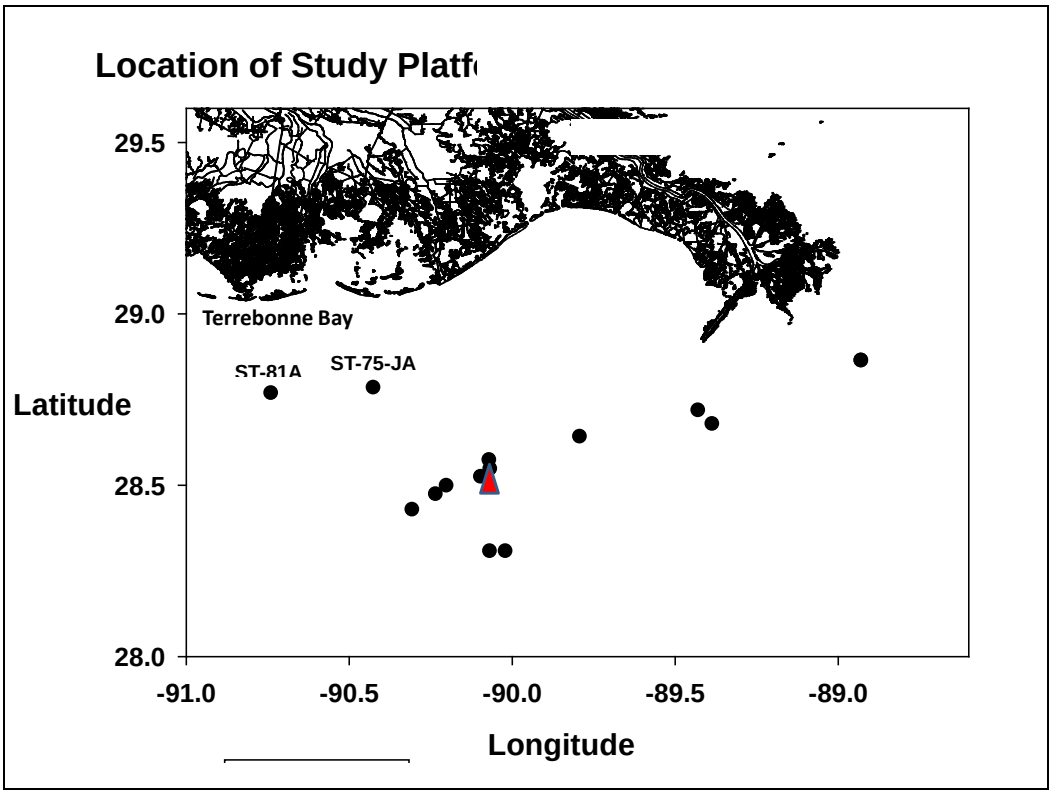



Figure 1. Map of the north-central Gulf of Mexico, showing locations of the 14 offshore energy platforms studied.
Platform GI-93-C (triangle) represents the site of first sighting of *T. micranthus* (Sammarco et al., 2010). MC-311A is suggested as the likely epicenter of colonization.

### 1.1.3. Objectives

The objectives of this part of this study were to quantify the abundance of *T. micranthus* on the initial site of observation (Platform GI-93-C) and to determine possible expansion, including degree, direction, and environment of expansion. This was accomplished by conducting surveys on GI-93-C and 13 other platforms in the vicinity of GI-93-C, extending from near the surface to the bottom of the platforms,

## 1.2. DEPTH DISTRIBUTION

### 1.2.1. Invasion of *Tubastraea* spp. into the western Atlantic Ocean

*T. micranthus* (Ehrenberg, 1834; Cairns and Zibrowius, 1997) is an ahermatypic scerlactinian 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 and Pichon, 1980), and elsewhere. It is a member of the Dendrophyllidae and is azooxanthellate (Schuhmacher and Zibrowius, 1985). It was estimated to have colonized the northern GOM around 2005 or earlier. It was first reported in 2010 (Sammarco et al., 2010), and has since been expanding its populations to other platforms in that region (Sammarco et al., 2014).

As an invasive coral species, *T. micranthus* is preceded by a congeneric species: *T. coccinea*. 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., 2014).

### 1.2.2. Depth distribution

The question arises as to whether this species is potentially harmful to native species and can disrupt native populations and community structure (Clout and Veitch, 2002a). This is a marine invasion, and many marine species possess swimming larvae dispersed by currents and often spend varying periods of time in the water column before 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*; Albins and Hixon, 2008; also see Clout and Veitch, 2002b). *T. coccinea* is highly fecund and is known to reproduce year-round (Glynn et al., 2008 a, b).

In the marine environment, accessibility is partially defined by depth and the new depth range of the target organism (Bax et al., 2002). Different depths may be reached by different techniques, and these techniques grow rapidly more expensive (and risky) with increasing depth.

### 1.2.3. Objectives

In this part of the study, we assessed the depth-distribution of *T. micranthus* on a set of energy platforms in the northern GOM, near the mouth of the Mississippi River. The objectives of the study were: 1) to determine the depth distribution on the platform of first observation; 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 an ROV.

## 1.3. COMPETITION FOR SPACE

### 1.3.1. Invasive species, the marine environment, and *Tubastraea micranthus*

Invasive species have long been regarded as problematic for the communities they have colonized (Secord, 2003). Data about the impacts of invasive species are disparate and, in some cases, equivocal (Gurevitch and Padilla, 2004). In some cases, they have displaced native species entirely (Mooney and Cleland, 2001). In others, they have become dominant in the community (Belote et al., 2003). In still others, they have adapted to their new environs, becoming an integral part of the community without causing local extinction or major changes to the community (Preston et al., 2012).

Over the past 70 years, there have been several invasions of coral species to the western Atlantic. A minor one was that of *Fungia scutaria* (Judith C. Lang, pers. comm., 1972; Paul W. Sammarco, pers. obs., 1973; Lajeunesse et al., 2005,), which was accidentally introduced to northern Jamaican waters in Discovery Bay. *Fungia* is a vagile Indo-Pacific fungiid coral and

lives primarily on soft-bottom (Russell-Hunter, 1968). It has not yet been reported to have any major effect on the benthic community and appears to have integrated well into the community, having invaded what was probably an open niche in its Caribbean soft-bottom environment (see Alamaru et al., 2009 for description of unique feeding habits). A second suite of coral species has also invaded the western Atlantic, all congeners of the genus *Tubastraea*. The Indo-Pacific species *T. coccinea* was first recorded in Puerto Rico during the 1940s, most likely on the hull of a ship going through the Panama Canal (Cairns, 2000). Its geographic range expansion throughout the tropical and sub-tropical western Atlantic required 60–70 yrs. More recently, *T. tagusensis* and *T. coccinea* were first observed to occur in the Tamoios Ecological Station Marine Protected Area (MPA) in Brazilian waters in 2011, with rapidly expanding populations (Silva et al., 2011).

We recently reported that populations of *T. micranthus* have invaded an area south of the Mississippi River mouth (Sammarco et al., 2010), colonizing offshore energy platforms in this region. They are also rapidly spreading throughout this region (Sammarco et al., 2014) and can occur to depths below the known depth-distribution of *T. coccinea* (Sammarco et al., 2012c).

### 1.3.2. The importance of competition for space

Population growth rates, rate of range expansion, and broad depth distributions are not the only characters that define potential success of a biological aquatic invasion (Griffiths, 1991; Johnson and Carlton, 1996; Wonham et al., 2000). Nor are rates of colony growth, reproduction, or mortality (MacArthur and Wilson, 1967). Certainly, local environmental variables will help determine the ability of a new foreign species to survive there including temperature and salinity (Dassuncao, 2009); nutrient concentrations (Alino et al., 1992, Engelhardt, 2011); and turbidity, sedimentation, and light (Thomsen and McGlathery, 2007); not to mention potential exposure to native diseases. Space availability can also be a factor of influence. Many factors contribute to the success or failure of an introduction. One of the primary factors influencing invasion success is the ability of the invading species to out-compete native species for local resources (Callaway and Aschehoug, 2000; Mangla et al., 2011; Mooney and Cleland, 2001). In the case of a benthic or demersal species, and particularly for sessile, epibenthic species, this means competition for space (Stachowicz et al., 2002; Sorte et al., 2010; McIntosh et al. 2006), which is critical to survival. If a species cannot compete successfully for space, it will not succeed in its invasion, despite high potential colony growth rates, reproduction rates, larval dispersal rates, etc. (MacArthur and Wilson, 1967; MacArthur, 1972).

Sessile epibenthic fauna use many mechanisms to compete for space. One is the chemical inhibition of one organism by another, or allelopathy, which has been demonstrated in numerous terrestrial plants (Rice, 1984; Qasem and Foy, 2001), Indo-Pacific alcyonacean soft corals on the Great Barrier Reef (Sammarco et al., 1983; Coll et al., 1990, 1992; Sammarco and Coll, 1992; Maida et al., 2001; Fleury et al., 2004), and between corals and algae (e.g., Ritson-Williams et al., 2013). Another is direct overgrowth of one species over another (Jackson and Buss, 1975; Jackson, 1977), as in *Millepora alcicornis* overgrowing *Gorgonia ventalina* (Wahle, 1980). Another is biological disturbance, for example, using currents to divert food away from another neighboring organism, as occurs between bryozoans, sponges, and other organisms (Buss, 1979; Best and Thorpe, 1986). One of the most effective means that marine organisms have of

expanding their territory, however, is extracoelenteric digestion (Lang, 1971, 1973; Sheppard 1979) or the development of sweeper tentacles (Richardson et al. 1979). This is a mechanism used by some scleractinian corals to defend and acquire space when dealing with other sessile epibenthic fauna, particularly other scleractinian corals. Mesenterial filaments are extruded from the gut of the coral, and extend some distance to touch a neighbor. Batteries of nematocysts housed in the filaments are discharged on the neighbor, resulting in death of that portion of the colony, leaving space for colony growth.

### 1.3.3. The importance of differences between Indo-Pacific and Atlantic species: comparative geological and evolutionary histories

The geographic origin of an invading species may also have an influence on the probability of success of invasion. This is particularly true when considering different oceans of origin, i.e., the Atlantic compared with the Pacific. Evidence suggests that marine species from the western Indo-Pacific are better adapted with respect to predator defense than their Atlantic counterparts (Vermeij, 1978). This is a function of the geological and evolutionary history and the differential extent to which the two regions have remained undisturbed (Stanley 1979, 1981, 1984, 1985, 1986; Sammarco and Coll, 1992). Palaentological data suggest that the western Pacific is an older, more stable, and less disturbed system, compared to the Atlantic (Kuhlmann, 1985). The Atlantic has experienced several major extinctions that the Pacific has not: one in the early Miocene, and one more recently in the late Pliocene and early Pleistocene, at the onset of the last glaciation. These extinctions were due primarily to major cooling events. Each represented a genetic bottleneck for the species living at those times and mass extinctions. This in turn resulted in a lower species diversity in the Atlantic, with species having broader niches and fewer specific mechanisms to deal with their prey and their neighbors in competition. Co-evolution of predator and prey, and among competitors, has not evolved to the level required for survival in the Pacific.

Phylogenetic radiation in the Indo-Pacific species was permitted to continue at a more constant rate than in the Atlantic, in the absence of these perturbations. Species diversity grew, in congruence with the stability-time hypothesis (Klopfer, 1959; Klopfer and MacArthur, 1960, 1961; Sanders, 1969; Slobodkin and Sanders, 1969). These new abundant species had narrower and narrower niches, becoming more effective, efficient, and aggressive with respect to competition and predation. When one of these Indo-Pacific species meets a species from the evolutionarily younger Caribbean fauna, provided that environmental conditions are agreeable to the invading species, the native species has a much lower chance of surviving the encounter. Thus, comparing competitive abilities is important for determining the ability of a new species to establish itself in a new environment and successfully expand its populations.

### 1.3.4. Objectives

Here, we have assessed the competitive abilities of the Indo-Pacific *T. micranthus* against other sessile, epibenthic Caribbean fauna occurring on the pilings of offshore oil and gas platforms in the northern Gulf of Mexico. We assessed the frequency of success and wins and losses in competition for space in this new invasive species with respect to other species it encounters during colony growth. For comparative purposes, we also did this for *T. coccinea.*

## 1.4 Duration

Because of field trip delays caused by poor weather conditions, this study ran for almost fouryears, including data collection, data analysis, graphic analysis, and writing. The data ultimately collected were voluminous, requiring us to break the research up into three sub-projects, each of which received attention in data collection, processing, analysis, graphing, and interpretation. Various reports were prepared during the course of the study and submitted to BOEM.

# 2. MATERIALS AND METHODS

## 2.1. POPULATION EXPANSION

### 2.1.1. Study sites and surveys

The study sites were Platform GI-93-C and 13 other platforms surrounding it within a 20 km radius (Fig. 1; Table 1). Specific platforms were chosen in consultation with BOEM. Surveys were performed using the M/V *Fling* (33 m, Gulf Diving, Inc., Freeport, Texas) and the R/V *Acadiana* (18 m, LUMCON, Cocodrie, Louisiana). The field portion of the study was conducted over two years, utilizing 12 days of ship-time. We spent approximately two-thirds of one day surveying each platform using an ROV.

We used LUMCON's Deep Ocean Engineering Phantom S2 ROV, which has 333 m of umbilical capable of surveying down to 170 m depth. We employed the techniques previously used successfully in earlier similar surveys (Sammarco et al., 2010, 2012a). ARACAR's SeaBotix LBV-300 and BOEM's similar ROV were also used as back-ups when the primary ROV required maintenance. All units were fitted with vertical and horizontal propulsion units, site-to-surface color video units, a topside monitor, lights, laser beams providing a spatial scale reference, and a sample retrieval unit (fixed grab).

### 2.1.2. Image processing

Imagery was processed using a Dell™ Precision™ 340 and T3400 desktop computers with a Pentium® 4 processor and a Dell™ Precision™ M4300 Workstation fitted with a duo-core processor and Microsoft® video imaging software. Image analysis software included Nero® 7.0, VideoLAN®, and Microsoft® Windows® Media Player®, capable of zoom and still-image capture. Images were analyzed at each 3 m interval within a video transect.

Data were collected for both *T. micranthus* and *T. coccinea* for comparative purposes. In the case of *T. coccinea*, population densities were so high (up to hundreds per still image) that counts were estimated visually using a $\log_5$ code system (0=1, 1=5, 2=25, 3=125, etc.), similar to that used in the field by Williams (1982) and Halford et al. (2004) for reef fish counts. Two laser dots of known inter-dot distance within the video field of view were used to standardize for both coral density (no. coral colonies per unit area) and coral colony size. A transparent 10 x 10 2.54 cm grid was placed over the computer screen to assist sampling and taking measurements. Mean colony densities were calculated for each platform along with standard deviations and 95% confidence limits.

Colony size was measured for all *T. micranthus* colonies. Colonies were assumed to be elliptical in shape, and measurements were made of the major and minor axes, as was done by Sammarco (1980). Estimated area was calculated as $A = \pi \times r_1 \times r_2$, where $r_1$ and $r_2$ are the major and minor radii, respectively for a two-dimensional ellipse. Mean colony size was calculated for each platform along with standard deviations and 95% confidence limits.

### 2.1.3. Data Analysis and Graphics

All quantitative data were logged in Microsoft® Excel® files and stored on the primary workstation. Data were backed-up on a 250G Western Digital® external hard-drive, updated daily as well as on the LUMCON computer network, which is backed-up regularly.

Table 1. List of 14 platforms in the northern Gulf of Mexico, near the mouth of the Mississippi River, video-surveyed by ROV for the ahermatypic invasive Indo-Pacific corals *T. micranthus* and *T. coccinea*.
Platform name, owner, and latitude and longitude of geographic location provided.

| Platform | | | | |
|---|---|---|---|---|
| **Number** | **Code** | **Owner** | **Latitude** | **Longitude** |
| | | | | |
| **1** | **GI-90A-1** | Apache Corp. | 28.575144 | -90.072429 |
| **2** | **GI-90A-2** | Apache Corp. | 28.575144 | -90.072429 |
| **3** | **GI-93C** | Apache Corp. | 28.548886 | -90.068677 |
| **4** | **GI-115A** | Walter Oil & Gas Corporation | 28.3076123 | -90.0219665 |
| **5** | **GI-116A** | Apache Corp. | 28.30928306 | -90.07054334 |
| **6** | **MC-109A** | Stone Energy Corporation | 28.86467752 | -88.93079054 |
| **7** | **MC-311A** | Apache Corp. | 28.642636 | -89.794241 |
| **8** | **SP-87D** | Apache Corp. | 28.72001853 | -89.43078669 |
| **9** | **SP-89B** | Apache Corp. | 28.680464 | -89.387596 |
| **10** | **ST-75-JA(B)** | Stone Energy Corporation | 28.76955709 | -90.74085664 |
| **11** | **ST-81A** | Stone Energy Corporation | 28.78656092 | -90.42747823 |
| **12** | **ST-185A** | Black Elk Energy Offshore Operations, LLC | 28.495501 | -90.203098 |
| **13** | **ST-185B** | Black Elk Energy Offshore Operations, LLC | 28.47493 | -90.235942 |
| **14** | **ST-206A** | Apache Corp. | 28.45372522 | -90.38341283 |

Coral density data were analyzed by parametric tests. Analyses included ANOVA and a posteriori Multiple Comparison Tests between Means–T-K, GT-2, and T' tests. Basic statistics (mean, s.d., n, range, $g_1$ – skewness, and $g_2$ – kurtosis) were calculated for colony size frequency distributions. Analyses were performed using BiomStat© 3.2 and 3.3 (Rohlf and Slice, 1996). In those cases where data were not normally distributed, they were transformed by square root of (Y+ 0.5) for assist in normalizing the data, allowing parametric statistics to be performed on them (Sokal and Rohlf, 1981).

Two-dimensional graphics were performed using SigmaPlot™ 10.0. Some data are presented within a geographic context in three dimensions, and these were constructed using SURFER® 8.0 (Golden Software). Data consisted of latitudes, longitudes, and the variate in question. Averages were determined by kriging, a geostatisical gridding method designed for use with irregularly spaced data, using a smoothing interpolator. Additional details may be found in Golden Software® (2002).

## 2.2. DEPTH DISTRIBUTION

### 2.2.1. Study sites and survey techniques

Platform GI-93-C served as a control platform of the study, because it was the location of first sighting and possessed the highest abundances of *T. micranthus* (Sammarco et al. 2010). Fourteen additional platforms surrounding it within a 20 km radius were also surveyed for *T. micranthus* (Fig. 1; Table 1; Sammarco et al., 2014). Some of these possessed this species, and a subset of these yielded population data sufficient in sample size to analyze for depth distribution; they were thus used in this study (Table 1).

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.

The camera of the ROV was always oriented at a horizontal angle to the substrate. That is, the images being captured were always on vertical surfaces, whether a vertical, horizontal, or diagonal strut was being surveyed. This eliminated the possibility of any changes in competitive advantage from target organisms being differentially oriented on different parts of the platform jacket.

### 2.2.2. Image processing

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 colony density data (Sammarco, 2012a), standardized to no./10 $m^2$. The total for each 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, before calculating densities of either species.

So that we could compare depth distributions, data were collected for both *T. micranthus* and *T. coccinea*. Total colony density and percent-cover data were collected. Mean colony density and percent-cover were calculated for each two-meter depth bin on each platform.

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.

## 2.3. COMPETITION FOR SPACE

All platforms surveyed for *T. micranthus* occurred within a 25 km radius south of the mouth of the Mississippi River (Figure 1; Table 1; see Sammarco et al., 2014). Some of these possessed this species. A subset of that group yielded population data sufficient in size to analyze *T. micranthus* with respect to competition for space. All 14 platforms were used for competition analysis in *T. coccinea*. On each platform, two to four vertical pilings were surveyed as well as two sets of horizontal struts, usually at depths of 13–17 m, and 21–27 m. The number of vertical pilings surveyed was dependent upon the number of pilings available for survey and wind and sea conditions.

### 2.3.1. Image processing and assessment of competitive state

In order to make comparisons regarding the capabilities of these two congeneric invasive species, data were collected for both *T. micranthus* and *T. coccinea*. Because *T. coccinea* population densities were extraordinarily high, competitive interaction data were collected only from up to five colonies per quadrat, selected haphazardly.

Evidence of either intra- or inter-specific competition involving corals and other sessile epibiota was recorded. The techniques used here were similar to those used by Sammarco (1980, 1982) and Sammarco and Carleton (1982). Sessile epibenthic organisms occurring within 8 mm of the target coral were assessed for interaction. An observation of overgrowth was assumed to be evidence of competition for space, as has been used in previous related studies (Jackson and Buss, 1975; Jackson, 1977). Competitive encounters were judged from the target coral's perspective. The competition variable was defined simply as the number of competitive wins over the total number of interactions within that taxonomic group.

### 2.3.2. Data handling and analysis

The test used to determine whether there were significant successful wins in a set of interactions (where the win frequency is significantly greater than 50%) was Fisher's Exact Test. Differences in competitive success between populations on the respective platforms were examined using a Goodness of Fit Test using the G-statistic, against a 1:1 expected ratio of win to loss (Sokal and Rohlf, 1981). Data were plotted as bar diagrams using SigmaPlot 10.0.

# 3. RESULTS

## 3.1. POPULATION EXPANSION

### 3.1.1. *Tubastraea micranthus*

Data derived from analysis of ROV videos revealed that *T. micranthus* had indeed spread to surrounding platforms. Of 14 platforms surveyed, this species was found on nine (Fig. 2). Densities varied by platform and was highest on the platform of initial sighting, GI-93-C, averaging approximately 15/m$^2$. ANOVAs and subsequent a posteriori tests revealed that densities on GI-93C and GI-116A were significantly higher than all other platforms Table 2). Details about inter-platform comparisons may be found in Table 2. *T. micranthus* did not occur on ST-185A&B, GI-94B, ST-81A, or ST-75JA(B).

When density data were placed into a geographic context, it could be seen that the peak density occurred to the southwest of the mouth of the Mississippi River (Fig. 3), next to two major safety fairways servicing the Port of New Orleans and the Port Fourchon (Sammarco et al., 2010). A second somewhat smaller peak in density could be seen south of GI-93-C. In general, densities fell off in all directions in near proximity to these points, with a minor peak west-southwest of the Mississippi River mouth. There was a moderate rise in densities to the east of the Mississippi River.

Patterns of average colony size for *T. micranthus* did not follow that of average density. The maximum average colony size was found on Platform MC-311-A (Fig. 4). It was significantly higher than on all other platforms (Table 3), suggesting that this may have been the site of original colonization. The reason for this is that these colonies may have had the longest time of opportunity for growth compared with the other platforms. The next largest average *T. micranthus* colony size was found on MC-109A, and it was significantly higher than the average colony size on SP-87D, GI-116A, and GI-93C. Average colony size on almost all other platforms was equivalent (not significantly different), except GI-115A versus ST-206A, and GI-93C compared with SP-87D. When these differences are placed into a geographical context, the three-dimensional representation of average colony size demonstrates that colony size not only peaks at MC-311-A, but it also drops off evenly from that point in all directions, with no secondary peaks in that region (Fig. 5).

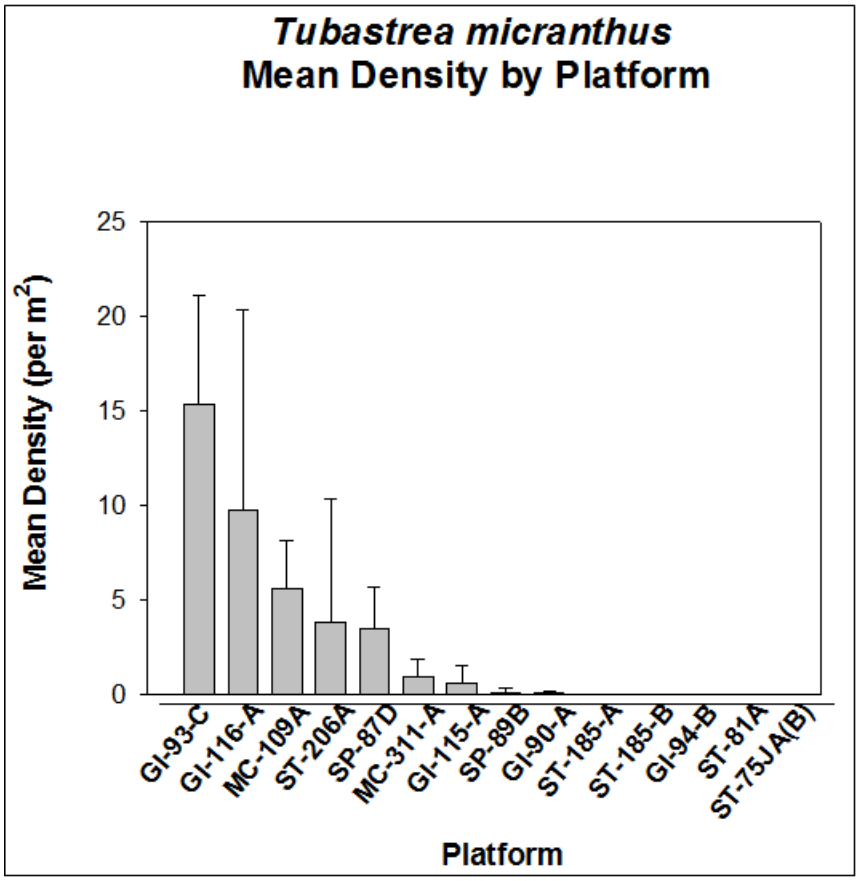



Figure 2. Density of *T. micranthus* on 14 offshore oil/gas platforms in the northern Gulf of Mexico. Densities shown in no./10 $m^2$ with 95% confidence limits.

In overview, most densities are highly significantly different from each other ($p < 0.001$, one-way ANOVA). Data transformed by square-root of (Y + 0.5) for purposes of normalization (Sokal and Rohlf, 1981). See Table 2 for details of pair-wise inter-platform comparisons and text for detailed discussion.

Table 2. Summary of results of a posteriori multiple comparisons of means tests performed on mean colony densities of *T. micranthus* on 14 energyplatforms in the northern Gulf of Mexico.

T', T-K, and GT-2 tests were used. Results of pairwise comparisons shown. Platforms are shown in order of density, high to low. An asterisk denotes a significant difference between coral densities on two given platforms.

| Platform Name | GI-93C | GI-116A | MC-109A | ST-206A | SP-87D | MC-311A | G-115A | SP-89B | GI-90A | ST-185A | ST-185B | GI-94B | ST-81A | ST-75JA(B) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| GI-93C | | | * | * | * | * | * | * | * | * | * | * | * | |
| GI-116A | | | | | | * | | | * | * | | * | | |
| MC-109A | | | | | | | | | | | | | | |
| ST-206A | | | | | | | | | | | | | | |
| SP-87D | | | | | | | | | | | | | | |
| MC-311A | | | | | | | | | | | | | | |
| G-115A | | | | | | | | | | | | | | |
| SP-89B | | | | | | | | | | | | | | |
| GI-90A | | | | | | | | | | | | | | |
| ST-185A | | | | | | | | | | | | | | |
| ST-185B | | | | | | | | | | | | | | |
| GI-94B | | | | | | | | | | | | | | |
| ST-81A | | | | | | | | | | | | | | |
| ST-75JA(B) | | | | | | | | | | | | | | |

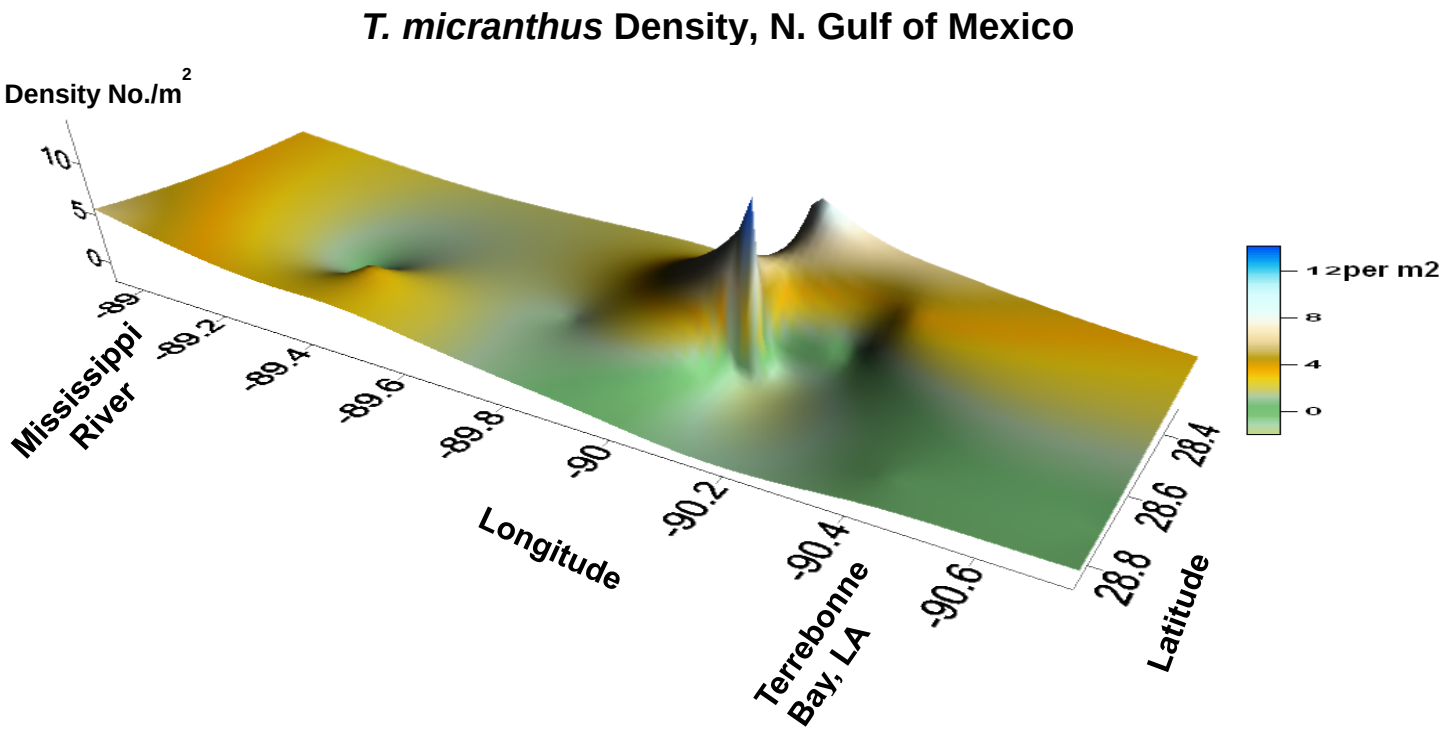



Figure 3. Geographic distribution of the density of *T. micranthus* in the northern Gulf of Mexico, south of the Mississippi River mouth.

Location of platforms shown by platform numbers. Platform codes of numbers shown in Table 1. Note the primary peak (at GI-93C), the secondary peak (at GI-116A).

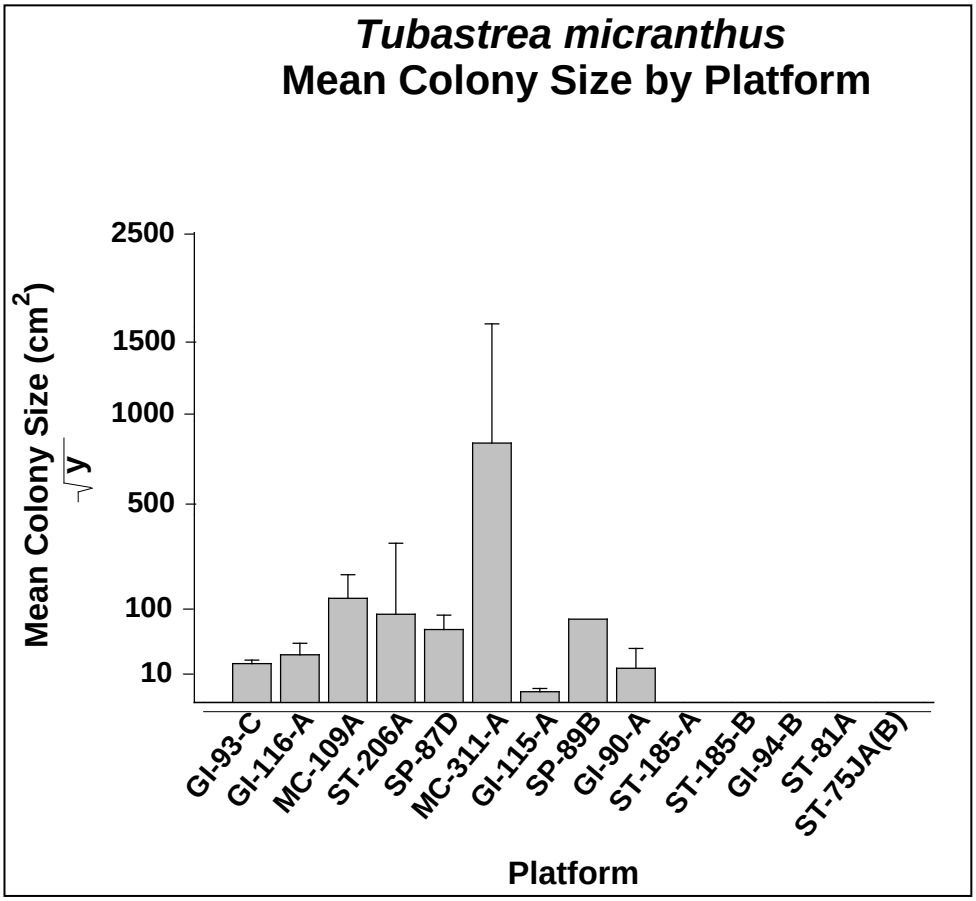



Figure 4. Mean colony size of *T. micranthus* in the northern Gulf of Mexico, south of the Mississippi River mouth.

Note that the largest average colony sizes are found on MC-311A, a site which occurs in blue water in Mississippi Canyon, unlike many of the other sites. Significant difference between colony sizes on different platforms ($p < 0.001$, one-way ANOVA; see Table 2 for detailed comparisons). Data transformed by square root (Y + 0.5) for normalization purposes.

Table 3. Summary of results of a posteriori multiple comparisons of means tests performed on average colony sizes of *T. micranthus* on 14 energy platforms in the northern Gulf of Mexico.

T', T-K, and GT-2 tests were used. Results of pairwise comparisons shown. Platforms are shown in order of average colony size, high to low. An asterisk denotes a significant difference between coral colony sizes on two given platforms.

| **Platform Name** | **MC-311A** | **MC-109A** | **ST-206A** | **SP89-B** | **SP-87D** | **GI-116A** | **GI-93C** | **GI-90A** | **GI-115A** |
|---|---|---|---|---|---|---|---|---|---|
| **MC-311A** | | * | * | * | * | * | * | * | * |
| **MC-109A** | | | | | * | * | * | | |
| **ST-206A** | | | | | | | | | * |
| **SP89-B** | | | | | | | | | |
| **SP-87D** | | | | | | | * | | |
| **GI-116A** | | | | | | | | | |
| **GI-93C** | | | | | | | | | |
| **GI-90A** | | | | | | | | | |
| **GI-115A** | | | | | | | | | |

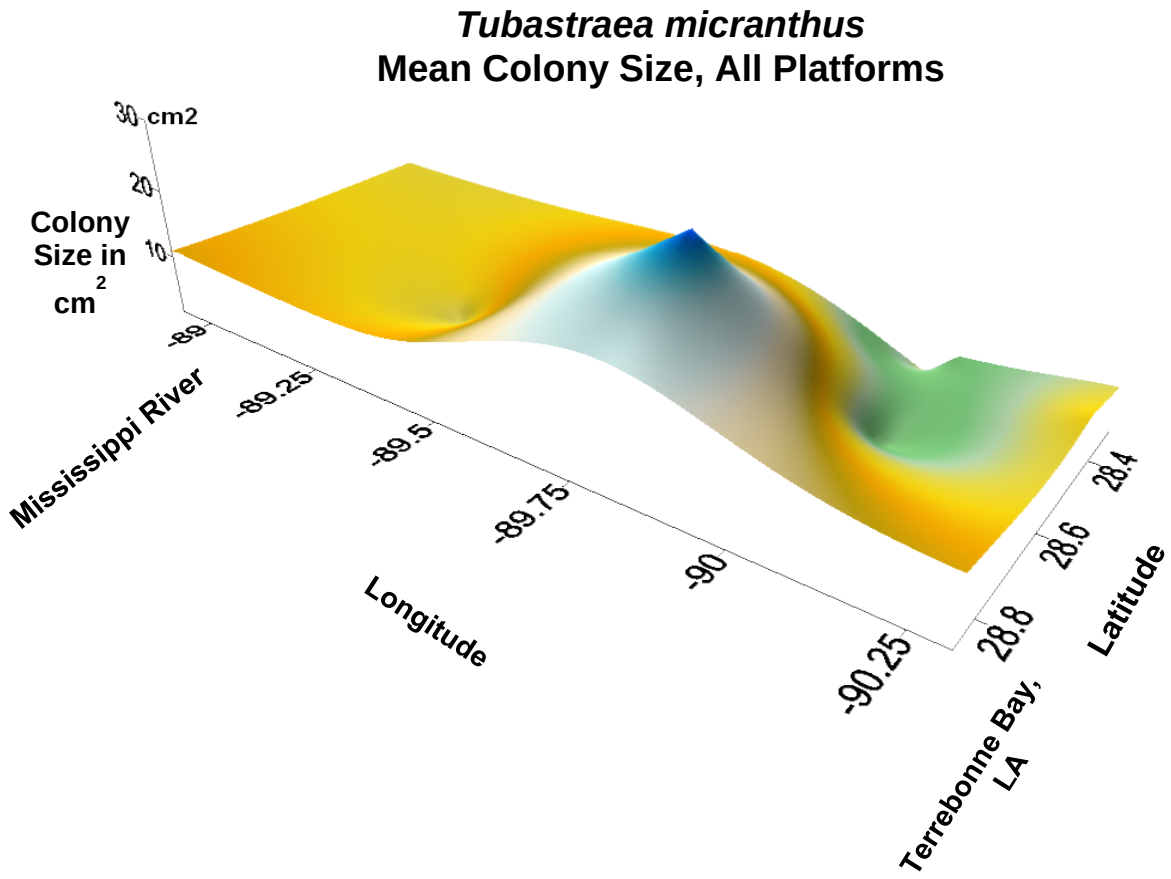



Figure 5. Geographic distribution of the mean colony size of *T. micranthus* in the northern Gulf of Mexico, south of the Mississippi River mouth.

Note the primary peak (at MC-311A, within Mississippi Canyon) and how average colony size decreases radially from that point, indicating that this site may be the initial site of colonization and may also possess the best environmental conditions for growth for this species.

Size-frequency diagrams were constructed for *T. micranthus* colonies on each of the platforms. In the case of Platform MC-109-A, it could be seen that a large proportion of the colonies - ~60% - were between one and 100 $cm^2$ in area (max. diameter = ~11 cm) in area (Fig. 6). Frequencies of larger average colony sizes fell off rapidly after this. This pattern of a logarithmic decrease in frequency of average colony sizes, heavily biased towards the smallest size frequency, was mimicked on all other platforms where *T. micranthus* occurred, as exemplified by GI-93C and GI-116A (Fig. 6).

### 3.1.2. *Tubastraea coccinea*

*T. coccinea* invaded the Caribbean approximately 70 years ago (Cairns, 2000). Its range extension has been broad, and its abundances have reached high levels, particularly more recently on artificial reefs such as the platforms in the Gulf of Mexico.

Densities of *T. coccinea* were much higher than those of *T. micranthus*, with the highest densities in this survey reaching about 300 colonies/$m^2$, 20-fold higher than that of the new invasive species: *T. micranthus* (Fig. 7). The platforms had significantly different densities. Platform ST-185B exhibited the highest concentrations of *T. coccinea*, which were equivalent to those on GI-116A, but higher than all other platforms (Table 4). Densities on GI-116A were higher than almost all other platforms. Densities on ST-206A were approximately equivalent to all other platforms except the above two plus MC-311A and ST-185A.

The geographic distribution of *T. coccinea* colony density in the study region is similar in pattern to that of *T. micranthus* (Fig. 8). The major peaks in both species occur southwest of the mouth of the Mississippi River, and densities decrease radially in all directions from there.

## 3.2. DEPTH DISTRIBUTION

Results from data based on density compared with 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* occurred at all depths surveyed, from near the surface to the deepest encountered in this study: 138 m (Fig. 9a). This was also evident if one measured abundance by percent-cover (Fig. 9b). The overall pattern of depth distribution was bi-modal, 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 (Fig. 9b).

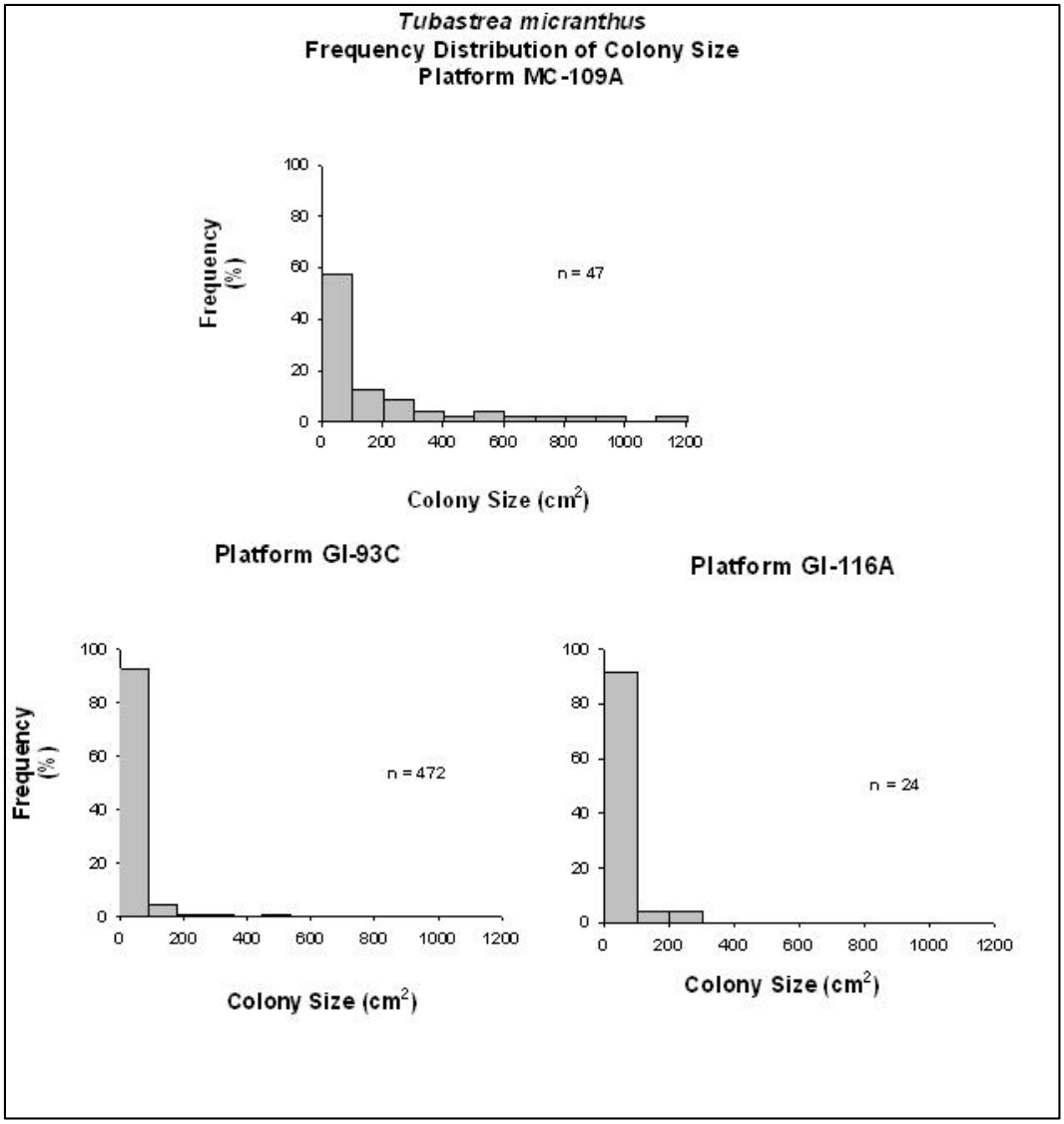



Figure 6. Size-frequency distribution of colonies of *T. micranthus* on three platforms in the northern Gulf of Mexico, near the Mississippi River mouth.

MC-109A (top), GI-93C (bottom left), and GI-116A (bottom right). Examplary of distributions found on all platforms. Note the over-representation of smaller-sized colonies, indicating explosive population growth with low doubling times. Platform MC-109A: Mean = 198.6 $cm^2$, s.d. = 281.14, $n_i$ = 47, $g_1$ = 1.92, $g_2$ = 3.36. Platform GI-116A: Mean = 34.7 $cm^2$, s.d. = 45.60, $n_i$ = 24, $g_1$ = 2.74, $g_2$ = 8.23. Platform GI-93C: Mean = 33.5 $cm^2$, s.d. = 94.18, $n_i$ = 472, $g_1$ = 7.19, $g_2$ = 63.11.

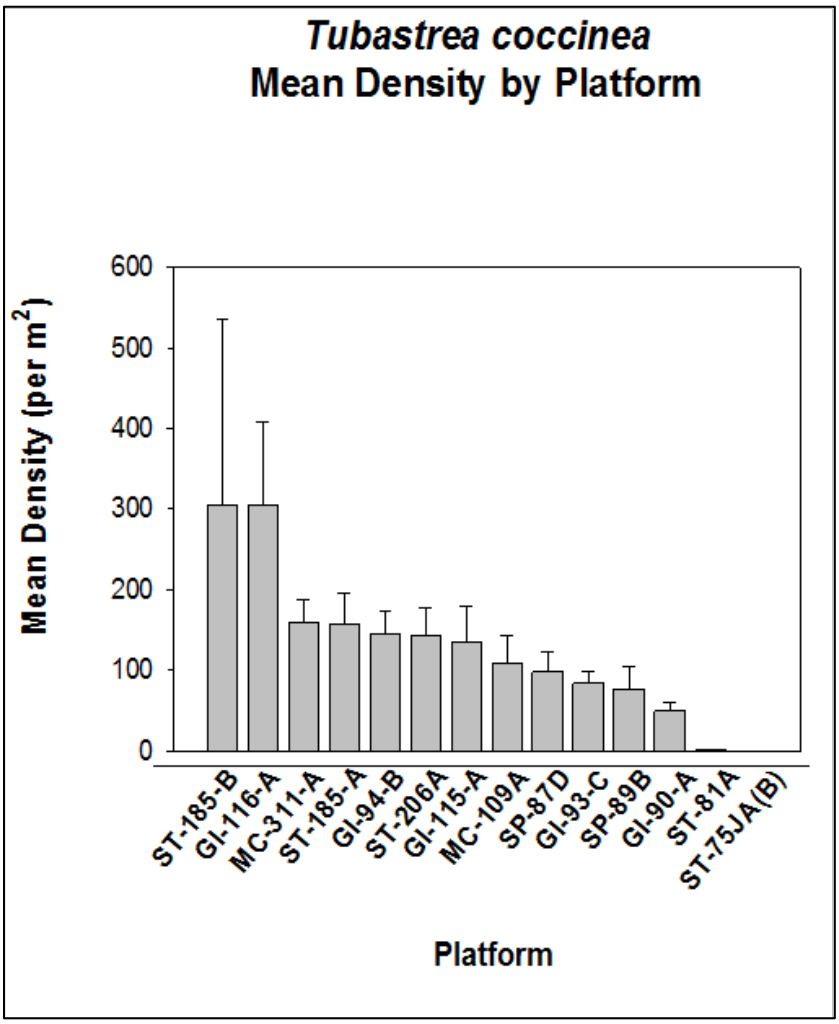



Figure 7. Density of *T. coccinea* in the northern Gulf of Mexico on 14 platforms off the mouth of the Mississippi River.

Densities shown in no./m$^2$ with 95% confidence limits. Densities are highly significantly different from each other ($p < 0.001$, one-way ANOVA). Data transformed via square-root of (Y + 0.5) for purposes of normalization (Sokal and Rohlf, 1981). See Table 4 for details of inter-platform comparisons.

Table 4. Summary of results of a posteriori multiple comparisons of means tests performed on mean colony densities of *T.* coccinea on 14 energy platforms in the northern Gulf of Mexico.

T', T-K, and GT-2 tests were used. Results of pairwise comparisons shown. Platforms are shown in order of density, high to low. An asterisk denotes a significant difference between coral densities on two given platforms.

| | ST-185B | GI-116A | MC-311A | ST-185A | GI-94B | ST-206A | GI-115A | MC-109A | SP-87D | GI-93C | SP-89B | GI-90A | ST-81A | ST-75JA(B) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **ST-185B** | | | * | * | * | * | * | * | * | * | * | * | * | * |
| **GI-116A** | | | * | * | * | | * | * | * | * | * | * | * | |
| **MC-311A** | | | | | | | | | | * | * | * | * | |
| **ST-185A** | | | | | | | | | | | | * | * | |
| **GI-94B** | | | | | | | | | | | | * | | |
| **ST-206A** | | | | | | | | | | | | | | |
| **GI-115A** | | | | | | | | | | | | | | |
| **MC-109A** | | | | | | | | | | | | | | |
| **SP-87D** | | | | | | | | | | | | | | |
| **GI-93C** | | | | | | | | | | | | | | |
| **SP-89B** | | | | | | | | | | | | | | |
| **GI-90A** | | | | | | | | | | | | | | |
| **ST-81A** | | | | | | | | | | | | | | |
| **ST-75JA(B)** | | | | | | | | | | | | | | |

## *T. coccinea*
## Mean Density, All Platforms

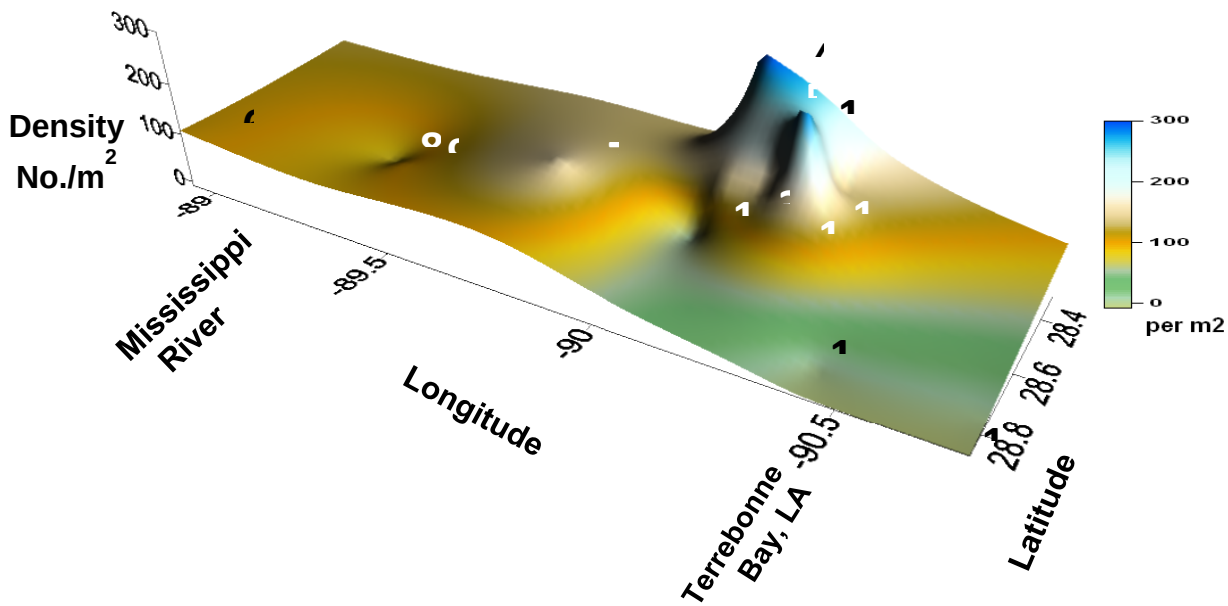



Figure 8. Density of *T. coccinea* in the northern Gulf of Mexico on 14 platforms off the mouth of the Mississippi River.

Densities shown in no./m$^2$ with 95% confidence limits. Densities are highly significantly different from each other ($p < 0.001$, one-way ANOVA). Data transformed via square-root of (Y + 0.5) for purposes of normalization (Sokal and Rohlf, 1981). See Table 4 for details of inter-platform comparisons.

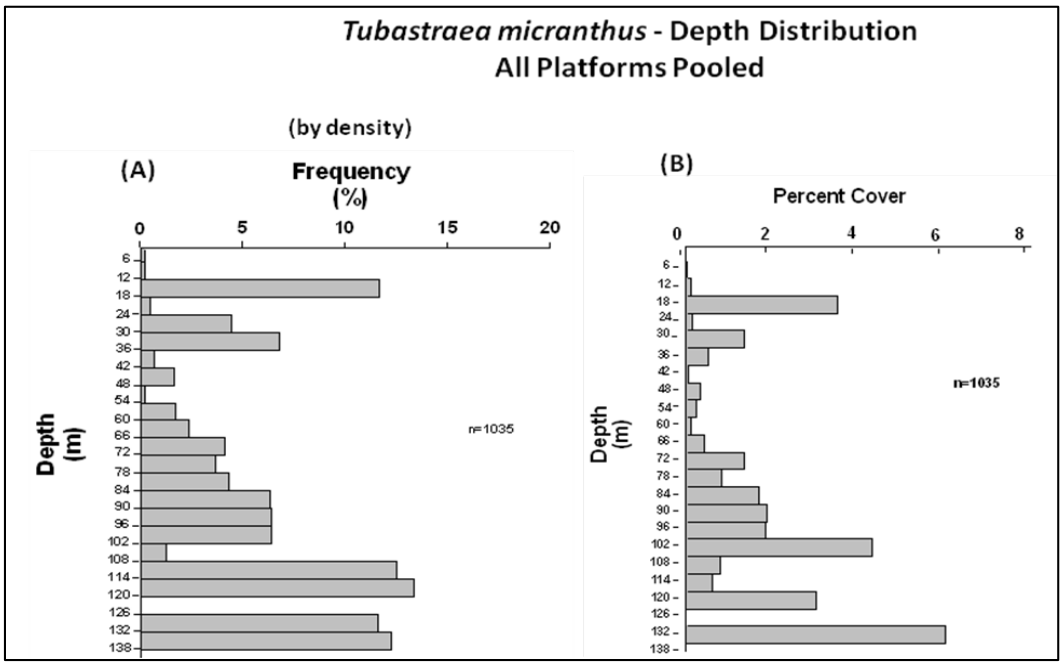



Figure 9. Depth distribution of *T. micranthus* in the northern Gulf of Mexico.

Data pooled from three production platforms: GI-93C, GI-116A, and MC-109A. (A) Distribution based on 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). g1 = 8.583, g2 = 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). g1 = 9.597, g2 = 113.657. Significant difference between *T. micranthus* distributions measured by density vs. percent-cover ($p < 0.001$, R x C Goodness of Fit test).

*T. coccinea* occurred in much higher numbers than *T. micranthus* on all platforms, and, 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 (Fig. 10). 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 (Fig. 10). 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 (Fig. 11a). The deeper distributions are southeast 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 (Fig. 11b).

When one examines the geographic pattern of these average depths based on average colony density in *T. coccinea*, it varies greatly from that of *T. micranthus*. First, it is relatively uniform across the study area (Fig. 12a). Second, 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 through colony density and percent-cover (Fig. 12b).

Examining patterns of depth distribution in *T. micranthus* on individual platforms based on coral density provides additional insight into the overall patterns. On GI-93C, the coral extended in distribution all the way to the bottom: 66 m (Fig. 13a). It also exhibited a clear peak average density in relatively shallow water at 18-24 m depth. By comparison, on 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 (Fig. 13b). Where it occurred on this platform, the distribution was relatively uniform. On GI-116A, *T. micranthus'* depth distribution was limited to mid-depths of 30–48 m (Fig. 13c). 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 (Fig. 14a). On MC-109A, the range of occurrence was once again 66–138 m depth, although percent-cover peaked at 102–108 m depth (Fig. 14b). On GI-116-A, the pattern of average percent-cover closely mimicked that generated by density data, concentrating at mid-depths, ranging from 30–48 m depth (Fig. 14c), but being absent from both very shallow and very deep waters.

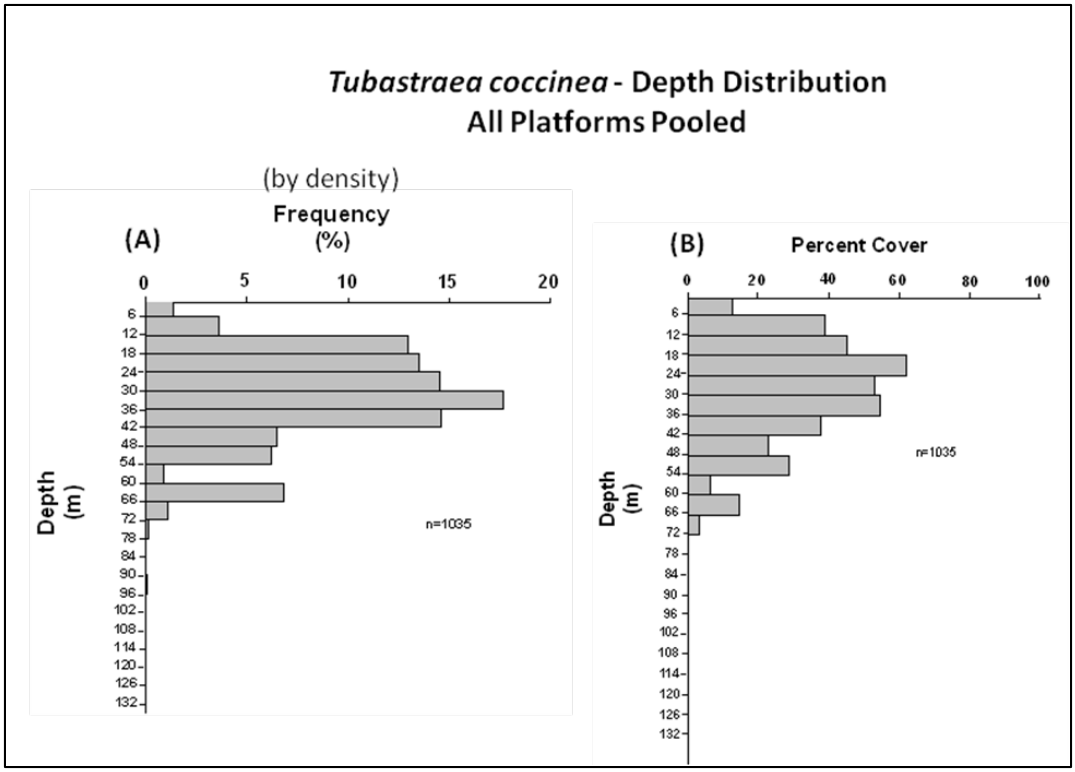



Figure 10. Depth distribution of *T. coccinea* in the northern Gulf of Mexico.

Data pooled from six energy production platforms: GI-94B, GI-116A, MC-311A, ST-185A, ST-185B, and ST-206A. (A) Distribution based on colony density in no./10 $m^2$ 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 through densitycompared with percent-cover ($p < 0.001$, R x C Goodness of Fit test). Significant difference between distributions of *T. micranthus* compared with *T. coccinea* whether measured by density or percent-cover ($p < 0.001$, R x C Goodness of Fit Test, in both cases).

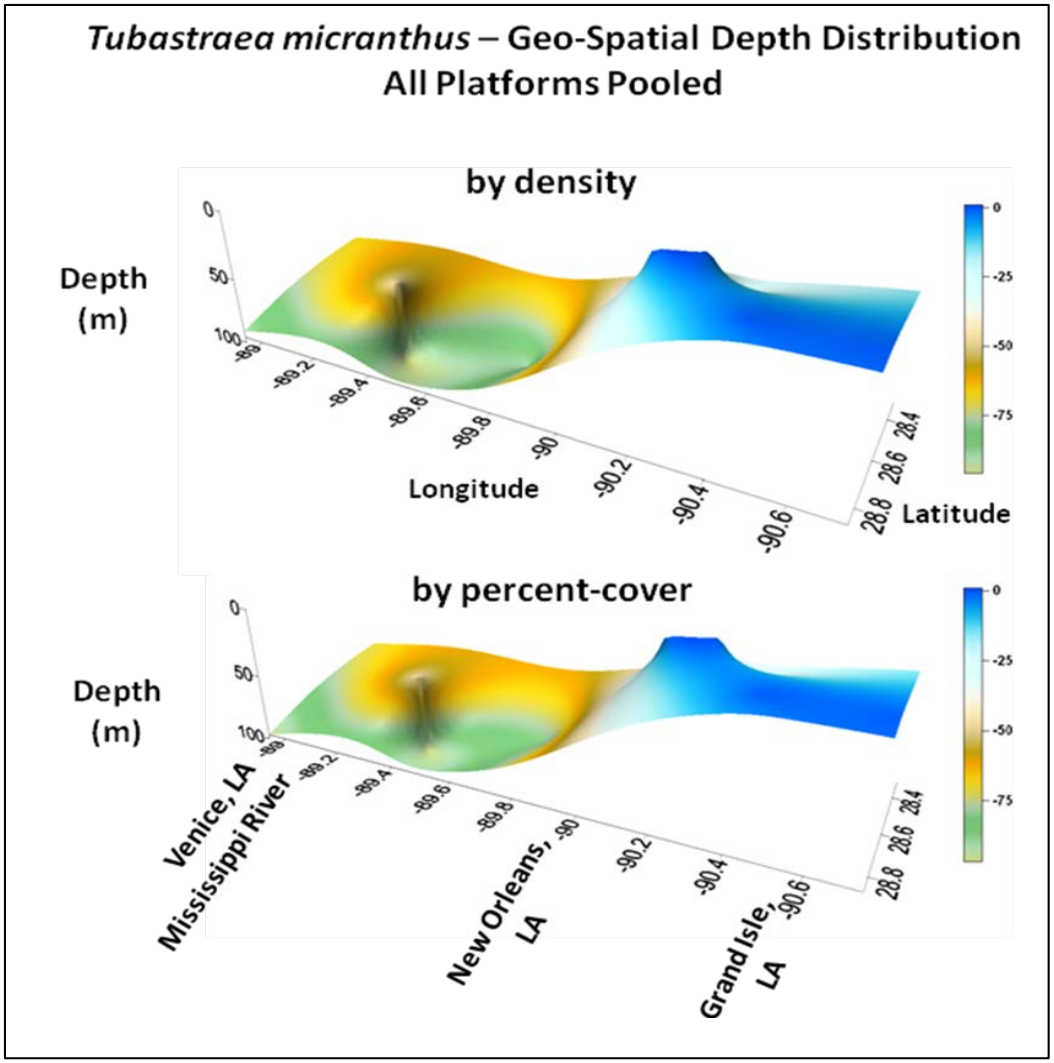



Figure 11. Geographic distribution of average depth of distribution for *T. micranthus* in the northern Gulf of Mexico.

(A) Data based on colony density in no./10 $m^2$. (B) Data based on percent-cover.

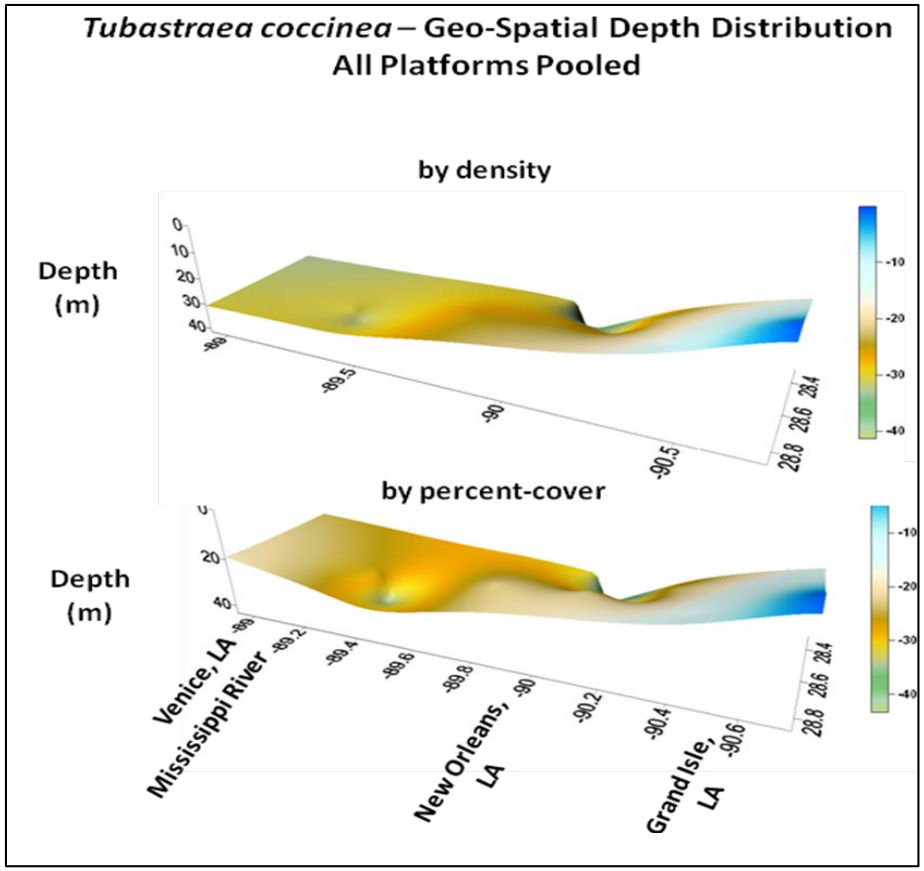



Figure 12. Geographic distribution of average depth of distribution for *T. coccinea* in the northern Gulf of Mexico.

(A) Data based on colony density in no./10 $m^2$. (B) Data based on percent-cover.

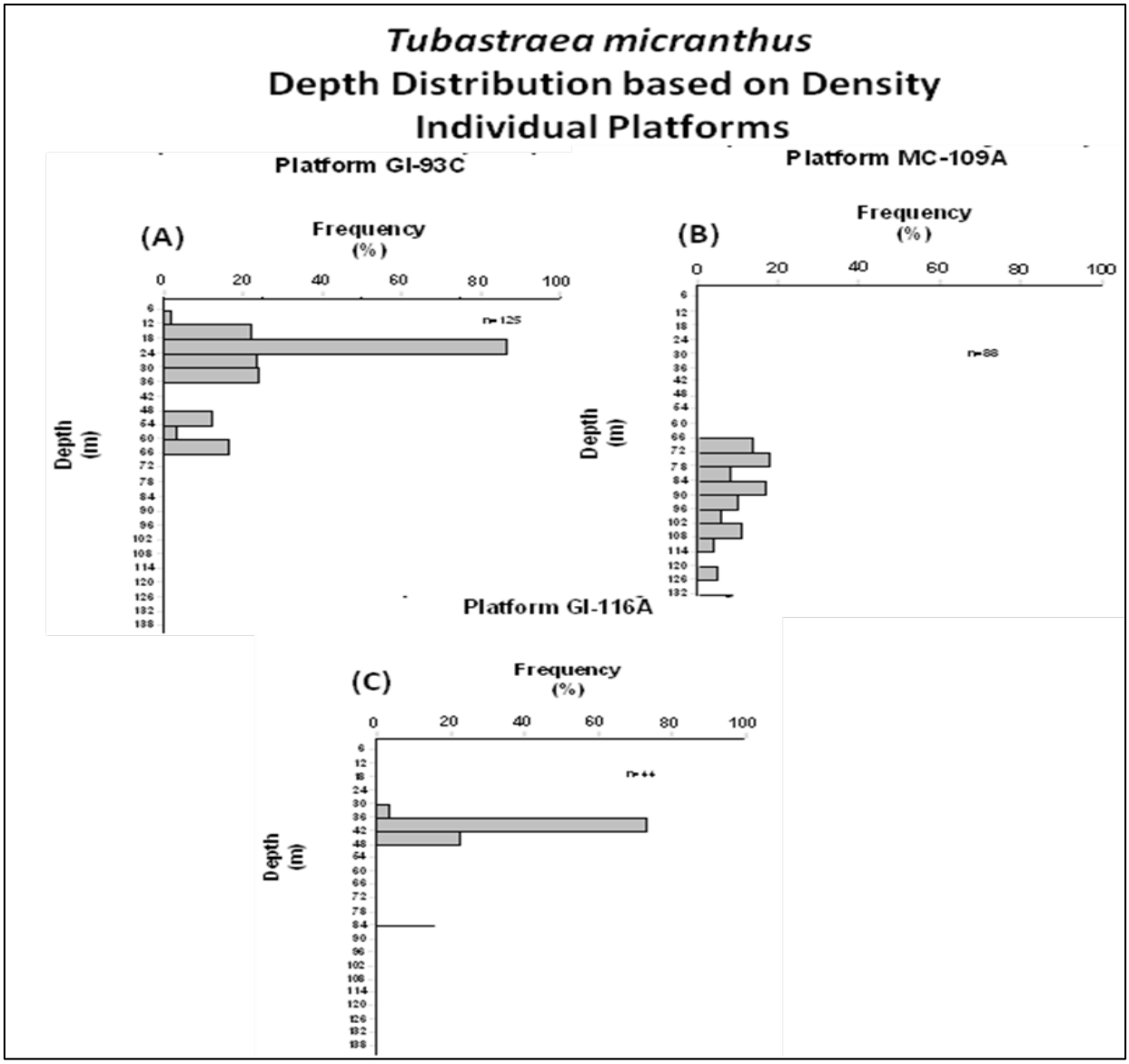



Figure 13. Depth distribution of *T. micranthus* observed on individual platforms in the northern Gulf of Mexico.

Data based on colony density in no./10 $m^2$. 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). $g_1 = 4.659$, $g_2 = 23.771$.

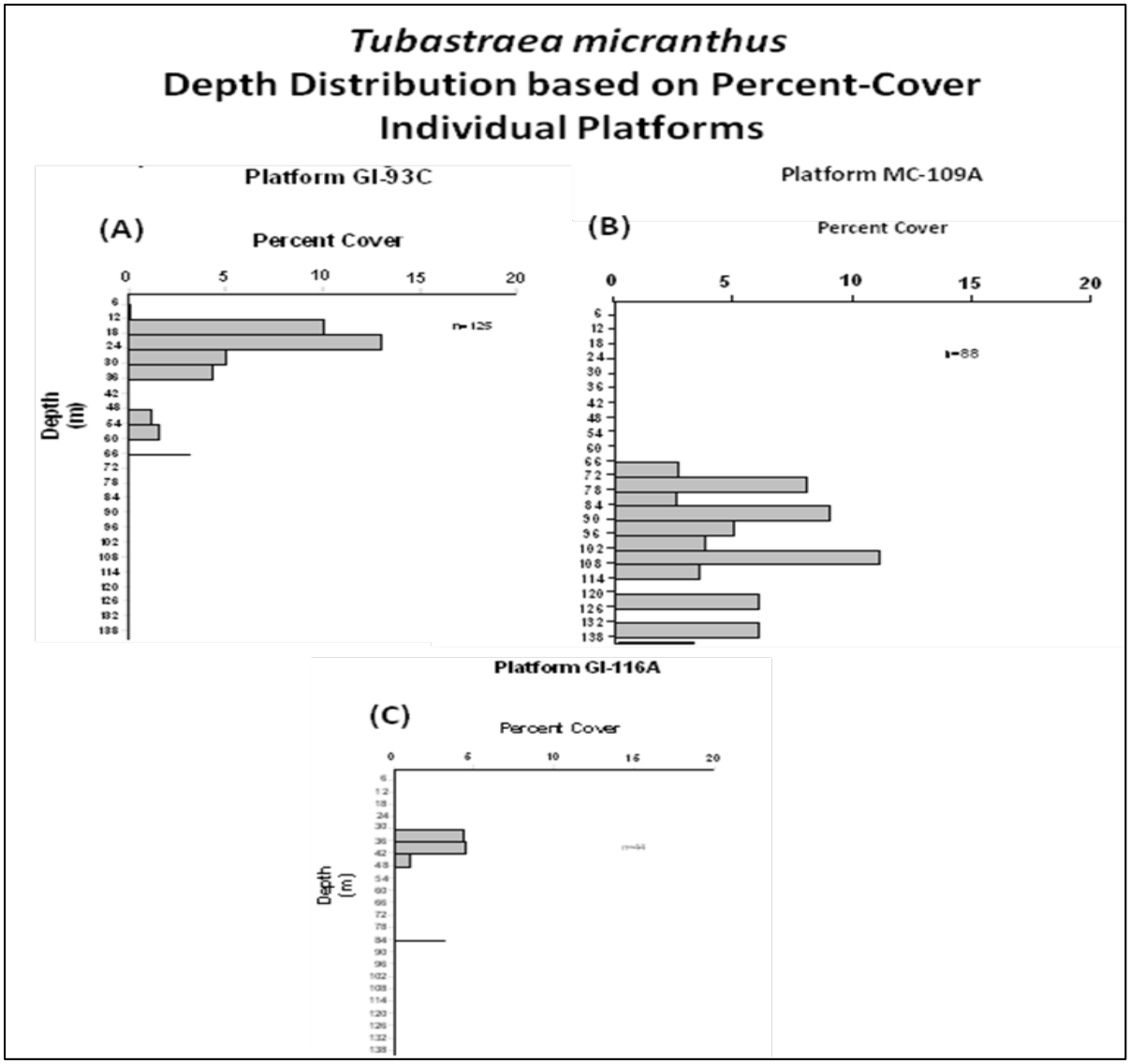



Figure 14. Depth distribution of *T. micranthus* observed on individual platforms in the northern Gulf of Mexico.

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). $g_1 = 4.403$, $g_2 = 19.336$.

*T. coccinea*'s depth distribution patterns on individual platforms were variable, but always remained within the shallower depths. On Platform GI-116A, *T. coccinea* exhibited its highest average densities at relatively shallow depths: 12–18 m (Fig. 15a). 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 (Fig. 15b). 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 (Fig. 15c).

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 (Fig. 16a). 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 (Figs. 16b&c). *T. coccinea* again extended all the way to the bottom.

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 (Fig. 17a). The pattern was similar on GI-94B, with a higher peak in colony density at 24–30 m depth (Fig. 17b). The pattern on Platform MC-311A was somewhat different. First, the maximum depth of the platform was 120 m. The maximum depth of colonization and growth in *T. coccinea* was 66–72 m (Fig. 17c). This underlines the fact that *T. coccinea* was distributed in relatively shallow water. Second, 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.

## 3.3. COMPETITION FOR SPACE

### 3.3.1. *Tubastraea micranthus*

From the ROV videos, it became evident that, on average, *T. micranthus* was a significantly better competitor for space than its associates (Fig. 18a). Its positive competitive abilities, however, varied significantly between populations. Competitive success varied from ~50% on GI-90A to ~90% on SP-87-D. On no platform, however, did *T. micranthus'* competitive success fall below 50%. This meant that, overall, it was winning in competition against the other sessile epibenthic fauna it encountered and that it could slowly dominate the community. With respect to its geographic distribution throughout the study area, the highest average win frequency occurred in the NE portion of the study area off Venice, Louisiana, and the lowest win frequency occurred in the SW, off Grand Isle, Louisiana (Fig. 18b).

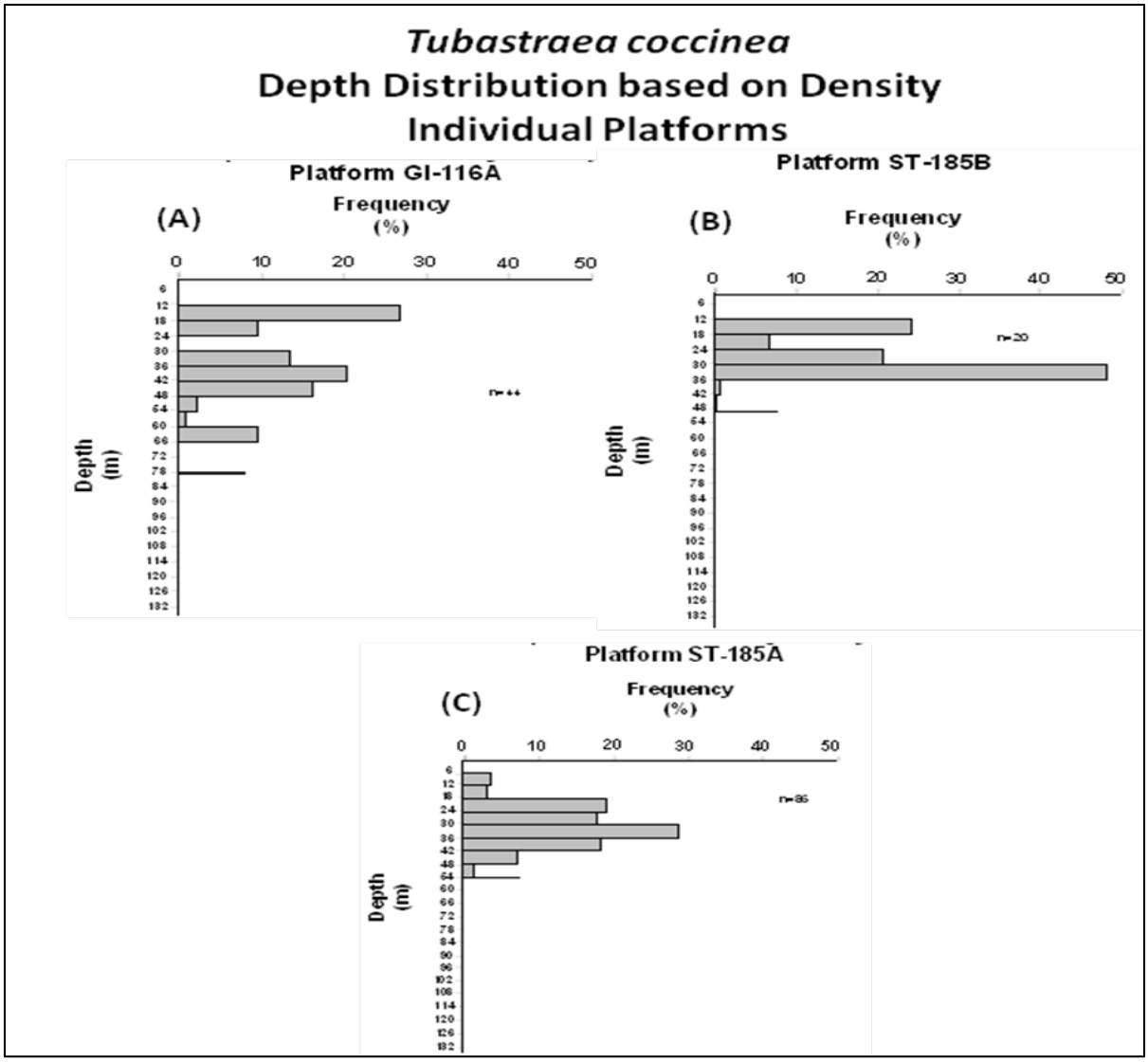



Figure 15. Depth distribution of *T. coccinea* observed on individual platforms in the northern Gulf of Mexico. Data based on colony density in no./10 $m^2$.

Heavy horizontal line represents depth of bottom. (A) *T. micranthus* 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). $g_1 = 3.639$, $g_2 = 14.634$. (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). $g_1 = 4.659$, $g_2 = 23.771$.

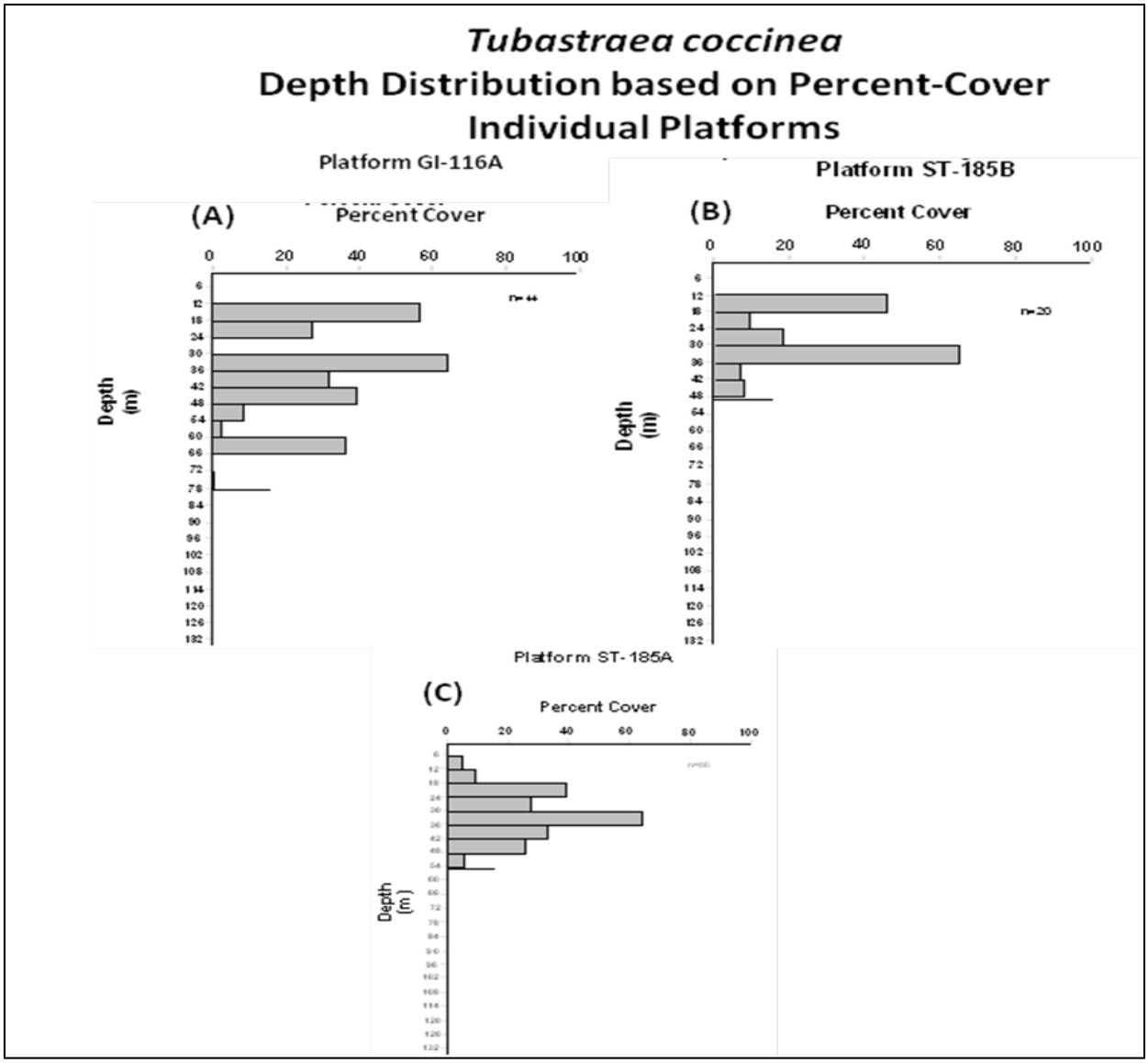



Figure 16. Depth distribution of *T. coccinea* observed on individual platforms in the northern Gulf of Mexico. Data based on percent-cover.

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). $g_1 = 0.827$, $g_2 = -0.750$.

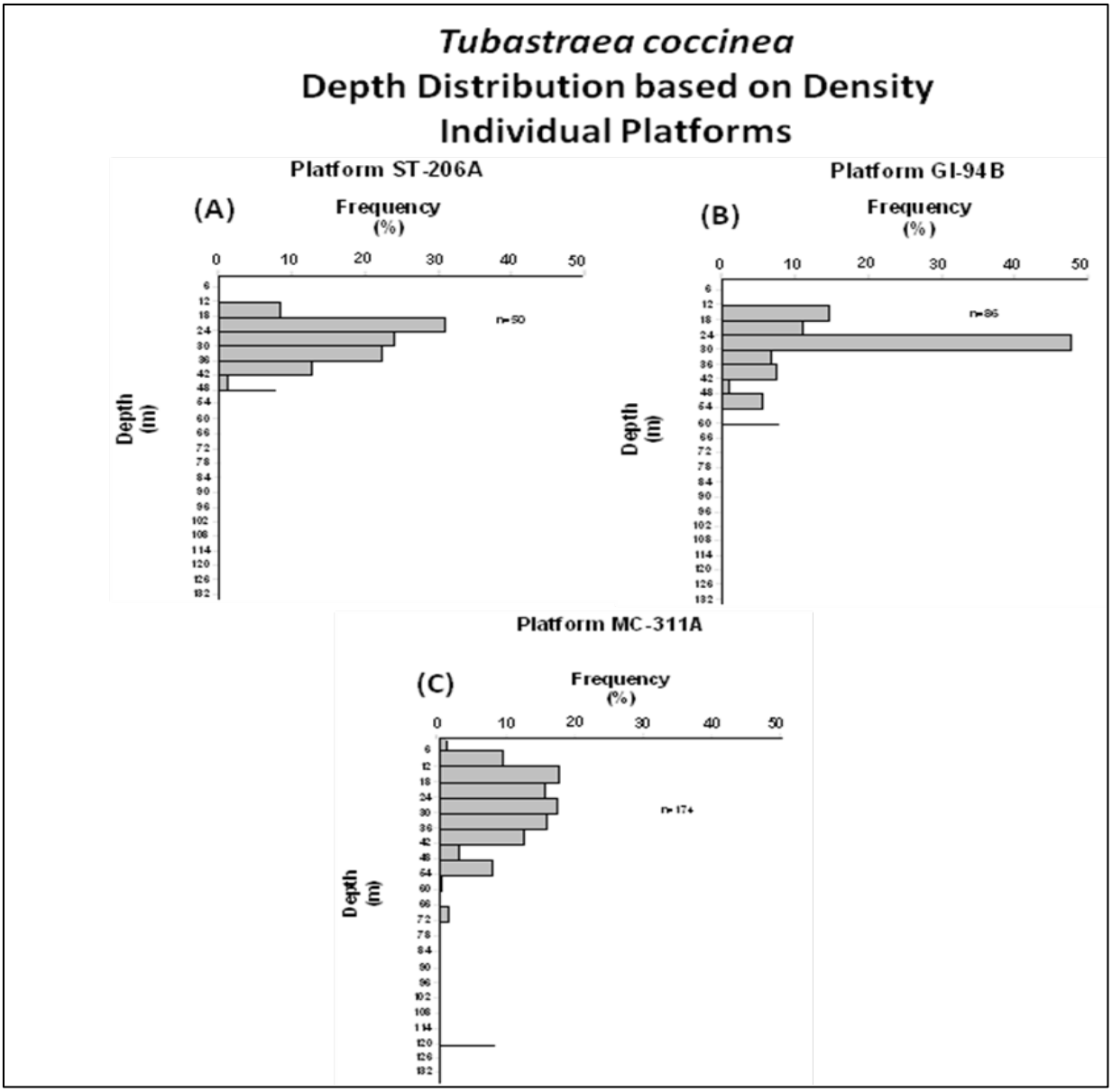
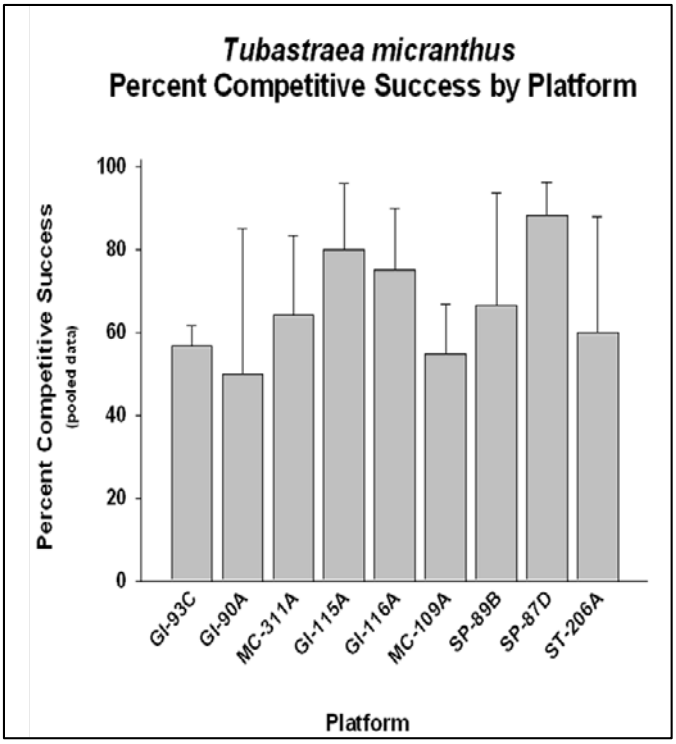



Figure 17. Depth distribution of *T. coccinea* observed on individual platforms in the northern Gulf of Mexico. Data based on density in no./10 $m^2$.

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) *T. micranthus* 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). $g_1 = 1.092$, $g_2 = 0.521$. (C) Depth distribution of *T. micranthus* 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). $g_1 = 2.837$, $g_2 = 14.899$.



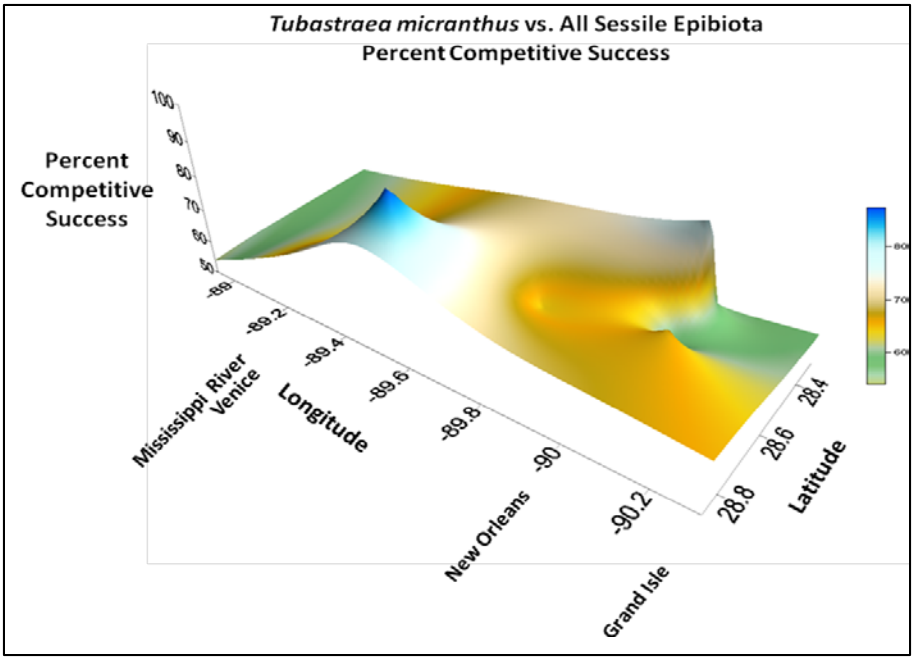




Figure 18. (A) Percent of wins in competition for space between *T. micranthus* and all other sessile epibiota, data pooled. Presented by platform. (B) Geospatial representation of the distribution of competitive wins in the study area.

(A) Percent competitive success plus 95% confidence limits shown. Tested for significant variation from 1:1 ratio of wins to losses. Competitive successes significantly higher than neutral outcome or losses ($p < 0.01$, Fisher's Exact Test). Also, significant difference between frequency of competitive success between platforms ($p < 0.001$, Goodness of Fit Test, G-statistic).

### 3.3.2. *Tubastraea coccinea*

Because *T. coccinea* was much more abundant and widely distributed on the platforms than *T. micranthus*, it became possible to assess it for its competitive ability against various epibenthic organisms. Due to low sample size, this was not possible in *T. micranthus.*

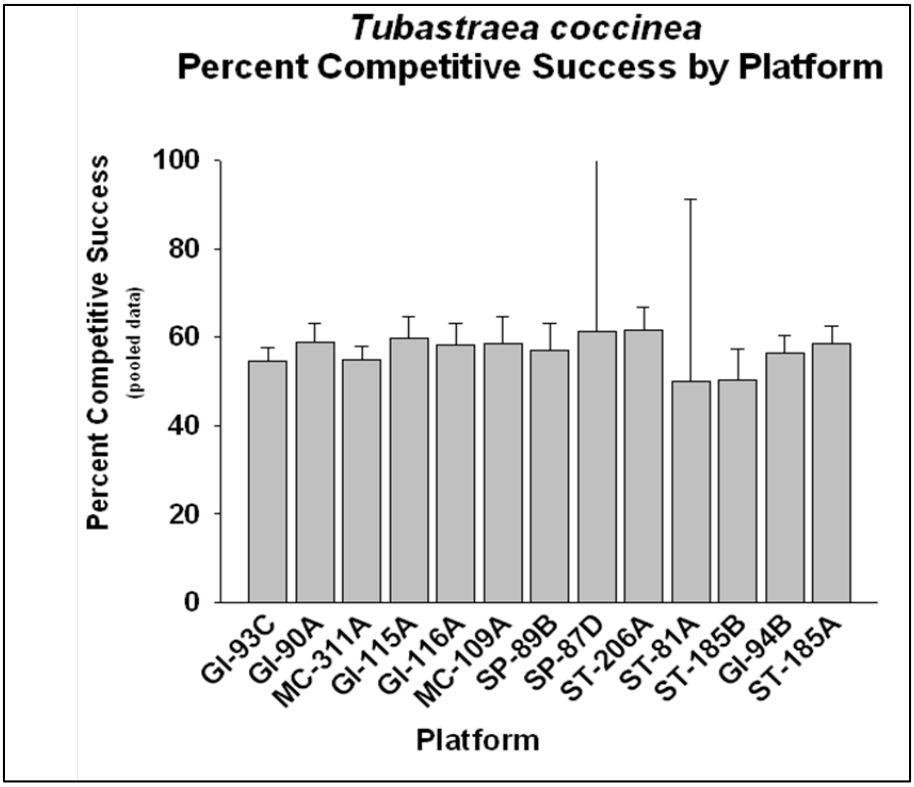
Competitive success in *T. coccinea* against all other sessile epibiota was highly significantly positive at an average of ~55% wins. There was significant variation between platforms (Fig. 19a), but that variability was actually quite low in magnitude, indicating a uniform ability of this species to compete for space. This uniformity was reflected in a geospatial analysis of the competitive abilities of this species (Fig. 19b).

When competition for space was examined specifically between *T. micranthus* against *T. coccinea*, from the perspective of *T. micranthus*, overall, the two species were found to be approximately equivalent in competitive abilities (Fig. 20). This response did not appear to vary between platform populations. The win frequency averaged ~50% on all platforms where both species were found actively competing with each other for space.

Several taxa emerged as common competitors of *T. coccinea*. The first taxonomic group observed to be an important competitor for space was the encrusting sponge *Xestospongia* sp. (with the commensal *Parazoanthus catenularis*). *T. coccinea* was significantly competitively superior to this sponge on all platforms, with an overall success rate of ~75%, ranging from 68-100% (Fig. 21a). Populations on each of the platforms followed this pattern, except for one, exhibiting no significant advantage. A geospatial analysis of the distribution pattern of *T. coccinea*'s competitive win frequencies indicates that it peaks in the SW part of the study area, with a single platform in the same vicinity also showing the lowest win rate (Fig. 21b).

The light grey encrusting sponge *Dictyonella finicularis* was also an abundant competitor for space with *T. coccinea*. The coral was significantly competitively superior to the sponge overall. Competitive success, however, was highly variable with respect to this organism, and significantly different between platforms. Competitive win frequencies varied between 45% and 100% between platform populations (Fig. 22a). The geospatial analysis revealed that the area of greatest competitive success was in the E, with the lowest competitive successes in the SW (Fig. 22b).

Even greater variability was observed in competition between *T. coccinea* and the white encrusting sponge *Haliclona vansoesti*, also common on these platforms. On average, *T. coccinea* did not have any significant competitive edge over this organism, with a mean success rate of 60% (Fig. 23a). However, the level of competitive success varied significantly between platforms, ranging from 30% to 100%; that is, there were significant levels of competitive success on individual platforms, with high variances between platforms. A geospatial analysis revealed that competitive ability peaked in the NE and SW, and was lowest in the W (Fig. 23b).



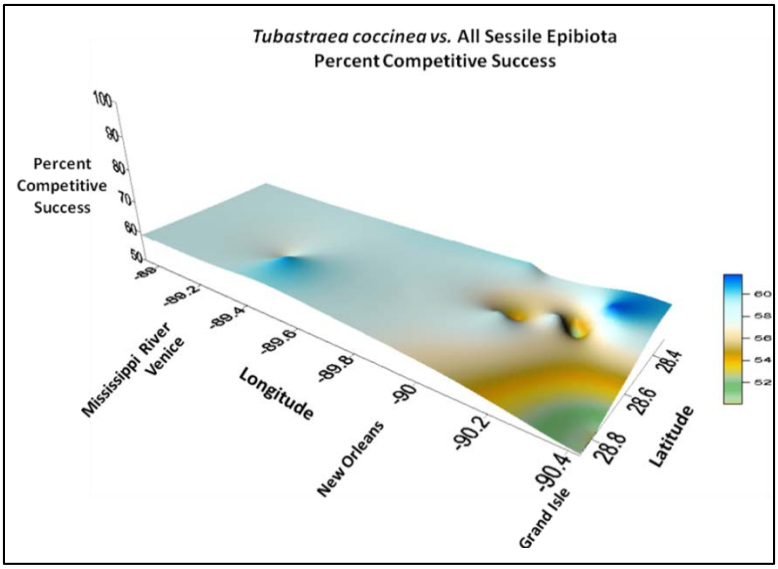




Figure 19. (A) Percent of successes in competition for space between *T. coccinea* and all other sessile epibiota, data pooled. Presented by platform. (B) Geospatial representation of the distribution of competitive wins in the study area.

(A) Mean plus 95% confidence limits shown. Tested for significant variation from 1:1 ratio of wins to losses. Competitive successes significantly higher than draws or losses ($p < 0.001$, Fisher's Exact Test). Also, significant difference between frequency of competitive success between platforms ($p < 0.001$, Goodness of Fit Test, G-statistic).

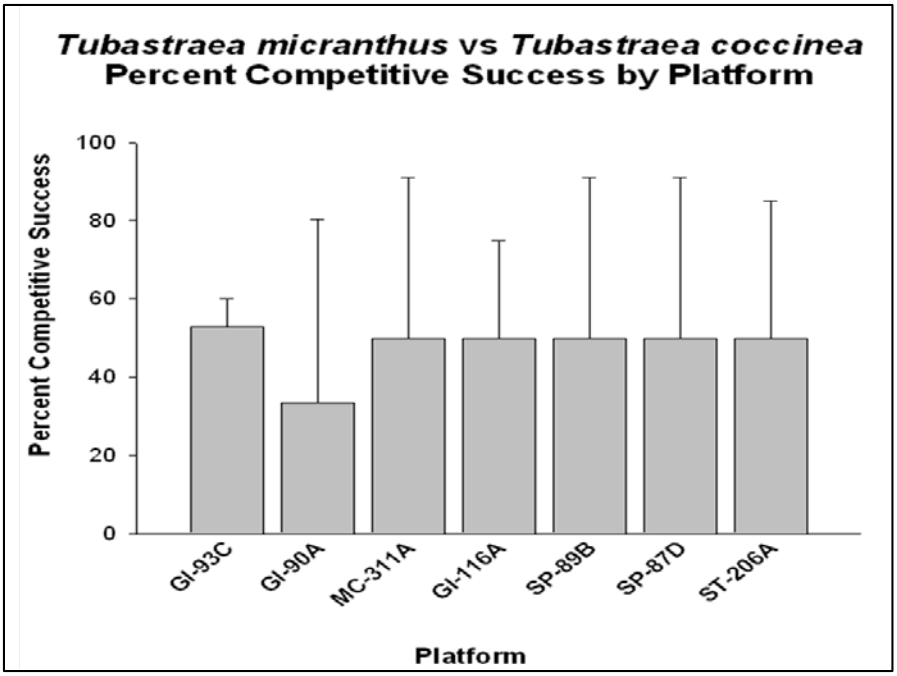
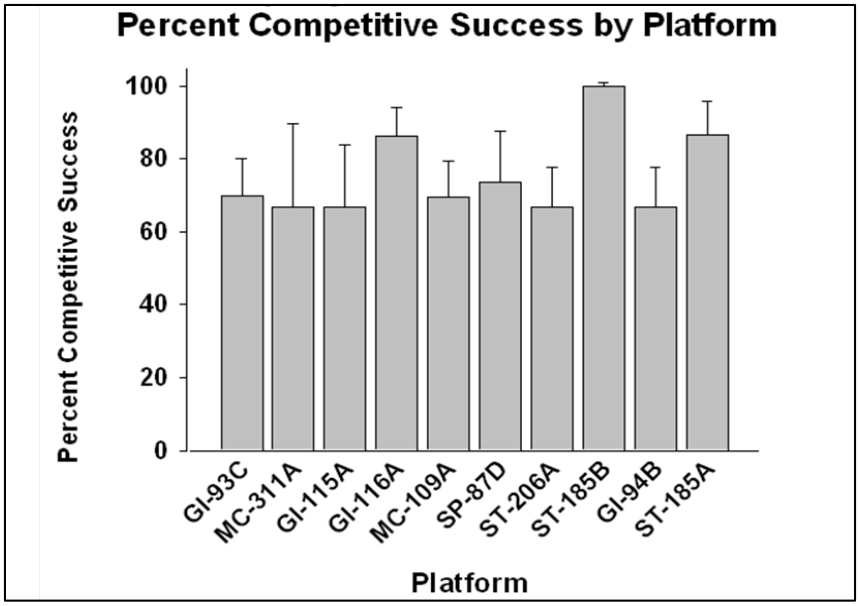



Figure 20. Percent of successes in competition for space specifically between *T. micranthus* compared with *T. coccinea,* from the former's perspective as the target organism. Presented by platform. Mean plus 95% confidence limits shown.



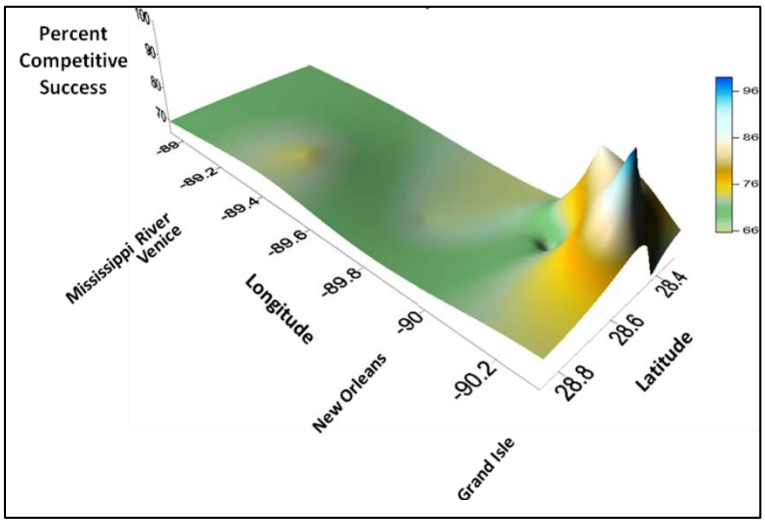
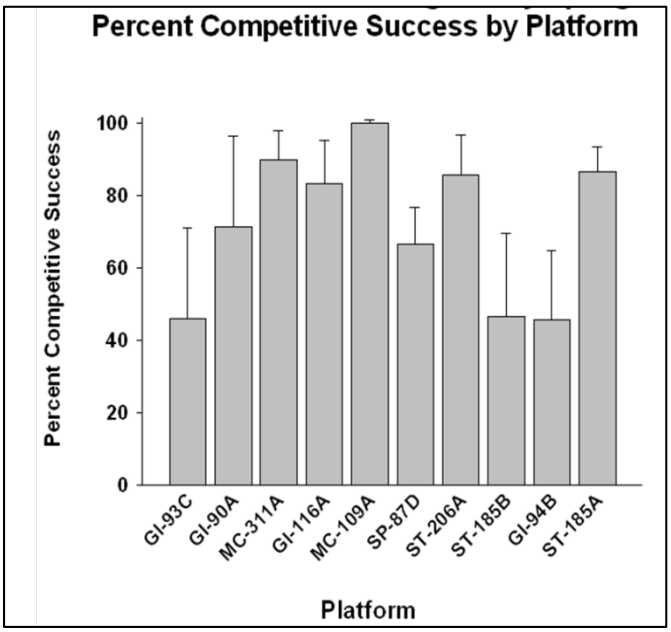




Figure 21. (A) Percent of wins in competition for space between *T. coccinea* compared with the encrusting sponge *Xestospongia* sp. (with the commensal *Parazoanthus catenularis*).). Presented by platform. (B) Geospatial representation of the distribution of competitive wins in the study area.

(A) Mean plus 95% confidence limits shown. Tested for significant variation from 1:1 ratio of wins to losses. Competitive successes significantly higher than draws or losses ($p < 0.001$, Fisher's Exact Test). Also, significant difference between frequency of competitive success between platforms ($p < 0.001$, Goodness of Fit Test, G-statistic).



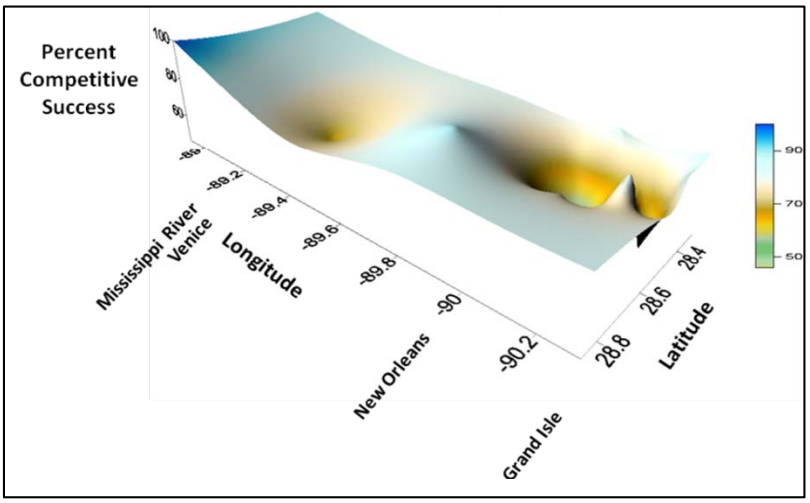
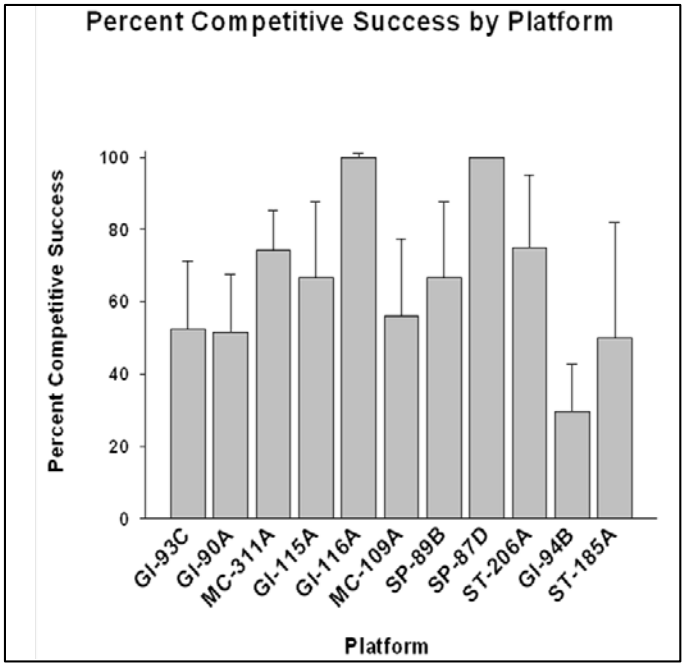




Figure 22. (A) Percent of successes in competition for space between *T. coccinea* and the light grey encrusting sponge *Dictyonella finicularis.* Presented by platform. (B) Geospatial representation of the distribution of competitive wins in the study area.

(A) Mean plus 95% confidence limits shown. Tested for significant variation from 1:1 ratio of wins to losses. Competitive successes significantly higher than draws or losses ($p < 0.001$, Fisher's Exact Test).Also, significant difference between frequency of competitive success between platforms ($p < 0.001$, Goodness of Fit Test, G-statistic).



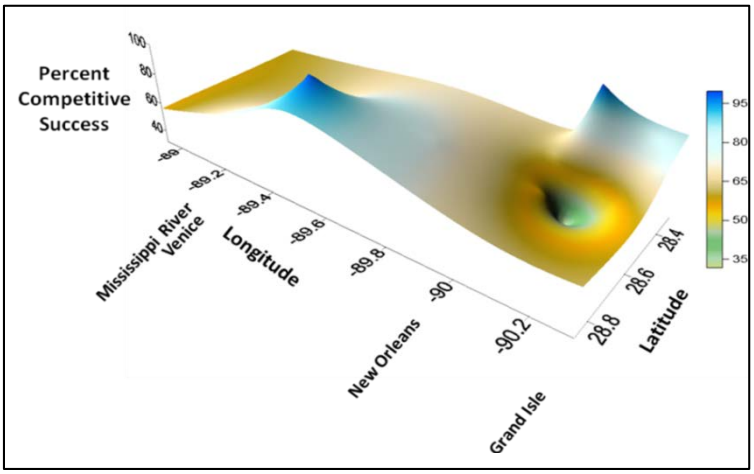



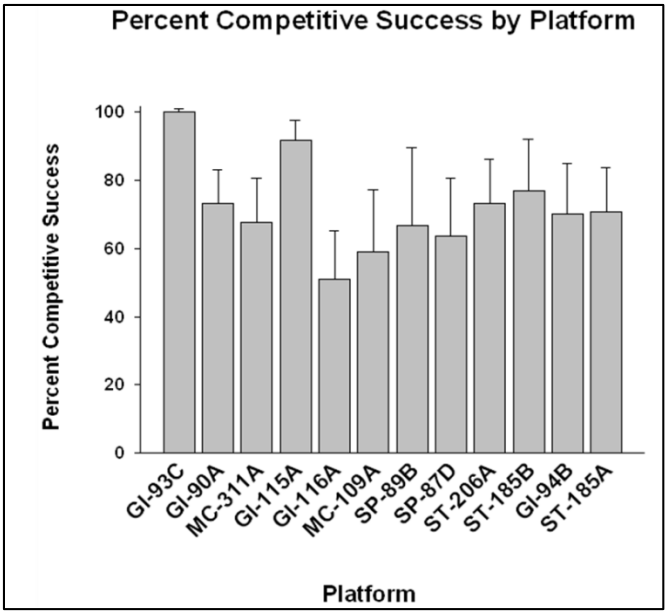

Figure 23. (A) Percent of wins in competition for space between *T. coccinea* and and the white encrusting sponge *Haliclona vansoesti*. Presented by platform. (B) Geospatial representation of the distribution of competitive wins in the study area.

(A) Mean plus 95% confidence limits shown. No significant difference between observed frequency of competitive success or loss, and an expected 1:1 ratio of the two ($p > 0.05$, Fisher's Exact Test). Significant difference between frequency of competitive success between platforms, however ($p < 0.001$, Goodness of Fit Test, G-statistic).

Another abundant competitor for space was the black encrusting sponge *Xestopongia carbonaria*, which occurred as numerous small colonies at all depths. *T. coccinea* was a formidable and significant competitor for space against this organism, averaging ~70% wins (Fig. 24a). This competitive advantage varied greatly and significantly between platform populations, however, ranging from 50–100% between platforms. A spatial analysis of competitive abilities indicated a peak in the SW portion of the study area (Fig. 24b).

The brown encrusting sponge *Mycale carmigropila* represented another abundant competitor for space with *T. coccinea*, and was generally larger in colony size than the *Xestopongia carbonaria*. Again, *T. coccinea* was on average significantly competitively superior to *Mycale carmigropila*, at a frequency of 60% (Fig. 25a). Competitive success varied significantly between platforms, ranging from 50–83%. *T. coccinea* was most competitively successful against this organism in the SW of the study area (Fig. 25b).

The red encrusting sponge *Phorbas amaranthus* was another primary competitor of *T. coccinea*. The coral was significantly successful in competition for space against this sponge, again averaging about 60% competitive wins (Fig. 26a). Success varied significantly between platforms, ranging from 45–100%; success was particularly strong on several platforms. The geospatial distribution of the coral's competitive abilities clearly peaked in the eastern portion of the study area (Fig. 26b).



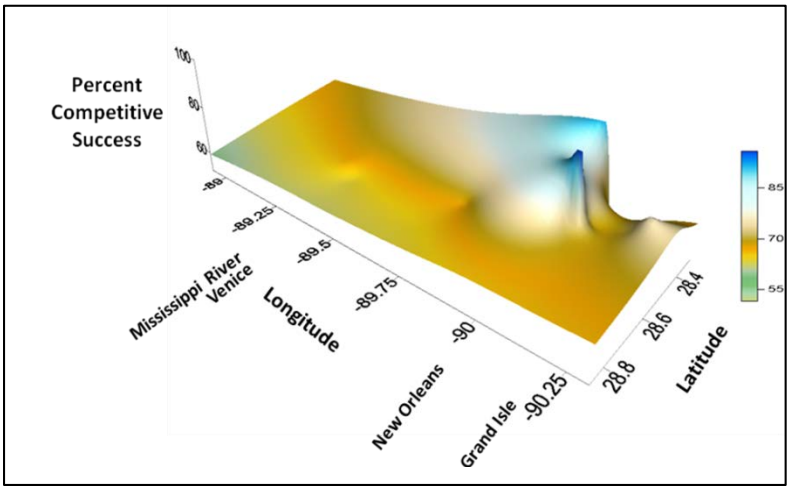
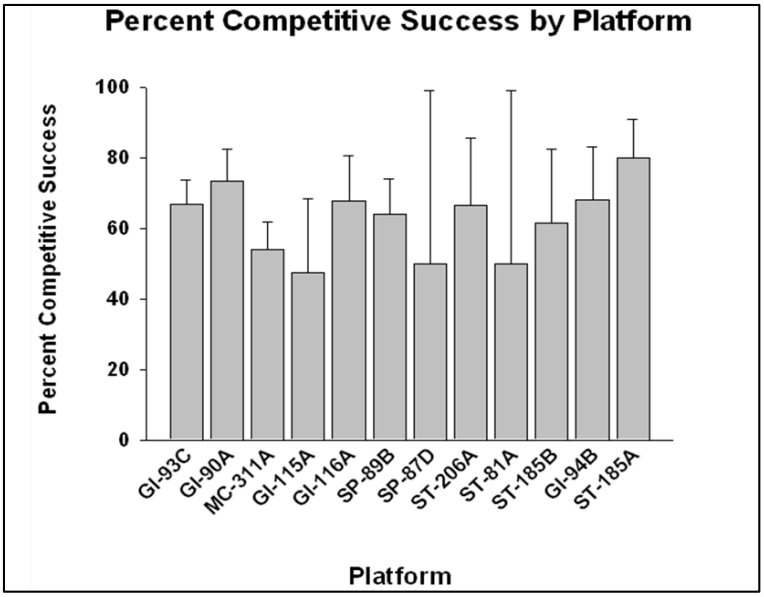




Figure 24. (A) Percent of wins in competition for space between *T. coccinea* and the black encrusting sponge *Xestopongia carbonaria*. Presented by platform. (B) Geospatial representation of the distribution of competitive wins in the study area.

(A) Mean plus 95% confidence limits shown. Tested for significant variation from 1:1 ratio of wins to losses. Competitive successes significantly higher than draws or losses ($p < 0.001$, Fisher's Exact Test). Also, significant difference between frequency of competitive success between platforms ($p < 0.001$, Goodness of Fit Test, G-statistic).



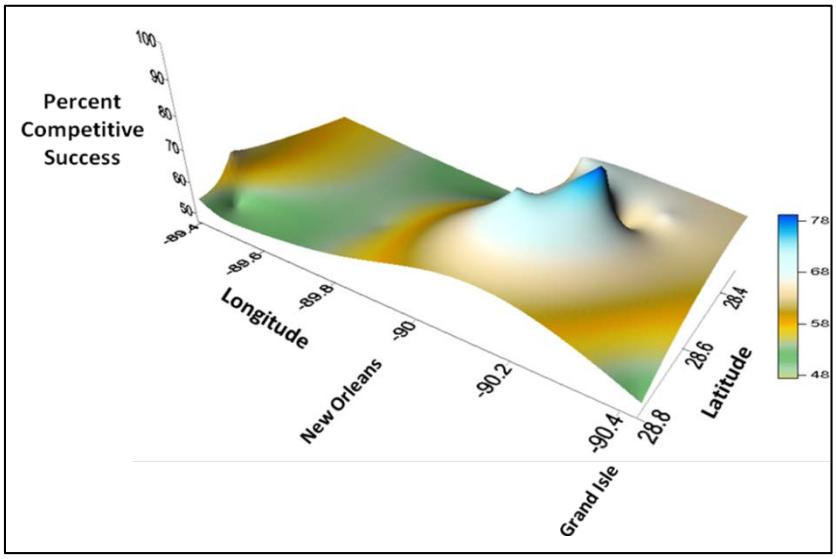
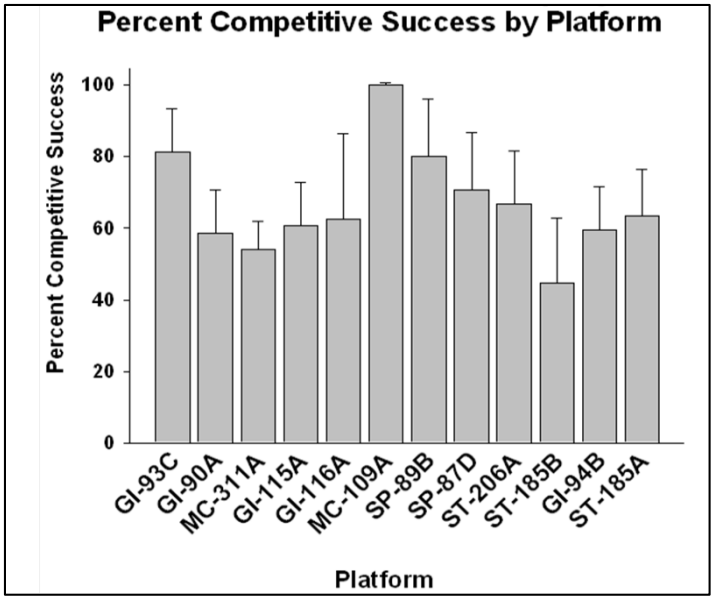




Figure 25. (A) Percent of wins in competition for space between *T. coccinea* and the brown encrusting sponge *Mycale carmigropila*. Presented by platform. (B) Geospatial representation of the distribution of competitive wins in the study area.

(A) Mean plus 95% confidence limits shown. Tested for significant variation from 1:1 ratio of wins to losses. Competitive successes significantly higher than draws or losses ($p < 0.001$, Fisher's Exact Test).Also, significant difference between frequency of competitive success between platforms ($p < 0.001$, Goodness of Fit Test, G-statistic).



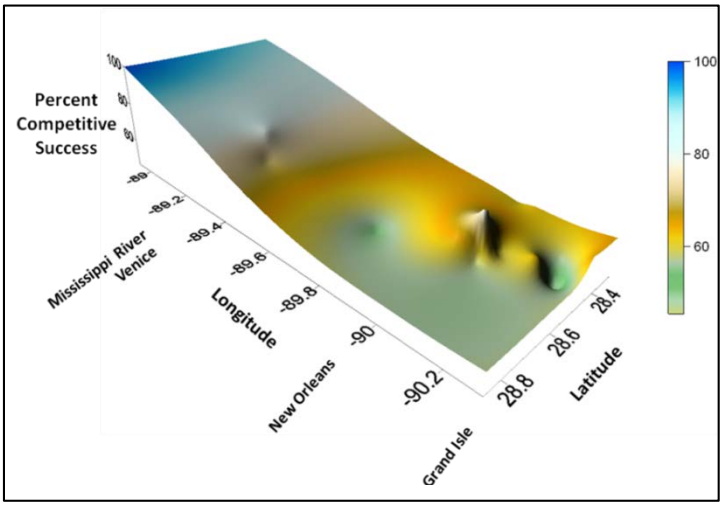




Figure 26. (A) Percent of wins in competition for space between *T. coccinea* and the red encrusting sponge *Phorbas amaranthus*. Presented by platform. (B) Geospatial representation of the distribution of competitive wins in the study area.

Mean plus 95% confidence limits shown. Tested for significant variation from 1:1 ratio of wins to losses. Competitive successes significantly higher than draws or losses ($p < 0.01$, Fisher's Exact Test). Also, significant difference between frequency of competitive success between platforms ($p < 0.001$, Goodness of Fit Test, G-statistic).

# 4. DISCUSSION

## 4.1. POPULATION EXPANSION

Data about the mean colony size of the *Tubastraea micranthus* colonies on these platforms have important implications for potential time and place of colonization by this species. They also have implications for definition of niche specificity and the population dynamics of this species. First, colony size did not peak at GI-93-C where the highest colony densities occurred; it peaked on the MC-311-A platform,  andwas significantly higher than all other survey platforms, and with average colony size clearly falling off in all directions from there. It is possible that these large colonies were afforded a longer period of time for growth, due to an earlier colonization time, and represent the oldest among the platform communities.

In addition, the environment of MC-311A is different from that of GI-93C. GI-93C occurs on the continental shelf in 64 m depth of water, and it periodically receives water from the Mississippi River plume as it meanders back and forth in this region. The plume is, of course, characterized by high turbidity, a high sediment load, high nutrients, and low salinity. On the other hand, MC-311A occurs beyond the edge of the continental shelf, at the head of Mississippi Canyon. It is more frequently characterized by blue water (low turbidity, low sediment load, low nutrients, and a more stable stenohaline environment; Rabalais et al., 1996; Weisberg and He, 2003; Green et al., 2006). Thus, one might hypothesize that *T. micranthus* grows better in a blue-water environment than a coastal one, subjected to typical coastal environmental variability. On the other hand, *Tubastraea coccinea*'s highest densities were found on ST-185B and GI-116A. Both of these sites have environments similar to GI-93-C, and are regularly subjected to water from the Mississippi River plume.

This observation raises an interesting point regarding potential impacts of *Tubastraea micranthus* compared with *T. coccinea*. *T. coccinea* invaded the Caribbean in the 1940s (Cairns, 2000; Humann and DeLoach, 2002; Fenner and Banks, 2004). Since that time, it has spread as far south as Brazil (Figueira de Paula and Creed, 2004) and as far north as the Flower Garden Banks (Fenner, 1999, 2001; Fenner and Banks, 2004), the Florida Keys (Shearer, 2008), and platforms in the northern Gulf of Mexico (Sammarco et al., 2012a). During this period, it has become evident that populations of this species are able to nearly monopolize artificial hard-bottom substrata such as offshore platforms. In no case, however, have there been reports of this species dominating natural coral reef environments, despite the fact that it has been reported to occur on these reefs (Sammarco, 2012b; Hickerson et al., 2006).

We propose that the reason for this deficit of colonies on natural reefs is that *T. coccinea* cannot compete well for space with the natural sessile epibenthic fauna and flora found on a coral reef. On the other hand, there may be naturally occurring predators there that suppress their populations when they occur fully exposed. On these natural reefs, the colonies observed tend to be found in their natural numbers and habitat, which is cryptic and in low numbers, with other ahermatypic corals. The concern here is that the natural environment for *T. micranthus* in the Indo-Pacific is on the upper surfaces of reef substratum, fully exposed (Schuhmacher, 1984). If and when this species encounters a natural coral reef, it is possible that it may be successful at outcompeting naturally occurring sessile epibenthic fauna and flora for space. Although some

studies have been done on the secondary metabolites of *T. coccinea* and *T. tagusensis* (Lages et al., 2010, 2012), to date, none have been done on *T. micranthus*. Its toxicity and degree of palatability to predators, which could potentially control its populations, are currently unknown.

The size-frequency distributions of *T. micranthus* are indicative of a population in an explosive growth phase (McNaughton and Wolf, 1979). In the case of MC-109-A, almost 60% of the colonies are between 1 and 100 $cm^2$ in area while the largest size colony was 1,200 $cm^2$. In addition, the size-frequency distributions were highly consistent from platform to platform; thus, this explosive aspect of population growth is occurring across all newly colonized platforms. The shape of this size-frequency distribution is similar to that of a "wide-based pyramid," described by human demographers to be indicative of human populations with a high growth rate and low doubling times, e.g., India, China, and Indonesia (Miller, 2000).

We believe that we have confirmed that *T. micranthus* has successfully invaded the Gulf of Mexico and is exhibiting signs of producing rapidly expanding populations in the region. Its congener, *T. coccinea*, has already demonstrated formidable capabilities in this area. Preliminary data on depth distribution and competitive abilities (see below) give cause for further concern about the invasion of *T. micranthus*. We believe that *T. micranthus* has the ability for extensive geographic expansion in the Caribbean. If introduced populations are left unchecked, the newly introduced populations will become well integrated into the original community, creating a new community structure and stable equilibrium defining a new set of ecological interactions between species (Mooney and Cleland, 2001; Krushelnycky and Gillespie, 2008).

## 4.2. DEPTH DISTRIBUTION

### 4.2.1. General discussion

Perhaps one of the first and most important results to emerge from this aspect of this study is the finding that *T. micranthus* has the ability to readily reach a depth of 138 m in its new environment. This is more than three times deeper than its reported depth range in its native Indo-Pacific habitat from 40 m (Anon., 2013) to 50 m (Cairns, 2013) in depth. These surveys were most likely performed by SCUBA, with its inherent depth limitations. 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. *T. coccinea*, on the other hand, appeared to be restricted to shallower depths. It primarily ranged from 1–78 m depth. Almost all 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 surveyed 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. First, *T. micranthus* exhibited its shallower depth distributions west of the study area, in the primary plume of the Mississippi River. Its deepest distributions occurred 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). *T. coccinea*, on the other hand, occurred in much shallower waters overall throughout the study region, but it 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, because both are azooxanthellate (Creed, 2006; Cairns, 2013). Temperature probably does not 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* colonized deeper habitats because of lack of space availability in shallower water due to dominance by *T. coccinea*; it was found in shallow water elsewhere. Coral larvae are known to be able to sense pressure (Stake and Sammarco, 2003). It could be that the larvae of these species simply have different preferences for depth ranges for settlement.

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 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 a small sample size effect.)

An analysis of *T. coccinea* populations on six platforms covering both shallow and deep sites, indicated that its depth distribution is clearly more limited than that of *T. micranthus*. *T. 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 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, including 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 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 before choosing one variable or the other as the basis for estimating depth distribution.

### 4.2.2. Implications of depth distribution

Whenever the eradication of a new invasive species is considered, population accessibility is one of the major factors that must be taken into consideration when assessing the potential efficacy of any such attempts (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 population which is not accessible to control or mitigation, the population could possibly still rebound. 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 and time. In addition, in the marine environment, the cost of access increases greatly with increased depth.

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 (Fonseca, 2001).

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. However, preliminary evidence, both field and laboratory, suggests that *T, micranthus* is highly aggressive and capable of outcompeting local sessile epifauna for space (Sammarco et al., 2012d,e; Hennessey and Sammarco, 2014).

## 4.3. COMPETITION FOR SPACE

Two major points may be drawn from the fact that *T. micranthus* is a better competitor for space than the various organisms it encounters on these offshore platforms. First, there is a high probability of success of invasion as this species overgrows and kills its sessile epibenthic neighbors (Vila and Weiner, 2004; Mangla et al., 2011). It should be recalled that the average competitive success frequencies against all species pooled, although variable, do not fall below 50%. Second, this success is variable between platforms. This suggests that we are observing these interactions very early in the successional development phase of these newly disturbed, disequilibrial benthic communities. A stable equilibrium, as defined by extended competitive interactions in the community, has not yet been achieved (MacArthur and Wilson, 1967, MacArthur, 1972). That is, natural selection has not yet eliminated the weaker *T. micranthus* colonies or the weaker members of the competing species. This process would appear still to be in progress at this point in time.

We have evidence to suggest that *T. micranthus* does not grow as well under conditions of high turbidity and high nutrients as *T. coccinea*. The results of the current study support this finding; *T. micranthus* did not compete well here under these turbid conditions. The lowest competitive success frequencies were observed in the SW part of the study region, in the plume of the Mississippi River. Also consistent with the above analytical results is the fact that when competition for space is considered from the perspective of *T. coccinea*, this coral species

performs best in competition in the SW, in the plume of the Mississippi River, and poorly in the NE, at the head of Mississippi Canyon, under blue-water conditions.

The fact that competitive abilities between *T. micranthus* and *T. coccinea* were almost exactly the same when in competition with each other is an indicator that *T. micranthus* may have a capacity for invasion similar to its predecessor. Thus far, there is no evidence indicating that one of these coral species will out-compete the other for space. Indeed, it would appear that they can be expected to coexist in their new environment.

When one considers *T. coccinea* and its competitive win frequency over all sessile epibiota on these platforms, we see some important differences arise between it and *T. micranthus*.The first concerns the average frequency of competitive success, which is 55% and significantly positive. This indicates that *T. coccinea* is still an important competitor in the western Atlantic and is most likely still slowly expanding its range there. Encroachment by *T. coccinea* on space held by other sessile epibiota is most likely slow and difficult; these older communities may well have reached an equilibrium. The *T. coccinea* populations would now appear to be adapted to their new environment. They have been integrated into the community and are coexisting with their neighbors. Competition for space has stabilized, permitting coexistence. The second point is the consistency of the competitive win frequency in this species. There is very low variability in the competitive win frequency between platforms. This reinforces the concept that the older coral populations have reached some level of equilibrium with respect to competitive efficacy in these communities.

Both congeneric coral species have numerous sessile epibenthic species with which they must interact and attempt to procure space required for living, growth, and reproduction. *T. coccinea* has clearly been very successful at this in the Caribbean, as is evident from its current geographic distribution. This study confirms that this competitive success is helping to maintain these populations in their new environments. The quantitative data regarding competition for space within each of the species observed is clear. For example, *T. coccinea* is a strong competitor for space with the encrusting sponge *Xestospongia* sp. (with the commensal *Parazoanthus catenularis*). Both competitors possess stinging nematocysts with which they are most likely capable of defending themselves, but *T. coccinea* is the stronger competitor.

*T. coccinea*'s competitive abilities were also strong with respect to the light grey encrusting sponge *Dictyonella finicularis* and the white encrusting sponge *Haliclona vansoesti*, both of which were encountered frequently. The high frequency of competitive success against these two organisms indicates that this sponge will most likely become less represented in the benthic community, at least on these artificial reefs, as time progresses. The high variability in the observed responses by various platform populations indicates that these competitive interactions have not yet come to equilibrium. In addition, it appears that *Dictyonella finicularis* has a higher probability of out-competing this invasive coral under conditions of high turbidity and nutrient concentrations. The opposite was true for the *Haliclona vansoesti*, which had less of a competitive advantage under those conditions. Competitive abilities in *T. coccinea* are species-specific (Sammarco et al., 1985).

*T. coccinea*'s competitive abilities appeared to be nearly equal to those of the black encrusting sponge *Xestopongia carbonaria*, the brown encrusting sponge *Mycale carmigropila*, and the red encrusting sponge *Phorbas amaranthus*. Thus, there are numerous species which appear to have survived competition for space with *T. coccinea* and will probably survive this coral's continuing expansion throughout the northern Gulf of Mexico and the Caribbean

In conclusion, it would appear that the scleractinian coral *T. micranthus* is as a formidable new invasive species for the northern Gulf of Mexico, as its predecessor, *T. coccinea*, was and continues to be. *T. micranthus* probably invaded during the mid-2000s, and its populations have already expanded from a single platform (Sammarco et al., 2014) to 9 out of 14 platforms in the region south of the Mississippi River mouth in less than a decade . It has also been shown that, unlike *T. coccinea*, it prefers deeper depths (Sammarco et al., 2012c). From the above documentation of *T. micranthus'* competitive abilities against native fauna and flora in the northern Gulf of Mexico, it would appear that its competitive abilities are comparable to *T. coccinea*. It has the potential for being another highly successful invasive species for the Gulf of Mexico and the Caribbean. We now have a deeper understanding of the magnitude of the threat this species may be to native fauna and flora.

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## The Department of the Interior Mission

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering the sound use of our land and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The Department also has a major responsibility for American Indian reservation communities and for people who live in island communities.

## The Bureau of Ocean Energy Management Mission

The Bureau of Ocean Energy Management (BOEM) works to manage the exploration and development of the nation's offshore resources in a way that appropriately balances economic development, energy independence, and environmental protection through oil and gas leases, renewable energy development and environmental reviews and studies.