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Determining the Geographical Distribution, and Genetic Affinities of Corals on Offshore Platforms, Northern Gulf of Mexico

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Author

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March 2014

Prepared under BOEM Cooperative Agreement
M05AZ10668 (32806-36188)
by
Louisiana Universities Marine Consortium
8124 Hwy. 56
Chauvin, Louisiana 70344

Published by

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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CITATION

Sammarco, Paul W. **2014**. Determining the geographical distribution and genetic affinities of corals on offshore platforms, Northern Gulf of Mexico. U.S. Dept. of the Interior, Bureau of Ocean Energy Management, Gulf of Mexico OCS Region, New Orleans, LA. OCS Study BOEM 2014-011. 75 pp.

ABOUT THE COVER

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ACKNOWLEDGEMENTS

Many thanks to those who assisted us with diving, sample collection, topside, laboratory, and other support: A. Atchison, A. Barker, G. Bunch, C. Chauffe, J. Collins, J. Conklin, J. Culbertson, B. DeFelize, T. Dempre, D. Dowdy, K. de Musert, T. Empey, C. Gentry, R. Harris, D. Hill-House, C. Horrell, S. Kolian, G. Kozlowski, H. Leedy, L. Logan, D. Marcel, Lt. Col. D. Perrenod, G. Rainey, C. Salmonsen, T. Sebastian, J. Sinclair, G. Speyrer, J. Van der Ham, K. Wheelock, and D. Woodall. H. Boudreaux, W. Hebert, C. Luke, S. Parrott, and B. Bourge assisted with accounting; J. Fontenot, A. Lirette, and F. Tung with data analysis; M. Dear of Aeigir, Inc. with ROV Operations; T. Bachmann, T. Berbner, T. Cothren, and L. Ong of the ADR German TV. We also thank the crew of the M/V *Fling* (Gulf Diving, Inc.): K. Bush, J. Byron, P. Combs, J. Denton, L. DeWeese, J. Dibble, D. Fanning, A. Felth, K. Foster, G. Harding, J. Heiser, Jason, S. Kerr, T. Kilpatrick, M. McReynolds, S. Richman, J. Smale, R. Travis, R. Widaman; and the oil, gas, and other companies and their staff who provided us access to their offshore platforms and other assistance: Anadarko Petroleum: J. Davidson, S. Hathcock, S. Jensen; Apache Oil: J. Bordelon, G. Thibodaux; Chevron Texaco Exploration and Production: D. Lucas, K. Mire, S. Ulm; Coastal Oil and Gas, Devon Oil: B. Gary, R. Hebert, V. Mile, B. Moody; Dominion Exploration and Production: B. Ventura, K. Schlogel, M. Sledge; El Paso Energy: C. Thornton, S. Lesiker; Forcenergy/Forest Oil: W. Fontenot, W. Myers, G. Ruiz; Kerr-McGee Oil and Gas: C. Bradford; Merit Energy: T. Lambert, P. Maiberger; Newfield Exploration: A. Comeaux, E. Haas, M. Prosper, J. Zernell; Noble Energy: S. Shuman; Offshore Energy; UNOCAL: D. Crusan, M. Hebert; Samedan Oil: R. Bemis, S. Berryhill, S. Mulbert, T. Spintzenberger, P. Tullos; and W&T Offshore: S. Schroeder; United Space Alliance: A. Knight. We thank J. Benzie for suggesting the use of AFLPs on coral tissue for the molecular genetics. We also thank L. Rouse of the Louisiana State University Coastal Marine Institute and the U.S. Department of Interior Bureau of Ocean Energy Management for their support and for funding this study under Cooperative Agreement #32806/TO#36188 to PWS.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ABBREVIATIONS, ACRONYMS, AND SYMBOLS

AFLP	Amplified Fragment Length Polymorphism
AFLPOP	Amplified Fragment Length Polymorphism Population Allocation Analysis
AMOVA	Analysis of Molecular Variance
ANOVA	Analysis of Variance
BOEM	Bureau of Ocean Energy Management
FGB	Flower Garden Banks
GOM	Gulf of Mexico
km	kilometers
m	meters
nmi	nautical miles
ft	feet
PCR	Polymerase Chain Reaction
pg	picograms
s	second(s)
SST	Sea surface temperature
STRUCTURE	Molecular genetic statistical analysis which analyzes for population genetic structure
x g	times gravity

EXECUTIVE SUMMARY

Cross-Shelf Platform Coral Study

There are approximately 3,200 oil and gas platforms in the northern Gulf of Mexico (GOM). These platforms provide hard substratum that extends from the bottom of the continental shelf up through the sea surface, in a region where such substratum has been rare in recent geological time. Major exceptions to this are the Flower Garden Banks (FGB), coral reefs which occur ~190 km S-SE of Galveston, Texas. Our previous Phase 1 study of 13 platforms surrounding the FGB provided evidence that suggests that the presence of these platforms were associated with substantial amounts of Caribbean reef fauna (Sammarco et al., 2004).

In the current study, we have determined the range of occurrence of corals on oil and gas platforms in the northern GOM, their distribution and abundance over this broad geographic range, and their species richness patterns. Thirty-five platforms along four transects, spanning from 20 km offshore to the edge of the continental shelf or beyond, were examined (Figure 4). Transect I was in the Matagorda Island (MI) lease area, extending S-SE from Corpus Christi, Texas; Transect II bisected the High Island (HI) lease area, running S from Lake Sabine, Texas to 10 km beyond the shelf edge; Transect III ran across the South Timbalier (ST) lease area, S of Terrebonne Bay, Louisiana; and Transect IV extended across the Main Pass (MP) lease area, S-SW from Mobile, Alabama. Transect II was closest to the FGB. Coral density and species richness data were also included from our previous Phase 1 study (Sammarco et al., 2004), encompassing an additional 13 platforms in the FGB area to provide as complete a picture as possible of these variables in the northern GOM. Visual surveys of corals were conducted down to a maximum depth of 37 m by teams of SCUBA divers. We attempted to determine whether extensive scleractinian coral populations have colonized these platforms by quantifying the distribution and abundance of scleractinian corals (hermatypic and ahermatypic) and determining population characteristics.

Corals occurred on many of the platforms in the northern GOM. Coral species richness (number of species) in the northern GOM peaked on the coral reefs of the FGB and was three times higher than the maximum species richness observed on any individual oil and gas platform. Coral species richness was very low on inshore platforms. Twelve species of coral were found, encompassing nine hermatypic corals and three ahermatypic corals. In order of abundance, the most abundant zooxanthellate hermatypic corals found on platforms were *Madracis decactis*, *Diploria strigosa,* and *Montastraea cavernosa*. The other hermatypes observed on platforms were *Porites astreoides, Madracis formosa, Colpophyllia natans*, *Stephanocoenia intercepta, Stephanocoenia michelinii*, and *Millepora alcicornis.* All were members of the Scleractinia, except for *Millepora,* which is a member of the Hydrozoa. The three ahermatypic corals found on platforms were *Tubastraea coccinea, Oculina diffusa*, and *Phyllangia americana.* All of these three were scleractinians. *T. coccinea* was the most abundant, by far.

The total density of hermatypic/zooxanthellate corals peaked on platforms in Transect III, south of Terrebonne Bay, Louisiana. These high densities extended to the north, toward shore in this region. Higher densities were also noted in the vicinity of the FGB, in Transect II. Coral densities on platforms dropped to low levels outside of this region. In no case were hermatypic corals observed within ~50km of shore. Densities of *M. decactis* were found to drive overall density of hermatypic corals, peaking on platforms in the north central GOM at the edge of the

continental shelf, south of Terrebonne Bay, Louisiana, in Transect III. Densities of *D. strigosa*, the second dominant in the platform coral community, peaked around the FGB. Its densities extended northward towards Port Arthur-Lake Sabine (Transect II). Densities of *M. cavernosa* were bimodal, with a higher peak near the FGB (Transect II) and a lower peak on east side of the Mississippi River mouth off Mobile, Alabama in Transect IV.

Density of all corals combined, including hermatypic/zooxanthellate and ahermatypic/ azooxanthellate types, was *four orders of magnitude* higher than density of hermatypes alone. This density peaked on platforms in the central and eastern regions of the northern GOM, with tens of thousands of colonies occurring south of Terrebonne Bay, Louisiana and Mobile, Alabama (Transects III and IV). This density pattern was driven entirely by ahermatypic/azooxanthellate corals, which far surpassed hermatypic corals in density. The pattern of total ahermatypic/ azooxanthellate corals in the northern GOM was driven entirely by densities of *T. coccinea*. Densities of this species were tens of thousands per 1,000 m^2.

Species richness (S, number of species) of ahermatypic corals was highest in the far western sector of the northern GOM, south of Matagorda Island, Texas (Transect I). In three of the transect areas, unlike the hermatypes, species richness peaked in mid-shelf and inshore areas. The peak in Transect I was further offshore. Richness generally decreased from west to east. The peak in Transect I indicated that the FGB were most likely not the source of ahermatypic corals in the northern GOM and that the ahermatypic corals are most likely derived from the southern GOM off Mexico or from the Caribbean.

Molecular Genetics Study

A previous study of 13 platforms surrounding the FGB (Sammarco et al. 2004) demonstrated that the presence of these platforms has facilitated the biogeographic extension of Caribbean reef fauna. However, there was a question about the origin of those corals and their genetic affinity with coral populations on the platforms and the FGB (Atchison et al. 2008). Earlier studies suggested that hermatypic coral populations were highly independent, most likely due to Founder Effect (Futuyma, 1998). Patterns of genetic affinity among coral populations throughout the entire northern GOM were not known. Here, we ask, "What are the patterns of genetic affinity in these populations for both hermatypic and ahermatypic corals?"

To determine the genetic affinity between coral populations across the northern GOM, we sampled coral tissue from populations of two species occurring on oil and gas platforms there: one hermatype, *M. decactis*, and one ahermatype, *T. coccinea*. The same transects used for the cross-shelf platform coral study were examined for the molecular genetics study (Figure 4; see section 2.1 for a description of the transects). Samples of *M. decactis* were taken from every colony encountered by teams of SCUBA divers, up to 30 samples per platform; thus, the entire population was sampled between depths of 8 m and 37 m. Because of the extraordinarily high abundances of *T. coccinea*, populations of this species were sub-sampled. Divers collected samples haphazardly, placed them in pre-labeled ZipLock® bags, and recorded the platform and depth from which the collection was made. The bags were returned to the support vessel and logged. A minimum of 30 samples of *T. coccinea* was collected from each platform.

Two cm^2 tissue samples were preserved in SED buffer (saturated NaCl, 250 mM EDTA, pH 7.5, 20% DMSO) to preserve the DNA and were returned to the laboratory for processing. Genetic variation was assessed using the DNA replication/polymerase chain reaction (PCR) technique of Amplified Fragment Length Polymorphisms (AFLPs). This is a DNA-fingerprinting technique that detects polymorphisms based upon the selective PCR amplification of a subset of numerous restriction fragments. These fragments are generated by two different restriction enzymes.

All samples were checked for zooxanthellar DNA contamination using PCR techniques developed by laboratories at the University of Buffalo and LUMCON (Brazeau et al. 2005; Atchison et al. 2005, 2008; Sammarco et al. 2012). Extra caution was taken in processing samples through all procedural steps to maximize repeatability of results. Samples were processed in large lots containing members from all populations to distribute any error potentially introduced by reaction conditions uniformly between populations in an unbiased fashion. All PCR reactions were run using one machine and the same thermal cycle profiles. The large number of polymorphic markers generated by AFLPs allowed for the use of highly sensitive statistical analytical techniques. We used the population allocation techniques AFLPOP and STRUCTURE.

STRUCTURE revealed that genetic affinity between *M. decactis* populations on the platforms was highest south of Port Arthur-Lake Sabine, Texas (Transect II), which was closest to the FGB, and decreased primarily with distance to the east. A slight increase in genetic affinity in the eastern sector (Transect IV) indicated some isolation between the populations from different sides of the Mississippi River (Transects III and IV).

STRUCTURE also revealed a similar genetic affinity pattern between populations of *T. coccinea*, which was highest in the west, off Matagorda Island, Texas (Transect I). Genetic affinity generally decreased to the east, although only slightly. A precipitous drop in genetic affinity off of Mobile, Alabama indicated a dramatic difference in populations between that area and other populations to the west of the Mississippi River, indicating that this hydrographic feature most likely represents a formidable barrier to coral larval dispersal in this region.

STRUCTURE identified a "point-drop" in genetic affinity for both *M. decactis* and *T. coccinea* off Terrebonne Bay, Louisiana. The point-drop was more pronounced for *M. decactis* than for *T. coccinea*, but indicated that a population very different from the others in the northern GOM exists here. It is possible that these populations could have been seeded from sources other than the FGB, possibly by the Loop Current derived from the Caribbean Current, or a jet current originating from the southern GOM.

AFLPOP analyses revealed that *M. decactis* populations off Terrebonne Bay, Louisiana and off Mobile, Alabama were almost 100% distinct from each other, exhibiting almost no cross-population recognition. Home population recognition on platforms within a transect was extremely high, but cross-site recognition between transects on either side of the Mississippi River was extremely low.

These results indicate that larval dispersal across the river mouth, and even between populations on platforms within a transect on either side of the river, was highly limited. This same trend of

no population recognition across the river mouth was even stronger in *T.coccinea*. However, self-allocation to home sites on platforms was more highly variable, and cross-site recognition between the platforms was higher than in *M. decactis*. This indicates that *T. coccinea* has higher effective larval dispersal and recruitment capabilities than *M. decactis* and therefore exhibits greater gene flow.

1.0 INTRODUCTION

1.1 EXPANSION OF CORAL COMMUNITIES THROUGHOUT THE NORTHERN GULF OF MEXICO THROUGH OFFSHORE OIL AND GAS PLATFORMS

1.1.1 General Background

Since the 1940s, approximately 40,000 oil and gas wells have been drilled in the northern GOM (Francois, 1993). There were 3,600 production platform structures servicing these wells in 2003, (Francois, 1993, Knott, 1995, Dauterive, 2000; Figure 1), and ~3,200 platforms remaining in 2011 (USDOI, BOEM, 2012). These platforms extend from the bottom of the continental shelf through the water's surface, and provide hard substratum for colonization by a variety of reef organisms (Gallaway and Lewbel, 1981; Driessen, 1989; Bright et al., 1991; Adams, 1996; Boland, 2002; K. Deslarzes, pers. comm.). The northern GOM has historically possessed little hard substratum in shallow water in recent geological time (Curray, 1965a,b; Blum et al., 2001; Frost, 1977, Schroeder et al., 1995, Blum et al., 1998). The Flower Garden Banks (FGB) is an important exception to this rule, because they have developed on top of large salt diapirs (Gross and Gross, 1995), rising to ~18 m of the water's surface. They possess a well-developed set of coral reefs, the only ones in the northern GOM (Rezak et al., 1985, Bright et al., 1992, Gittings, 1992, 1998; Sammarco et al., 2002, Sammarco and Atchison, 2002, 2003).

The FGB are considered to be among the most isolated coral reefs in the western Atlantic (Bright, 1981; Rezak et al,. 1985, Snell et al., 1998; Sammarco et al., 2004). They occur ~110 nmi south-southwest of Galveston, Texas (Rezak et al., 1985) and have a healthy coral community, as has been inferred from observations of high coral cover (Aronson et al., 2005; Precht et al., 2008), mass coral spawnings (Bright et al., 1992; Gittings et al., 1992), and high recruitment levels (Gittings, 1992; Sammarco and Brazeau, 2001; Brazeau et al., 2011 Sammarco et al., 2012b).

There are 37 named banks protected by BOEM on the continental shelf of the northern GOM (Hickerson et al., 2006; Schmahl and Hickerson, 2006), including the FGB (Figure 2). Most banks, other than the FGB, occurring offshore in "blue water" (e.g., Rankin-1, Rankin-2, Bright, Geyer, Elvers, Claypile, etc; Rezak et al. 1985, Lugo-Fernandez et al., 2001, G. Boland, pers. obs.) are too deep or lack other appropriate environmental conditions for development of true coral reefs (actively growing reefs built entirely of calcium-carbonate, secreted by hermatypic corals). However, some banks do possess populations of reef-building corals, including Stetson, Bright, Sonnier and MacNeil Banks (Schmahl et al., 2005; Hickerson et al., 2006).

Sea level in the GOM has been variable throughout recent geological history (Curray, 1965 a,b; Blum et al., 2001; Frost, 1977, Schroeder et al., 1995, Blum et al., 1998). When sea level was 30 m below the present level, during the late Pleistocene and the Holocene epochs, banks known to exist now may well have supported coral reefs. It is possible that the northern GOM supported dozens of reefs at the edge of the continental shelf since that time (Rezak et al., 1985).

The FGB now share the northern GOM with thousands of oil and gas production platforms, providing thousands of artificial islands with substrate suitable for settlement that otherwise would not exist. Over a period of decades, benthic communities, including hermatypic

scleractinian corals, have developed on these platforms (Bright et al., 1991; Sammarco et al., 2004; G. Boland, pers. comm., unpub. data; K. Deslarzes, pers. comm.).

There is no question now that these oil and gas platforms harbor hermatypic scleractinian corals (Bright et al, 1991; Boland, 2002; Sammarco, 2002a,b, 2003, 2005; Sammarco et al., 2004; K. Deslarzes, pers. comm.; pers. obs.). In fact, it is possible that these platforms have increased the stability of the coral community on the Banks and on the platforms themselves in this region (Sammarco et al., 2004; Atchison et al., 2006, 2008). Observations of scleractinian corals on platforms were originally made in the 1980s (T. Bright, Q. Dokken) and 1990s (Bright et al., 1991, Boland 2002, K. Deslarzes, pers. comm.; pers. obs. all authors). Quantitative data were collected in later studies (Sammarco et al., 2004). Platforms have clearly assisted in the biogeographic expansion of corals in the northern GOM (Sammarco et al., 2004; Atchison et al., 2008; Brazeau et al., 2011). Population expansions of this sort have been well-documented in both terrestrial and marine environments, by "leap-frogging" or "stepping stone" mechanisms (Elton, 1958, Futuyma, 1998; Gold et al., 2001). A good example is the expansion of reef fish populations in association with the introduction of oil and gas platforms (Shinn, 1973; Winfield, 1973; Sonnier et al., 1976, Boland et al., 1983, Shinn and Wicklund, 1989, Love et al., 2000, Pattengill et al., 1997, Rooker et al., 1997, Childs, 1998; Schroeder et al., 2000).

Coral reefs are experiencing a severe decline in health globally. Mass coral mortalities caused by bleaching, disease, poor fishing techniques, nutrient enrichment, etc. (Sammarco, 1996, Souter and Linden, 2000, Hughes et al., 2003, McClanahan et al., 2008, Sammarco, 2009, Sammarco and Strychar, 2009, 2010, Strychar and Sammarco, 2010). We now have evidence that demonstrates that at least in one system, the GOM, coral populations are expanding their distributions through the colonization of oil and gas platforms.

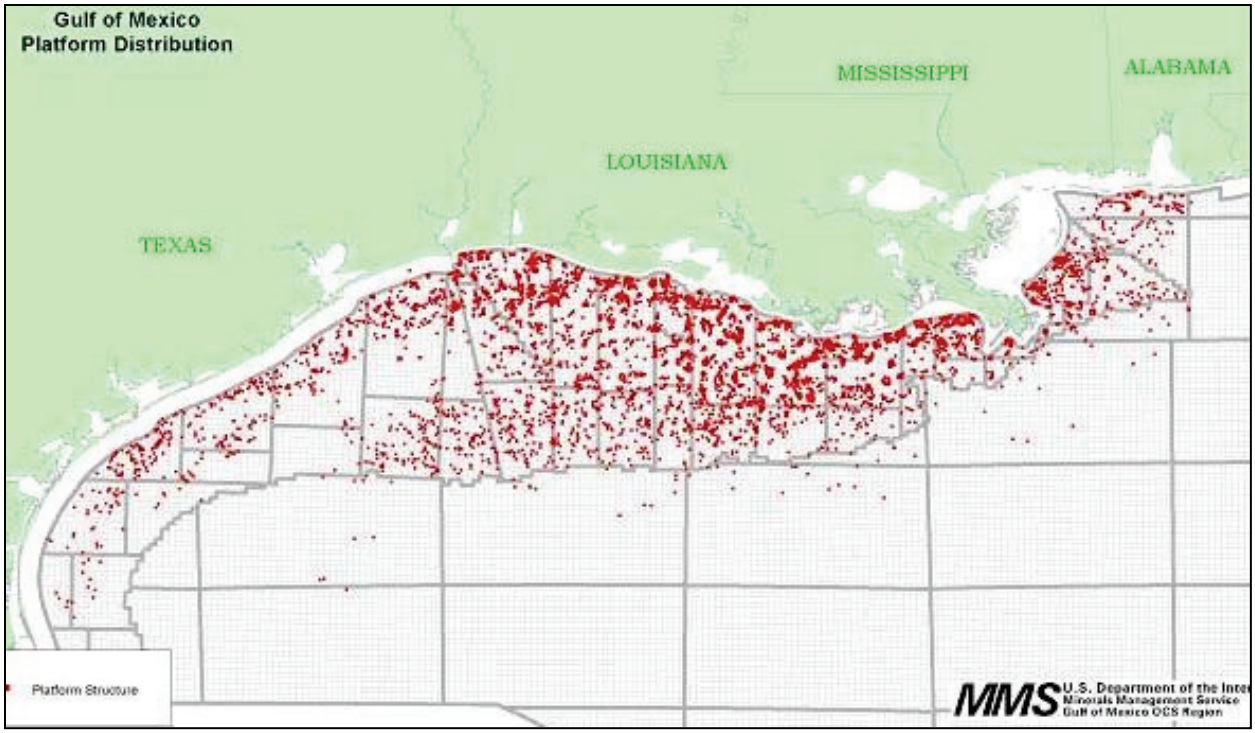


Figure 1. Map of the northern GOM, indicating locations of oil and gas platforms in 2003.

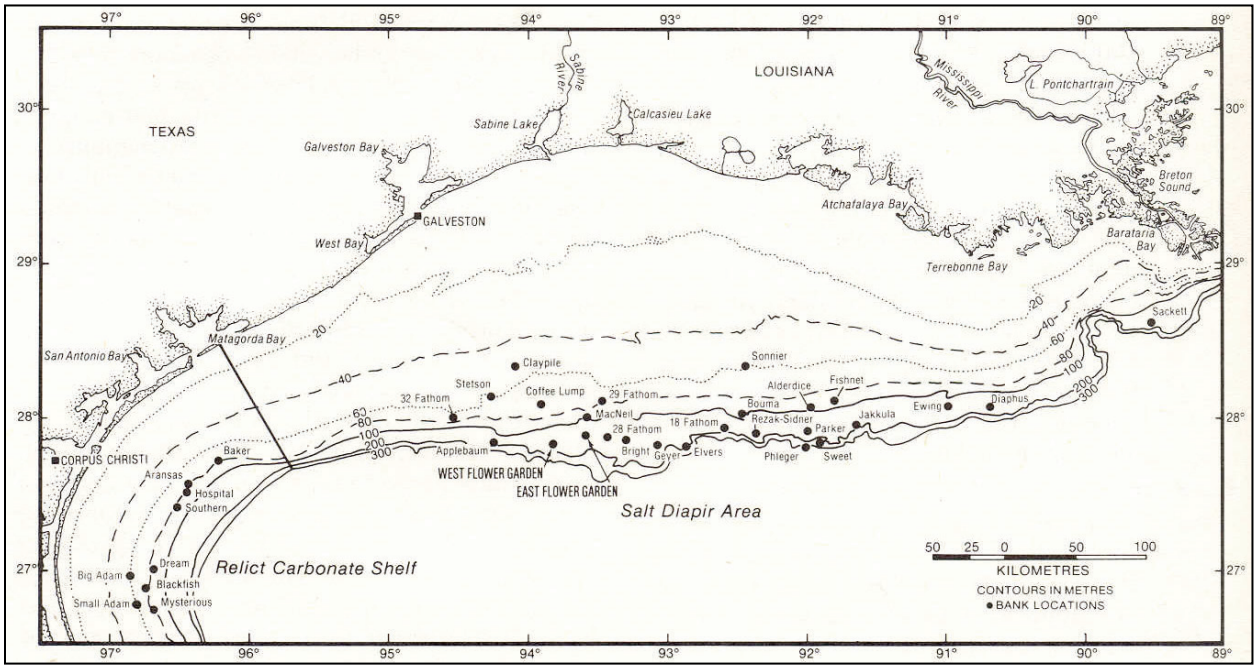


Figure 2. Map depicting location of the East and West FGB, and other major banks on the continental shelf of the northern GOM (from Rezak et al., 1985).

1.1.2 Coral Larval Dispersal and Gene Flow

Exchange of coral larvae would probably have been relatively high in the late Pleistocene and Holocene epochs because of the broad distribution of the many shallow, submerged banks in the

northern GOM at that time. Original expansion of these coral populations would most likely have followed the "Island Model" of gene flow (one way gene flow from a large continental "mainland" population to smaller island populations; see Futuyma, 1998 for description). As sea level rose over the next 6,000–10,000 years, the reefs drowned. The FGB became two of the few true coral reefs in the northern GOM remaining. Some of the shallowest reefs nearest to the FGB are those off the northern coast of Yucatan Peninsula (Alacran and associated reefs, 650 km); Tampico, Mexico (700 km); and the Florida Keys (1,090 km).

Adult corals are sessile; therefore, colonization of remote habitats such as the FGB by corals is achieved by larval dispersal (Sammarco, 1994). Because the FGB are isolated by hundreds to thousands of kilometers from neighboring coral reefs (Rezak et al., 1985), the probability of colonization by larvae from neighboring reefs is small (Sammarco and Brazeau, 2001). Coral larvae can travel hundreds and possibly thousands of kilometers to successfully settle on remote reefs (Richmond, 1981, 1987), but the probability of actually reaching a distant target site and of settling successfully there is low. A single platform in 33 m of water can present ~8,100 sq m of hard surface to the surrounding waters (Shinn, 1974). In the absence of these platforms in the northern GOM, survivorship of coral larvae derived from the FGB or other reefs in the region would be lower due to larval mortality after extensive dispersal, attempts to settle on soft bottom, or being transported into nearshore habitats unsuitable for settlement (low salinity, low temperature, high turbidity, etc.).

Gittings (1992) conjectured that because of self-seeding of coral larvae within the Bank system, the FGB were self-sustaining. Sammarco and Brazeau (2001), Atchison (2003, 2005, 2008), Brazeau et al. (2005, 2011), Atchison et al. (2008), and Sammarco et al. (2012) have presented molecular genetic data to support this hypothesis, suggesting that self-seeding is dominant there at multiple spatial scales. Brazeau et al. (2005) presented evidence for self-seeding based on comparisons between adult populations of *Agaricia agaricites* from the FGB, the Florida Keys, and the Bahamas, and also using newly-settled spat collected from the FGB (Brazeau et al. 2008, 2011). We have found similar results by examining 13 platforms for corals and attempting to determine genetic population structure and genetic affinities in *Madracis decactis, Diploria strigosa,* and *Montastraea cavernosa* from the FGB and those platforms bearing these species within a 45 km radius of that site (Atchison et al., 2008; Brazeau et al., 2008). Lugo-Fernandez (1998; Lugo-Fernandez et al., 2001) has described meso-scale circulation patterns near the FGB which could support self-seeding there (also see Sammarco and Heron, 1994 for a general discussion).

External sources for seeding the FGB have yet to be confirmed. Larvae may be derived from the Tampico region or Bahia de Campeche, Mexico (Salas-de-Leon et al., 1998) by transportation by the Western Boundary Current (Vidal et al., 1999); or possibly from the Cozumel and Cancun regions by transportation north by the Caribbean Current into the GOM or by jets traveling north from the Alacran region and then west by the Loop Current (Sturges and Blama, 1976, Hamilton et al., 1999; Lugo-Fernandez and Gravois, 2010). It is also possible that currents may transport larvae from the Florida Keys, including the Tortugas Bank and Pulley Ridge (Jarrett et al., 2000; also see Meyers et al., 2001) to the western GOM (see Section 4.1.1 below for discussion and Figure 18 for graphic representation of currents). However, our data on the molecular genetics of coral spat at the FGB suggest that corals are not seeded from the eastern GOM (Brazeau et al.,

2005). Our earlier studies indicated that the FGB spat are 100% differentiable from adults from the Bahamas and Florida Keys.

A high degree of self-seeding is not necessarily a sign of long-term ecosystem stability, for self-seeding carries with it risk. For example, in the late 1970s and early 1980s, reefs of the Pacific coast of Panama–well isolated from those of the central and western Pacific–suffered mass coral mortality because of bleaching caused by El Niño and associated high sea surface temperatures (SSTs) (Glynn, 1994). Two hydrocoral species were driven locally extinct (Glynn and de Weerdt, 1991). Re-seeding of these communities must come from neighboring communities and may require long periods of time, particularly if remote. Time required for population regeneration is determined, in large part, by the density of adults. It is also determined by the balance between cross-seeding (connectedness between coral communities) and self-seeding.

1.1.3 Objectives

The objectives of this study were as follows:

- To determine the extent to which coral communities have developed on oil and gas platforms in the northern GOM;
- To determine population densities of the coral species on those platforms;
- To determine the geographic pattern of distribution of those populations; and
- To examine patterns of coral species richness on platforms along and across the continental shelf of the northern GOM.

1.2 GENETIC CONNECTIVITY IN CORALS ACROSS THE NORTHERN GULF OF MEXICO, WITH RESPECT TO OIL AND GAS PLATFORMS AND THE FLOWER GARDEN BANKS

1.2.1 Background: Genetic Affinity in Coral Populations

Before the 1940s, the bottom of the GOM was characterized by terrigenous, sandy muds with little habitat diversity (Rezak et al. 1983, Scarborough-Bull 1989). During that decade, offshore drilling for oil and gas began and the number of production platforms increased steadily, spreading southward across the continental shelf of the GOM. Those platforms served as substrate for colonization of numerous marine organisms, and this has been continuing. The platforms extend up from the seafloor through the euphotic zone and above the water's surface, creating "islands" and providing hard substrate in open water (Shinn, 1974) that would otherwise not be available to benthic, demersal, and pelagic marine organisms. It has been estimated that a 200 ft. platform jacket can provide acres of hard substrate, supporting algae, barnacles, mussels, and other sessile epibenthic invertebrates (Driessen, 1989; Scarborough-Bull, 1989). In earlier studies, we and others have documented the presence of both hermatypic (zooxanthellate, reef-building) and ahermatypic (azooxanthellate, non-reef-building) scleractinian corals on many of these platforms (Sammarco et al., 2002, 2003, 2004, 2006; Sammarco et al., 2004; also see Bright et al., 1991).

The only true coral reefs in the northern GOM are the FGB NOAA Flower Garden Banks National Marine Sanctuary (Dokken et al., 2002), located ~190 km SE of Galveston, Texas. These banks are now surrounded by oil and gas platforms. The FGB are defined by two banks: the East Bank (27º54'32" N, 93º36' W) and the West Bank (27º52'27" N, 93º48'47" W; Bright et al., 1984; Rezak et al., 1983; see Figure 3). They approach the water's surface to within 18m (Lugo-Fernandez et al., 2001). Calcium carbonate reefs have developed on the caps of the FGB (Bright et al., 1984; Dokken et al., 1999) which are productive (Rezak et al., 1985) and healthy, being characterized by 24 species of hermatypic corals (Bright et al,. 1984; Gittings et al., 1992, Lugo-Fernandez et al. 2001; Dokken et al., 2002). The closest reefs to the FGB are the Lobos-Tuxpan system that are located 13 km off Cabo Rojo, Mexico, $\geq$ 640 km away (Hagman et al., 1998; Dokken et al., 2002; Sammarco et al., 2004; Figure 2). Other banks do exist on the northwestern GOM shelf, such as Stetson, Sonnier, 32 Fathom, etc. (Figure 2), but they do not qualify as true coral reefs because they are not biogenic in origin (i.e., composed of calcium carbonate that has been accreted by corals). Although corals exist there (Schmahl et al., 2005; Hickerson et al., 2006), they occur in deeper waters and are responsible for only a low percent-cover of the bottom (Rezak et al., 1985; Lugo-Fernandez et al., 2001; Schmahl, 2003; Sammarco et al., 2004; G. Boland, pers. obs.). It is possible that coral populations on the deeper banks could be a source of larvae for platform colonization, but the densities of corals are much lower than those of the FGB; and thus their potential as a larval source for recruitment on platforms in the region would be comparatively low.

Here, we focused on one hermatypic and one ahermatypic scleractinian coral species which occur on the platforms in the northern GOM and also on the FGB. We attempted to determine the degree of genetic connectedness among the natural and platform populations on a large geographic scale, covering most of the northern GOM. Through earlier surveys, we found that two species were abundant enough to provide sample sizes sufficient for meaningful comparative molecular genetic analyses. The corals we studied were *M. decactis* (Lyman, 1859; Pocilloporidae; hermatype) and *Tubastraea coccinea* (Lesson, 1829; Dendrophylliidae; ahermatype). Both of these corals reproduce by brooding. *M.decactis* is a simultaneous hermaphrodite and planulates monthly from March to December with a peak occurring from Sept. to Nov. (Vermeij et al., 2003). *T. coccinea* generally produces planulae sexually (Glynn et al., 2008) but can also produce them asexually (Ayre and Resing, 1986; Shearer, 2008). In addition, *T. coccinea* is highly effective at producing new colonies asexually through the formation of "runners" (Vermeij, 2005; Pagad, 2007).

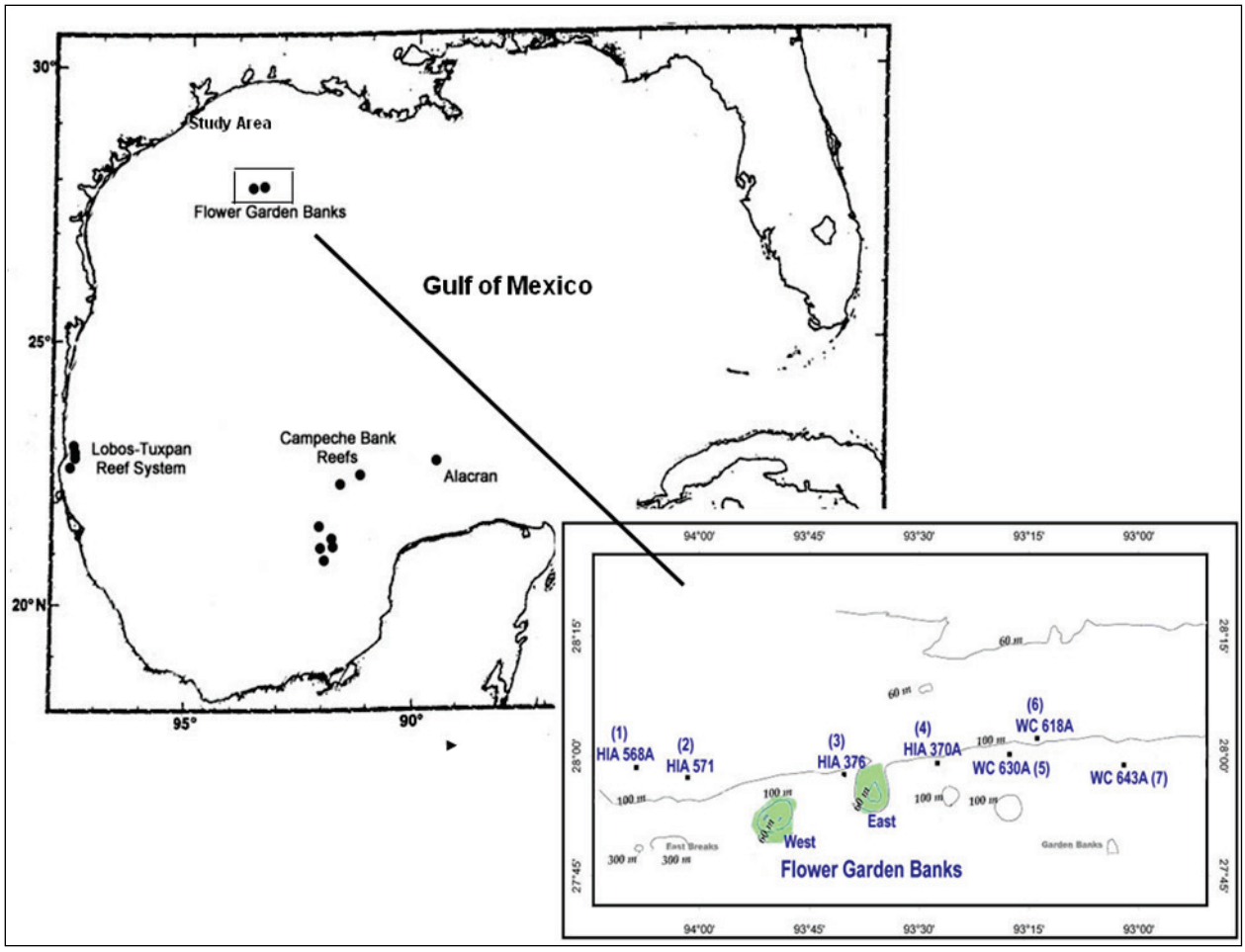


Figure 3. Map of the GOM depicting the locations of the FGB and their nearest neighboring reefs. Inset: The FGB and a sub-set of the numerous oil and gas production platforms around them (see Sammarco et al., 2004).

Regarding reproduction in these two coral species, fully-developed larvae derived from brooding corals have the capability to settle in ≥ 4 hours (Harrison and Wallace, 1990). Such species can become reproductively mature at ages of 1–2 years. Brooders generally planulate on a monthly cycle and can release larvae up to 8–10 times per year (e.g., *Porites astreoides*; McGuire, 1998). Planulae are released during a spawning event that may extend over a period of days. Data from some coral studies suggest that brooders are adapted for short-distance dispersal, while broadcast spawners (release of sperm and eggs into the water column for fertilization and larval development) are more effective at longer-distance dispersal (Baums et al., 2005). Nevertheless, the potential for long-range dispersal between planulae produced by these two types of corals is most likely comparable once the planulae have become fully developed (Sammarco and Andrews 1989, Sammarco 1994).

In the western Atlantic, *T. coccinea* is considered to be one of the most successful species to invade the Atlantic Ocean from the Indo-Pacific and is the single, most successful invasive coral in this ocean. The only other known invasive corals of species in the Caribbean are *Fungia scutaria* (Lajeunesse et al., 2005; J.C. Lang, pers. comm.; P.W. Sammarco, pers. obs. 1973) and

Tubastraea micranthus (Ehrenberg, 1834), a much more recent introduction to the region just south of the Mississippi River mouth (the Grand Isle [GI] lease area; Sammarco et al., 2010). Figueira de Paula and Creed (2004) have also reported the introduction of *Tubastraea tagusensis* to Brazil, along with that of *T. coccinea.* Thus, the total number of introduced species to the western Atlantic Ocean is now four.

T. coccinea by far represents the most successful invasion. It was first recorded in Puerto Rico in 1943 and then in Curacao, Netherlands Antilles in 1948, occurring on ships' hulls (Cairns, 2000). This coral appeared in Belize and Mexico in the late 1990s and early 2000s (Fenner, 1999; Humann and DeLoach, 2002). Its spread progressed to Venezuela, northern GOM, and the Florida Keys (Fenner, 2001; Fenner and Banks, 2004; Sammarco et al., 2004); Brazil (Figueira de Paula and Creed, 2004); and Colombia, Panama, the Bahamas, and throughout the Lesser and Greater Antilles (Humann and DeLoach, 2002). In terms of sheer numbers, *T. coccinea* is clearly the most abundant scleractinian coral, hermatypic or ahermatypic, in the northern GOM on artificial substrata (Sammarco et al., 2004, 2007a,b,c). Hundreds of thousands of colonies may be found on a single platform (e.g., 28/m^2; Sammarco et al., 2007a; Sammarco, 2008). It has also been found on some of the deeper banks of the northern GOM, but its abundances were low there (Schmahl, 2003; Hickerson et al., 2006; Schmahl and Hickerson, 2006).

The genetic affinities among populations of the scleractinian corals *M. decactis* and *T. coccinea,* were examined by sampling populations derived from the FGB and a large number of platforms across the continental shelf of the northern GOM from Matagorda Island, Texas to Mobile, Alabama. The FGB occur west of center of the range sampled. We will examine the degree of connectedness between coral populations on the platforms in this region, and between those platforms and the natural reefs. We will attempt to determine the degree of genetic distinctness for each population on a platform or reef, and thus the degree of connectivity or affinity between the platforms, and between the platforms and the FGB. We will also attempt to infer information about the comparative effectiveness of dispersal and colonization by these two brooding species, and relate it to an island-hopping strategy of colonization as described by MacArthur and Wilson (1967; also see Maltagliati et al., 2002; Atchison, 2005; Baums et al., 2005; Atchison et al. 2008). Here, we expand the analyses of Atchison et al. (2006, 2008), who worked on *M. decactis* and *D. strigosa* (a broadcasting coral) in a more restricted region around the FGB. We include the ahermatypic, invasive brooding species *T. coccinea*, and analyze data covering a much broader geographic range. We also use a more conservative statistical analytical approach to analyze the data, based on extensive simulations.

1.2.2 Objectives

The objectives of this portion of the study were as follows:

- To determine the degree of genetic affinity between adult coral populations of the hermatypic scleractinian coral species *M. decactis* on oil and gas platforms throughout most of the northern GOM and the FGB;
- To determine the degree of genetic affinity between adult coral populations of the ahermatypic scleractinian coral species *T. coccinea* on oil and gas platforms throughout most of the northern GOM and the FGB;

- To compare variation in genetic affinity between adult coral populations of the same species on different platforms;
- To determine the degree of genetic affinity between adult coral populations of the same species on the platforms compared with the FGB; and
- To use data on patterns of genetic variation to infer comparative colonization potentials for the two target species.

1.3 DURATION

This initial phase of the study ran for four years, from 2004 through 2008. A variety of issues, including hurricanes, resulted in cruise delays and extended the study two years beyond the projected original date of completion. The first three years were spent surveying the platforms and sampling coral populations on the selected platforms. Distribution and abundance data about adult coral populations were analyzed. Tissues from adult colonies were genetically finger-printed and statistical analyses of the data were performed. Various reports were prepared during the course of the study and submitted to BOEM.

2.0 MATERIALS AND METHODS

2.1 ADULT CORAL COMMUNITY SURVEYS ON THE PLATFORMS

To address questions about the distribution of adult coral populations on platforms throughout the northern GOM on oil and gas platforms, we initiated a set of field surveys and experiments, followed by laboratory analyses. These surveys were conducted on offshore platforms between Madagorda Island, Texas and Mobile, Alabama, a distance of ~3,000 km. We sampled an area from ~20 km offshore to the edge of the continental shelf. Platforms were sampled along four cross-shelf transects spaced at approximately equal intervals along the GOM coast (Figure 4). A number of study platforms were examined along each of these transects, as follows:

1. Transect I From Corpus Christi, Texas; bearing = 125° SE;
2. Transect II From Port Arthur-Lake Sabine, Texas; bearing = 170°S;
3. Transect III From Timbalier Island, Louisiana; bearing = 180°S;
4. Transect IV From Mobile Point, Alabama; bearing = 19°S.

There were several reasons for choosing the position of these transects. First, they cover the breadth and width of the shelf where platforms exist, particularly the shelf edge. Second, they cover enough of the shelf to potentially provide northern boundary information about coral colonization and survival. They also provide information on coral colonization and growth on platforms near the edge of the shelf. The second transect was designed to bisect our previous study area and provide additional data for comparison. In fact, coral density and species richness data from the first phase of this study have been included in the analyses and graphs to provide as complete a picture as possible of geographic patterns in these variables in the northern GOM (see Sammarco et al., 2004 for details). We chartered a dive vessel (M/V *Fling*, Freeport, Texas) and surveyed a total of 28 oil and gas platforms over a period of three years (Table 1). Surveys were conducted with teams of SCUBA divers during the summer and fall seasons of 2004–2007. Divers examined the platform jacket from the surface to a depth of 37 m. Data were collected on numbers of scleractinian and hydrozoan corals, depth of occurrence, and species identification.

Abundance data were standardized to density using approximate area surveyed. Architectural structural drawings of the platform jackets were obtained from a number of oil and gas companies whose platforms were sampled. Platform jackets (support structures) were placed into categories, based on number of primary pilings (3, 4, 6, 8, etc.). Total surface area was estimated for each platform. The surface area for each 3 m interval of depth was also determined, in order to compensate for additional surface area added by horizontal support structures that typically occurred at 10–15 m and 24–27 m. The molecular genetics of corals from another thirteen platforms around the FGB were considered in an earlier study and also used here. The details of these results may be found in Atchison (2005) and Atchison et al. (2008). Unfortunately, the techniques used in that study were updated here and precluded direct joint analysis and comparison of results. The current study used the most up-to-date AFLP techniques available at the time of the study.

Standard parametric univariate statistical analyses were performed on the data using BIOMStat V3.2 and V3.3, SigmaPlot 10.0, and SAS. Data were transformed by square-root where necessary for purposes of normalization (Sokal and Rohlf 1994). Only significant results are

discussed. Surfer V.8.6 was used to generate three-dimensional graphs from coral density and species richness data collected in the field. In some cases, kriging and interpolation of values resulted in the generation of negative numbers in the graphs. These were generally restricted to land areas.

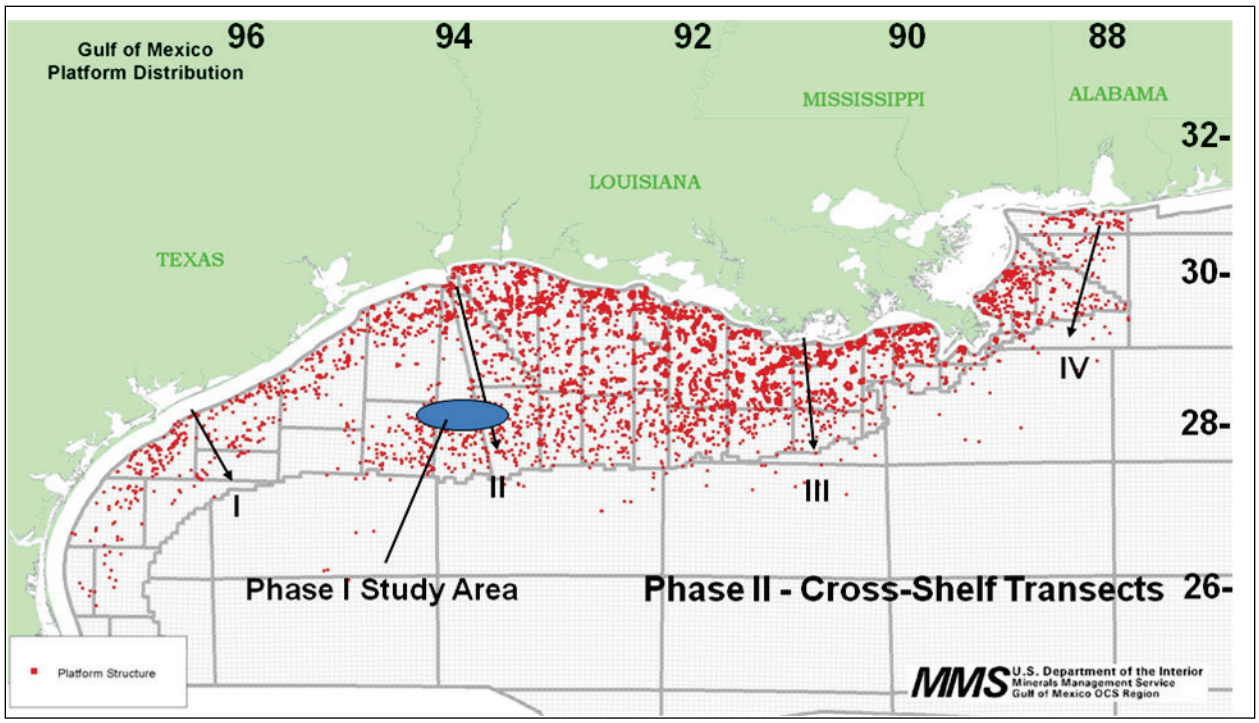


Figure 4. Map of the oil and gas platforms in the northern GOM, indicating the four cross-shelf transects. The oval represents the study area sampled for Sammarco et al., 2004.

Table 1.

Details of the 41 oil and gas production platforms studied in the northern GOM along four cross-continental shelf transects from Matagorda Island, Texas to Mobile, Alabama, including the 14 sampled in a previous study

Platforms surveyed throughout the northern Gulf of Mexico, with geographic locations												
Gulf of Mexico												
Far Western Sector			Western Sector			Central Sector			Near Eastern Sector			
Platform	lat.	long.	Platform	lat.	long.	Platform	lat.	long.	Platform	lat.	long.	
Platforms sampled 2003-2006												
BA-104-A	27.8669	-96.0334	GB-189-A	27.7786	-93.3095	SS-277-A	28.2993	-91.0876	MP-144-A	29.2924	-88.6691	
BA-A-133-A	27.8545	-96.0364	GB-236-A	27.7611	-93.1377	ST-163-A	28.5720	-90.4996	MP-159-1	29.6491	-88.4647	
BA-133-D	27.8388	-96.0282	HI-A-237-A	28.6678	-93.8857	ST-165-A	28.5767	-90.5769	MP-236-B	29.4054	-88.5844	
MI-A-4A	27.9042	-96.0892	HI-A-287-A	28.3610	-93.7690	ST-188-CA	28.5010	-90.3808	MP-265-A	29.3467	-88.2816	
MI-618-A	28.0222	-96.3071	VC-312-1	29.1872	-93.5822	ST-190-A	28.4663	-90.4461	MP-288-A	29.2398	-88.4095	
MI-651-A	28.0222	-96.3071	VC-414-A	28.7579	-93.3878	ST-292-A	28.2141	-90.4203	MP-289-B	29.2585	-88.4415	
MI-672-A	27.9942	-96.2596	VC-522-A	28.3759	-93.4912	ST-295-A	28.1963	-90.5413				
MI-672-B	27.9688	-96.2909										
			Additional Platforms included in (sampled 2000-2003)									
			EC-317B	28.2084	-92.9519							
			HIA -30A	28.0962	-93.4784							
			HI-A-349B	28.0703	-93.4691							
			HI-A-368B	27.9620	-93.6709							
			HI-A-370A	27.9855	-93.4584							
			HI-A-376A	27.9620	-93.6709							
			HI-A-382	27.9132	-93.9351							
			HI-A-385C	27.9168	-93.9168							
			HI-A-386B	27.9717	-93.5178							
			HI-A-568B	27.9763	-94.1439							
			HI-A-571	27.9556	-94.0271							
			VC-618	28.0367	-93.2312							
			VC-630A	28.0034	-93.2941							
			VC-643A	27.9814	-93.0342							

2.2 TECHNICAL CONSIDERATIONS AND ALTERATION OF ORIGINAL PLAN

Because of a variety of reasons, survey plans needed to be altered. Poor or severe weather conditions frequently caused truncation or cancellation and re-scheduling of cruises. This resulted in changes in survey dates and number of platforms to be surveyed per transect. Statistical analyses were adjusted accordingly to accommodate changes in experimental design.

2.3 DETERMINING GENETIC CONNECTIVITY BETWEEN CORAL POPULATIONS ON PLATFORMS IN THE NORTHERN GULF OF MEXICO AND ON THE FLOWER GARDEN BANKS

2.3.1 Study Site

Twenty-eight oil and gas platforms were surveyed for hermatypic corals off the coasts of Texas, Louisiana, and Alabama. The same transects used for the cross-shelf platform coral study were examined for the molecular genetics study; (see section 2.1 for a description of the transects and Figure 4 for their location). *Madracis decactis* and *Tubastraea coccinea* were the target species for the coral genetic connectivity study. All platforms surveyed had been deployed for 15–26 years, because it has been determined that a minimum of 15 years is associated with the development of substantial adult coral populations (Sammarco et al., 2004).

2.3.2 Sample Collection

Tissue was collected from all *M. decactis* coral colonies on the platforms between 5 and 37 m depth. This represented a total population for these depths. Sub-samples were taken for *T. coccinea*, since, in most cases, the populations were very abundant. Divers collected samples randomly, placed them in pre-labeled ZipLock® bags, and recorded the platform and depth from which the collection was made on slates with underwater data-log sheets. The bags were returned to the support vessel and logged. A minimum of 30 samples of *T. coccinea* were collected from each platform. At the East and West FGB, coral tissue samples of both *M. decactis* and *T. coccinea* were also collected by SCUBA divers randomly within a 50 m radius of Buoy #2.

Tissue samples, two cm^2 in area, were collected by SCUBA divers from the growing edge of adult corals of the two target species using small hammers and chisels. Total population sizes of *M. decactis* on the platforms were small, and sample sizes represent the total populations of this species on each platform between 5 and 37 m. The samples returned to the ship and sealed in plastic freezer bags containing SED buffer (saturated NaCl, 250 mM EDTA, pH 7.5, 20% DMSO) to preserve the DNA. This preservative allows tissue samples to be stored at room temperature, eliminating the need for storage in liquid nitrogen. The samples were then placed in additional SED buffer, placed in ice chests, and returned to the laboratory.

2.3.3 Molecular Technique used to Determine Genetic Affinity, Amplified Fragment Length Polymorphism

The technique we used to conduct molecular genetic analysis was Amplified Fragment Length Polymorphism (AFLP). This is a DNA-fingerprinting technique (Sunnucks, 2000) that detects polymorphisms based upon the selective PCR amplification of a subset of numerous restriction fragments generated by two different restriction enzymes (Vos et al., 1995; Mueller and Wolfenbarger, 1999). AFLPs tend to be highly polymorphic, but they are not co-dominantly expressed. They are commonly used in studies of commercial crop species and other economically important species; but they have not been widely use in animal studies (Bensch and Akesson, 2005). However, AFLPs can provide something that many other approaches cannot because alternate techniques are limited by the number of polymorphic markers produced.

AFLPs have been used successfully to estimate migration rates (He et al., 2004), species boundaries (Lopez et al., 1999; Fukami et al., 2004), and degree of parental contributions to populations (VanToai et al., 1997). AFLPs are not ideal for all population genetic applications (Sunnucks, 2000). They do, however, perform extraordinarily well for population assignment or allocation studies (Blears et al., 1998; Mueller and Wolfenbarger, 1999; Brazeau et al., 2005, 2011), where the number of polymorphic loci is more important than allelic diversity (Bernatchez and Duchesne, 2000).

It is possible that some genetic variation detected using AFLPs may not be derived from the target organism (Sunnucks, 2000). This has been an area of concern with corals, which possess endosymbiotic zooxanthellae. Here, however, we have used zooxanthella-specific PCR primers to confirm for each sample that any contamination by zooxanthellar DNA is at levels far below those necessary for AFLP (i.e., 5–10 pg of zooxanthellar DNA in a background of coral DNA;

Brazeau et al., 2005). In a previous study, Brazeau et al., 2005 assessed this potential problem. We spiked coral DNA preparations with zooxanthellar DNA and tested for detection. The amount of zooxanthella DNA detectable by our zoozanthella-specific PCR assay (4.8 pg) is five to six orders of magnitude less than the usual amount of coral DNA present in each sample (minimally 50–100 ng). More important, the detection limit of our assay for zooxanthellae contamination (0.48 pg) is well below (~200,000 fold) the amount of DNA necessary to generate AFLP bands. Attempts to generate AFLP bands using pure zooxanthellar DNA in amounts ranging from 0.48 to 480 pg were unsuccessful. Thus, we determined that coral samples showing no detectable zooxanthellae-PCR product would surely have too little zooxanthellar DNA to contribute any substantial numbers of AFLP bands, confounding the coral bands.

2.3.4 Preparation of Coral Tissue Lysates for Genetic Analysis

DNA was isolated by macerating samples lightly in SED buffer and spinning at 16g for 5 min in a centrifuge min to pellet the zooxanthellae from the homogenate. The DNA was then purified using the Wizard® SV Genomic DNA Purification System (Promega Corporation), following the manufacturer's instructions for animal tissue. All samples were checked for zooxanthellae DNA contamination using the PCR techniques described in Brazeau et al. (2005) and Atchison et al. (2006, 2008).

AFLPs, like other similar molecular genetic techniques, generate a subset of markers from a large population of markers. Of the subset obtained from a given AFLP experiment, a portion is often sensitive to specific reaction conditions. Thus, extra caution is required in processing samples through all procedural steps to maximize repeatability of results. Here, we processed samples in large lots containing members from all populations. This helped to distribute any error potentially introduced by reaction conditions uniformly between populations in an unbiased fashion. Also, all PCR reactions were done using one machine and the same thermal cycle profiles.

2.3.4.1 Genomic Coral DNA digestion and adapter ligation

A restriction-ligation "master mix" was prepared using the following reagents (measures are per sample): 1.1 µl T_4 DNA ligase 10X buffer (30 mM Tris-HCl, pH 7.8 / 10 mM $MgCl_2$ / 10mM dithiothreitol (DTT) / 1mM ATP), 1.1 µl of 0.5 M NaCl, 0.5 µl bovine serum albumin (BSA; 1 mg/ml), 1.0 µl Mse I adapters (50 µM), 1.0 µl EcoRI adapter (5 µM), 0.25 µl Mse I (4U/µl; New England BioLabs), 0.25 µl of EcoRI (20U/µL; New England BioLabs), and 0.33 µl of T_4 ligase (3 U/µl; 10 mM Tris-HCl, pH 7.0 / 50mM KCl / 1mM DTT / 0.1 mM EDTA / 50% glycerol). Sequences for the Mse I and EcoRI adapters and PCR primers are listed in Table 2. To each new 1.7 ml tube, 5.5 µl of the restriction-ligation mixture plus 5.5 µl (500 ng genomic DNA) of the purified genomic was added, centrifuged for 15 s, and incubated at room temperature overnight. At the end of the restriction-ligation reaction, 189 µl of TE buffer (10 mM Tris-HCl, pH 8.0 / 0.1 mM EDTA) was added (10-fold dilution), serving as the template for the next-step, pre-selective amplification.

2.3.4.2 Pre-selective (PS) Amplification of Coral DNA

A second "master mix" was made for pre-selection (PS) amplification, using the following reagents (per sample measure given): 8.1 µl of nuclease-free water, 2.0 µl of 10X PCR buffer (15 mM Mg^{++} in buffer), 0.8 µl of 5 mM dNTP's, 2.0 µl of *Eco*RI PS primer (2.75 µM), 2.0 µl of

*Mse*I PS primer (2.75 µM), and 0.1 µl of Thermostable (Taq) DNA polymerase (5U/µl), for a total volume of 15.0 µl. 15 µl of the pre-selective amplification master mix was added to each 0.5 ml tube, and 5 µl of each of the diluted restriction ligation reactions samples was vortexed and centrifuged for 15 s. Amplification was performed using a 2-min initial incubation at 72ºC, followed by 20 cycles of 20 s denaturation at 94ºC, 30 s annealing at 56ºC, and 2 min extension at 72ºC. Last steps were 2 min final extension at 72ºC, and 30 min final incubation at 60ºC. After the cycling was completed, 180 µl of TE buffer was added to each tube, which consisted of the templates for the final step, selective amplification.

Table 2

Sequences of the adapters and arimers used in the AFLP protocol

	Name	**Sequence**
Adapters *Eco*RI	*EcoF*	5'-CTCGTAGACTGCGTACC
	EcoR	5'-AATTGGTACGCAGTCTAC
Adapters *Mse*I	*MseF*	5'-GACGATGAGTCCTGAG
	MseR	5'-TACTCAGGACTCAT
Pre-selective primer	*Eco*RI **A**	5'-GACTGCGTACC AATTC **A**
Pre-selective primer	*Mse*I **C**	5'-GATGAGTCCTGAG TAA **C**
Selective primers	*Eco*RI	5'-GACTGCGTACCAATTC **ACT**
(Set 1)	*Mse*I	5'-GATGAGTCCTGAGTAA **CAG**
Selective primers	*Eco*RI	5'-GACTGCGTACCAATTC **ACC**
(Set 2)	*Mse*I	5'-GATGAGTCCTGAGTAA **CTT**
Pre-selective and selective nucleotides are indicated in bold.		

2.3.4.3 Selective Amplification of Coral DNA

In the final step, a selective amplification "master mix" was made, containing the following components: 8.1 µl of nuclease-free water, 2.0 µl of 10X PCR buffer (with Mg^{++} at 15mM), 0.8 µl of 5mM dNTP's, 2.0 µl of *Eco*RI selective primer (0.46 µM), 2.0 µl of *Mse*I selective primer (2.75 µM), and 0.1 µl of Taq DNA polymerase (5U/µl) for a total volume of 15.0 µl. To each 0.5 ml micro-centrifuge tube, 5 µl of the diluted pre-selection PCR reaction was added to each corresponding tube, mixed, and centrifuged for 15 s. Samples were placed in the thermocycler, and the cycle profile was performed as indicated: 2 min initial denaturation at 94ºC, followed by 1 cycle of 20 s denaturation at 94ºC, 30 s annealing at 66ºC, and 2 min extension at 72ºC. Next, there were 9 cycles: 20 s at 94ºC, initial 30 s at 66ºC (reduced 1ºC/cycle), and 2 min at 72ºC. Final cycle consisted of 20 cycles: 20 s at 94ºC, 30s at 56ºC, and 2 min at 72ºC, followed by a 30 min final incubation at 60ºC.

The products of the selective PCR were separated on a 5% polyacrylamide (sequencing) gel. Banding patterns were analyzed using Kodak Digital Image Analysis software (Eastman Kodak Co. Scientific Imaging Systems; Bonin et al., 2004). Bands were assigned to bins based upon 20 base-pair (bp) size intervals. The Selective PCR reactions were repeated three times for each sample. These "repeat" reactions were run on different days with populations mixed in each run. Bands were considered present if they appeared in two of the three runs; conversely, bands were scored as absent if two out of the three reactions yielded no band. Of the bands included in the study, >90% yielded the same result in all three PCR runs. These inclusion criteria helped to exclude bands that were overly sensitive to reaction conditions.

2.3.5 Statistical Analyses

With respect to the molecular genetics section of the study, two statistical analyses were used to assess population differentiation: AFLPOP population allocation analysis (Version 1.1; Duchesne and Bernatchez, 2002), a statistical analytical procedure designed particularly to analyze data generated by AFLPs, and STRUCTURE Version 2.0 (Pritchard et al., 2000). We have reported the development of these techniques and their application to the analysis of Caribbean corals earlier (Brazeau et al., 2005).

AFLPOP uses AFLP presence/absence data to calculate log-likelihood values for any individual's membership in a reference population, based upon their banding patterns. The reference population is that target population (e.g., from one platform) against which all other colonies from other sites are compared for genetic affinity. Each individual is allocated to the population showing the highest likelihood for that genotype (Duchesne and Bernatchez, 2002; He et al., 2004). Population assignment tests for individuals, based on genetic differentiation among populations, have provided the most promising statistical methods used to estimate contemporary long-distance dispersal (He et al., 2004). When the individual is assigned to a population different from the site from which it was collected, it is interpreted as evidence of dispersal. One major advantage of using these types of assignment methods is that populations do not have to be sampled exhaustively (He et al., 2004). In an AFLPOP simulation, an individual was chosen randomly from the entire population, population marker frequencies were then calculated without that individual, and then the individual is assigned to the new data set. For each simulation run, this was repeated 500 times. Average assignments to a given site were subsequently calculated as a percent value, based on 10 repeats of these 500 iterations.

The AFLPOP program allows the user to set a log-likelihood threshold for each assignment. A log-likelihood threshold set to 0.0 will result in the assignment of a colony to the population with the highest likelihood value. Atchison (2005) and Atchison et al. (2006, 2008) found that this may yield potentially misleading results. This is because there may be more than one population with nearly-equal likelihood values. Here, we also performed simulations using 1.0 as the comparative log-likelihood threshold in the analysis. This approach is more conservative and removes potentially spurious groupings. With the threshold set to 1.0, assignment of a colony to a population was not made unless the probability of the given assignment was 10 times more likely than the next most probable assignment. If this threshold was not met, the individual was not assigned to any population; in that case, it was designated "Criteria for Allocation Not Met" (CANM). This does not necessarily imply that the sample could not be assigned to any population with high probability; it only means that there may have been at least two populations

with nearly equivalent probabilities of assignment. It could also mean that the individual fits none of the populations well; in that case it could have been derived from an outside population (Atchison et al., 2006, 2008). In this study, we focus primarily on cases where clear assignments have been made, including self-allocations to sites of origin, and cross-population allocations.

STRUCTURE uses Bayesian techniques and Monte Carlo simulations to assign samples to populations. Unlike AFLPOP, in which assignment is based solely upon marker frequencies, STRUCTURE makes assignments that minimize deviations from the Hardy-Weinberg (H-W) equilibrium, which assumes that the population giving rise to the recruits constitutes a large, randomly mating population. Using this approach, the program calculates probabilities of individual assignment, estimates of F_{ST} (Wright's measure of population subdivision – a measure of genetic distance between populations; Neigel, 2002), and probable paternity, grand-paternity, etc., relationships. The program can accommodate dominant marker data such as those generated by our AFLP technique. The entire data set was subjected to several preliminary runs in order to evaluate parameter estimates used by Markov Chain Monte Carlo (MCMC) iterations for stability. STRUCTURE also called for definition of the parameter MIGPRIOR before running. This parameter is the prior probability of a spat being identified as coming from an external source. It was run at two levels, for comparative purposes, 0.05 and 0.50, taking into account different potential estimated migration rates. Once these parameters were set, data were analyzed using a burn-in period of 500,000 iterations, followed by another 100,000 MCMC repetitions.

The genetic variables derived from this study were analyzed using additional parametric and non-parametric statistical techniques. The software used for analyses was BIOMStat V. 3.2 and SigmaPlot V. 10.0. Percent data were transformed by arcsine (square-root of Y) before analysis for normalization purposes, if necessary.

3.0 RESULTS

3.1 ADULT CORAL COMMUNITIES ON PLATFORMS THROUGHOUT THE NORTHERN GULF OF MEXICO

3.1.1 Coral Species Composition

Twelve species of scleractinian corals were found on the platforms surveyed. Nine were hermatypic/zooxanthellate corals, and three were ahermatypic/azooxanthellate species, as follows:

Hermatypic/Zooxanthellate

- *Madracis decactis* (Lyman, 1859)
- *Diploria strigosa* (Dana, 1848)
- *Montastraea cavernosa* (Linnaeus, 1766)
- *Porites astreoides* (Lamarck, 1816)
- *Madracis formosa* (Wells, 1973)
- *Colpophyllia natans* (Houttyn, 1772)
- *Stephanocoenia intercepta* (Lamarck, 1816)
- *Stephanocoenia michelinii* (Milne Edwards et Haime, 1848)
- *Millepora alcicornis* (Linnaeus, 1758)

Ahermatypic/Azooxanthellate

- *Tubastraea coccinea* (Lesson, 1829)
- *Oculina diffusa* (Lamarck, 1816)
- *Phyllangia americana* (Milne Edwards and Haime, 1849)

For comparative purposes, the FGB are reported to have 24 species of hermatypic corals and 2 spp. of ahermatypic corals (Rezak et al., 1985).

3.1.2 Coral Species Richness: Number of Species

To facilitate interpretation of geographic trends in the data, results are presented in three-dimensional graphic format.

When one considered the distribution of number of coral species on oil and gas platforms in the northern GOM, particularly including the number of species on the FGB, an interesting pattern emerged. First, a clear peak in hermatypic coral species richness emerged at the FGB which fell off precipitously in all directions with respect to the number of corals on the platforms (Figure 5). Note the peak of diversity at the FGB and how it slopes away in all directions, but is extended towards the north, towards shore, off Port Arthur-Lake Sabine, Texas (Transect II). Unexpectedly, the distribution was skewed to the west, towards Transect I, in the far western sector near Matagorda Island, as opposed to the east, where prevailing currents flow. That is, there appeared to be more species to the west of the FGB than to the east. Three other features were apparent in this figure. The higher species richness appeared to be limited to the edge of the continental shelf for all transects, and fell off gradually as one moved closer to the coast.

Also, coral species richness peaked in the western sector (in Transect II off Lake Sabine-Port Arthur, Texas), near the FGB, with some additional minor peaks on platforms at the mid-shelf. In addition, there were no hermatypic coral species on the northern half of the shelf in the central or western sectors of the northern GOM (Transects I, II, and III). This "no coral zone" was compressed, however, in the Main Pass lease area, to the east of the Mississippi River mouth (Transect IV).

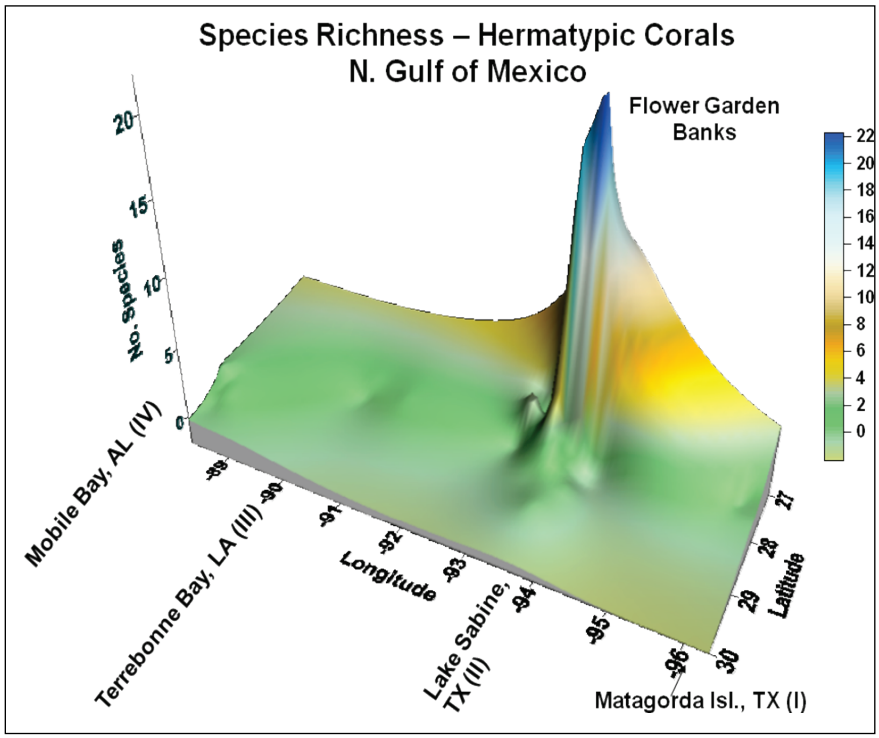


Figure 5. Species richness of hermatypic scleractinian corals in number of species on oil and gas platforms in the GOM and on the FGB.

3.1.3 Coral Distribution and Abundance

3.1.3.1 Hermatypic/Zooxanthellate Scleractinian Corals

The distribution and abundance patterns of hermatypic corals in the northern GOM did not mimic the species richness pattern (Figure 5 compared with Figure 6). In the case of overall hermatypic coral density, there is a clear peak south of Terrebonne Bay in Transect III, which extends to some degree inshore, but otherwise in all directions. There are some other minor peaks around the FGB off Lake Sabine-Port Arthur, in Transect II. Hermatypic corals are present throughout the northern GOM on platforms, albeit at very low densities in most cases, and except at the inner coastline. This report focuses on the three dominant species found on platforms in the GOM: *M. decactis*, *D. strigosa*, and *M. cavernosa*.

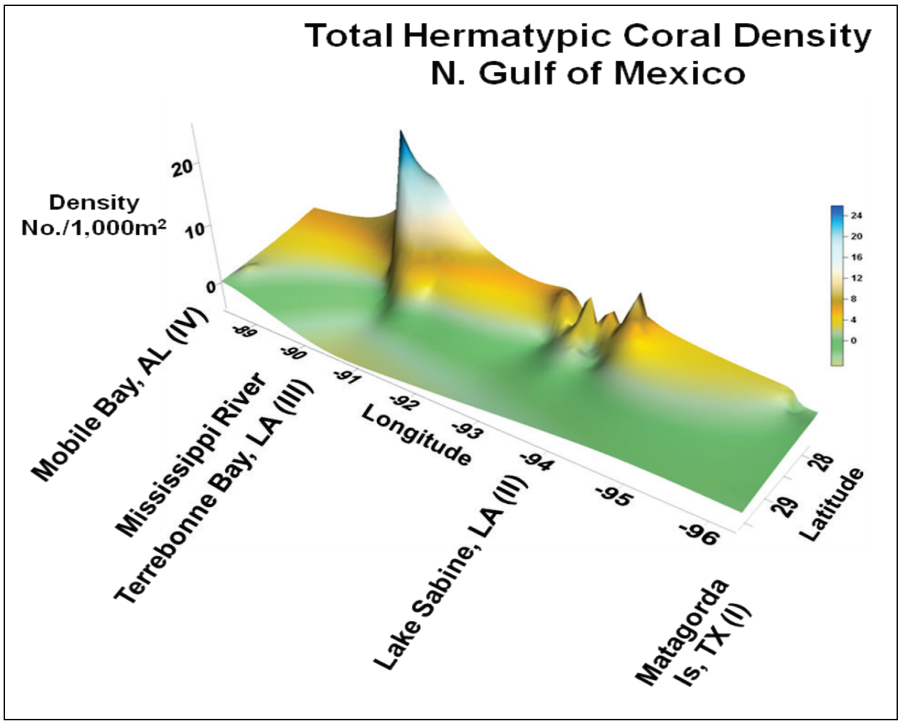
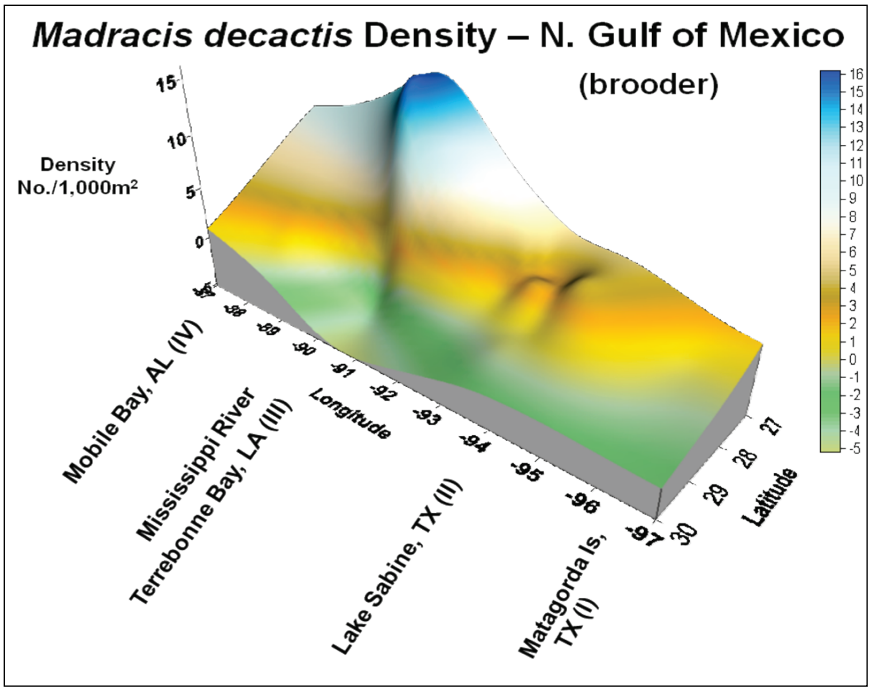


Figure 6. Total coral density of hermatypic scleractinian corals in no.per 1,000 m-2 on oil and gas platforms in the GOM.

3.1.3.1.1 *Madracis decactis*

The dominant coral in the hermatypic scleractinian coral community found on platforms in the northern GOM was *M. decactis*. Its pattern of distribution was similar to that of all hermatypic corals and was responsible for driving that pattern. No peak was observed around the FGB (Figure 7).

Rather, it occurred on platforms near the shelf edge east of the FGB, off of Terrebonne Bay, Louisiana (west of the mouth of the Mississippi River; Transect III). At this longitude, its distribution was skewed to the north, reaching within 40 km of the coast. Its distribution also was skewed to the east into Main Pass lease area (Transect IV), again with highest densities occurring at the edge of the shelf, but reaching moderate densities towards the coast. Densities of *M. decactis* were lower in the western half of the study area. Densities on platforms around the FGB (Transect II) were moderate, and only 1–2 colonies were found in the far western sector, and only at the shelf edge (Transect I).



Note: Negative numbers exhibited on the Z-axis are due to interpolation calculations performed by SURFER; these occur generally over land areas.

Figure 7. Density of the hermatypic scleractinian coral *M. decactis* on oil and gas platforms in the northern GOM, shown in no. per 1,000 m-2.

3.1.3.1.2 *Diploria strigosa*

D. strigosa, was the second dominant species in the hermatypic scleractinian coral community found on platforms, although its densities were relatively low. Its individual densities peaked at ~2/1,000 m^2 on a platform near the FGB and on several platforms at and beyond the outer edge of the continental shelf (Figure 8). This peak was at the southern end of the cross-shelf transect in the west, off Lake Sabine-Port Arthur, Texas (Transect II). Coral densities fell dramatically to zero with distance from that area. It was absent in all other sectors.

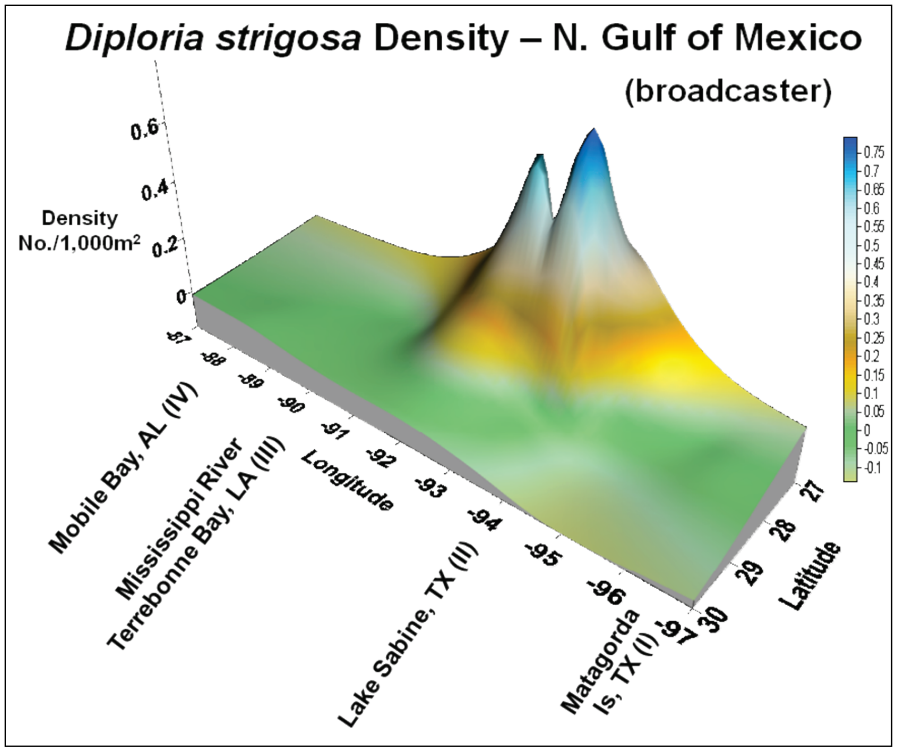


Figure 8. Density of the hermatypic scleractinian coral *D. strigosa* on oil and gas platforms in the northern GOM.

3.1.3.1.3 *Montastraea cavernosa*

The third-ranking dominant coral in the hermatypic scleractinian coral community on platforms in the northern GOM was *M. cavernosa*. Its average densities, overall, were low and bimodal in nature, peaking at ~0.25/1,000 m^2 on platforms just to the east of the FGB off Lake Sabine-Port Arthur, Texas (Transect II; Figure 9). A second minor peak occurred in the eastern Main Pass lease area, off Mobile Bay, Alabama, in Transect IV. However, because only one colony was found, densities were negligible. This species was absent in the far western and central sectors (Transects I and III), off Matagorda Island, Texas and Terrebonne Bay, Louisiana. In the west (Transect II), however, their distribution did reach northward, more than halfway across the shelf. Note that, similar to that of *D. strigosa*, the density peaks east of the FGB, at the edge of the continental shelf.

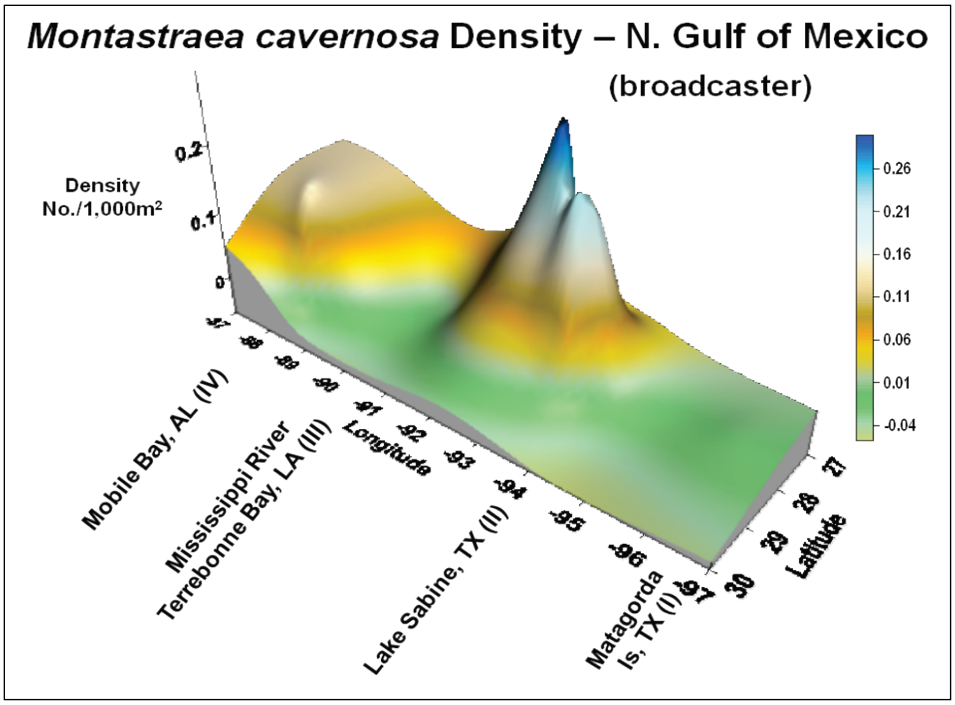
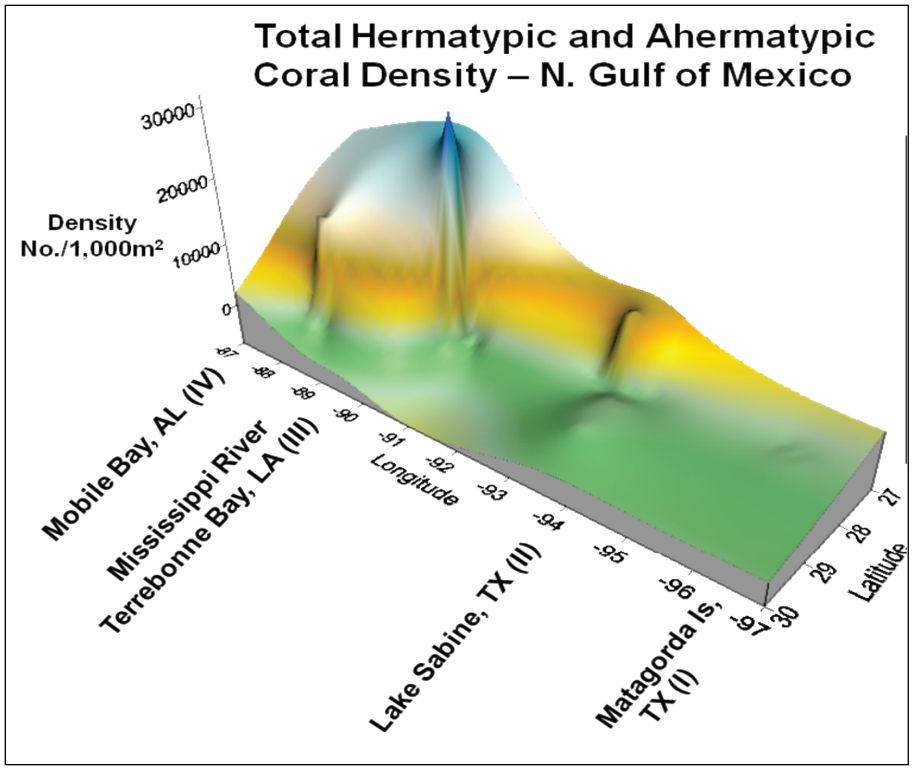


Figure 9. Density of the hermatypic scleractinian coral *M. cavernosa* on oil and gas platforms in the northern GOM.

3.1.3.2 Total Scleractinian Corals

If one combines the densities of all scleractinian corals on the platforms, including both hermatypic/zooxanthellate and ahermatypic/azooxanthellate corals, the distribution varies greatly from that of the scleractinian corals alone (Figure 6; Figure 10). There is a clear density peak in Transects III and IV in the central and eastern regions. The highest densities occur near the shelf edge, but they also extend northward to within 35 kms of the coastline off Mobile, Alabama. The densities are skewed to the west, where they show a small peak again at the shelf edge near the FGB. Note that the peak average density of all corals occurring on platforms near the shelf edge in the central sector, off Terrebonne Bay, Louisiana, is approximately 35,000 corals/1,000 m^2, a much greater density than observed for the hermatypic corals.

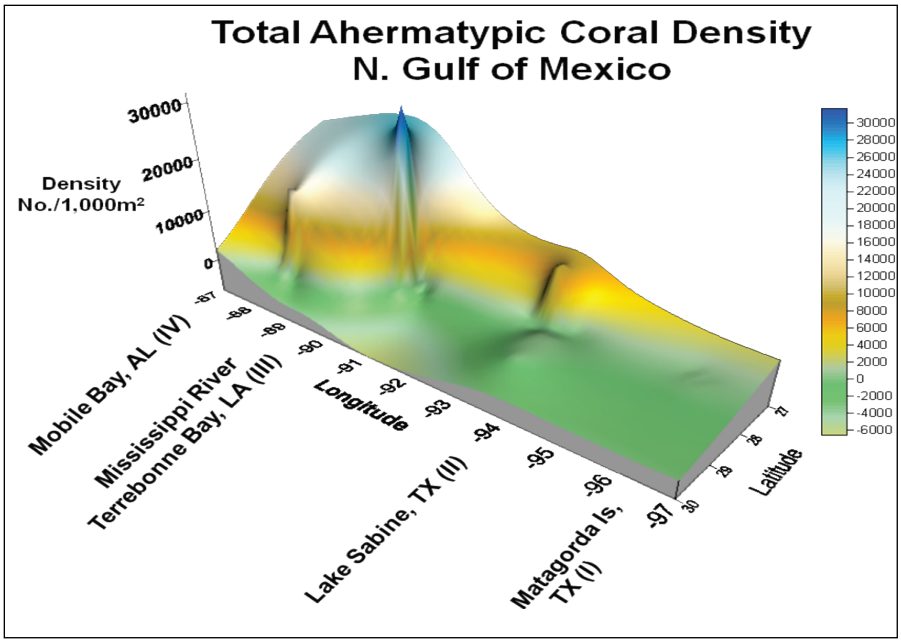


Note: See scale on Y-axis, compared to earlier graphs (Figs. 7-10).

Figure10. Total coral density of all scleractinian corals, hermatypic and ahermatypic, on oil and gas platforms in the GOM.

3.1.3.3 Ahermatypic/Azooxanthellate Corals

The density of ahermatypic/azooxanthellate corals in the northern GOM mimicked precisely the pattern exhibited by all scleractinian corals (Figure 11; compare with Figure 10). This implies that the ahermatypic corals are by far driving the overall coral distribution and abundance pattern in this region. The pattern of distribution mimics almost precisely that of all scleractinian corals, shown in Figure 9. Peaks occur in the central and near-eastern sectors, off Terrebonne Bay, Louisiana and Mobile, Alabama, on either side of the Mississippi River.



Note: See scale on Y-axis, compared to earlier graphs. Negative numbers exhibited on the Z-axis are due to interpolation calculations performed by SURFER; these occur generally over land areas.

Figure 11. Density of all ahermatypic scleractinian corals in the GOM.

3.1.3.3.1 Species Richness of Ahermatypic Compared with Hermatypic Corals

The distribution of ahermatypic/azooxanthellate coral species – Species Richness (S) - on platforms across the northern GOM did not follow the pattern exhibited by the hermatypic/scleractinian corals. Rather than showing a distinct peak at the FGB, it exhibited a series of peaks, one on each of the four cross-shelf transects (Figure 12). Considering the number of species under consideration here (three), these peaks are relatively low compared to the distribution of hermatypic species, implying a much more equitable distribution of species across the shelf. In addition, they generally did not occur at the shelf edge, but peaked approximately at the mid-shelf. The peaks decreased in size from west to east. The widest representation of all three ahermatypes was observed in the west, off Matagorda Island (Transect I).

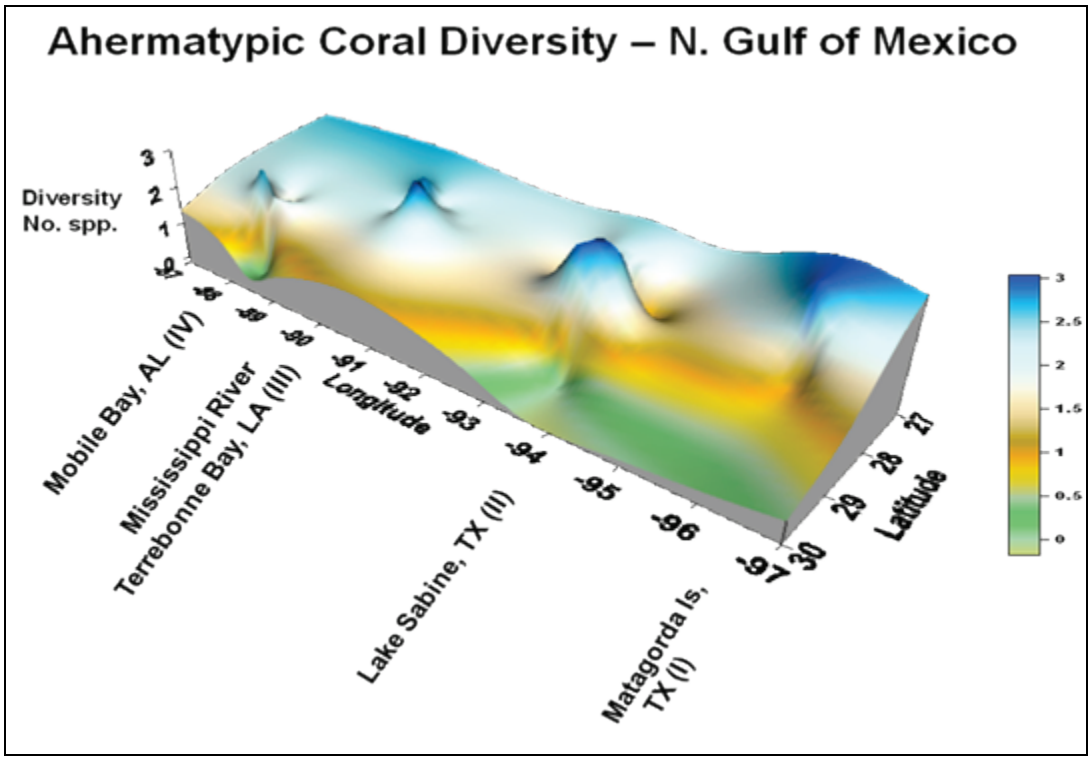
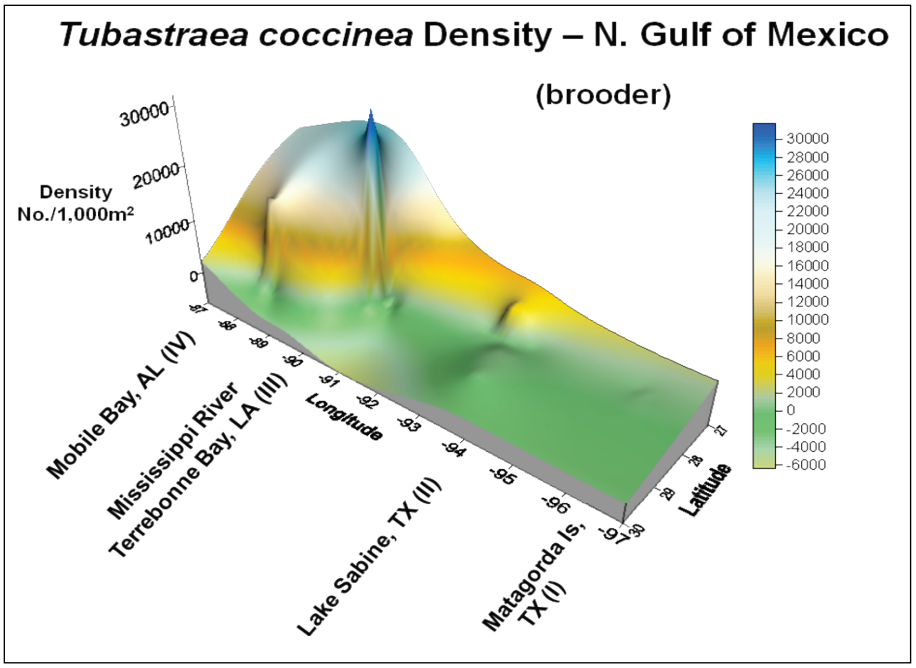


Figure 12. Species richness (number of species - S) of ahermatypic corals in number of species on oil and gas platforms across the northern GOM.

3.1.3.3.2 Tubastraea coccinea

The densities of the ahermatypic/azooxanthellate *T. coccinea* on platforms were orders of magnitude higher than any other coral analyzed in this study. The individual densities of this species reached upwards of 40,000 colonies per 1,000 m^2. This density occurred on one platform in the central region off Terrebonne Bay, Louisiana, at the shelf edge (Transect III). This coral species clearly dominated the northern GOM, whether considering hermatypes, ahermatypes, or both groups combined.

When one considers the specific distribution and abundance of *T. coccinea* alone, it is quite clear that this species followed the precise pattern of all ahermatypic corals and indeed all corals combined, whether hermatypic or ahermatypic (Figure 13). *T. coccinea* is clearly driving the distribution and abundance on platforms in the northern GOM of ahermatypic corals as well as all corals combined through its sheer numbers. Its densities peaked on the outer half of the continental shelf in the central region (Transect III), off Terrebonne Bay, Louisiana, occupying the outer half of the shelf. Its second highest peak was in the eastern region (Transect IV), in the Main Pass area, off Mobile, Alabama. It was present in the west (Transect II, off Lake Sabine), on the outer half of the shelf, with densities reaching ~3,000/1,000 m^2. *T. coccinea* densities dwindled dramatically, however, in the west (Transect I), occurring in tens to hundreds of colonies per 1,000 m^2, being sparsely distributed only on the outer half of the shelf.



Note: Negative numbers exhibited on the Z-axis are due to interpolation calculations performed by SURFER; these occur generally over land areas.

Figure 13. Density of *T. coccinea*, the dominant ahermatypic coral on oil and gas platforms in the northern GOM.

3.1.3.3.3 Oculina diffusa

The ahermatype *O. diffusa* was present in all sectors of the GOM sampled. Its densities were highest on platforms just beyond the shelf edge in the western sector off Lake Sabine-Port Arthur, Texas (Transect II), where individual densities almost reached 6,000 per 1,000 m^2 (Figure 14). This species also occurred there at the mid-shelf, but at much lower densities. The second highest density of this species was observed offshore in the far-western sector off Matagorda Island (Transect I), but densities reached no higher than ~150/1,000 m^2. Although this species was present in the central and far-eastern sectors, the densities there were quite low. The pattern of distribution follows that of *D. strigosa* (Figure 9) and *M. cavernosa* (Figure 10), indicating that the FGB may be the source of larvae.

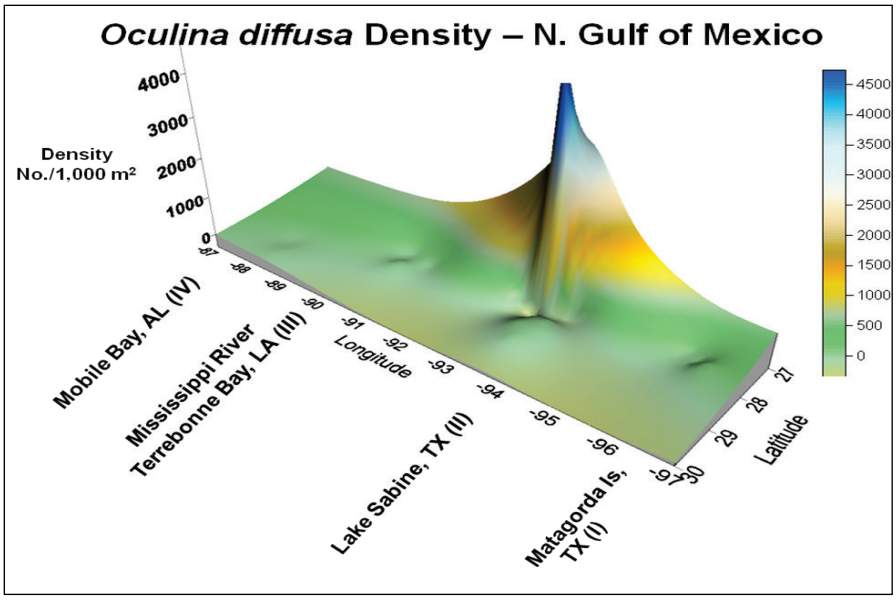


Figure 14. Density of *O. diffusa* on oil and gas platforms in the northern GOM.

3.1.3.3.4 Phyllangia americana

P. americana was the least abundant ahermatypic coral encountered on platforms. Its densities were generally low, never surpassing ~10/1,000 m^2. Its densities were highest in the western GOM (Figure 15). In the far western sector, off Matagorda Island (Transect I), they were abundant on platforms across the continental shelf. In the west, off Lake Sabine-Port Arthur, Texas (Transect II), they occurred inshore, peaked at the midshelf, and were absent off the edge of the shelf. In the central region, off Terrebonne Bay, Louisiana, they occurred in varying densities over the continental shelf. In the eastern sector, they only occurred towards the outer edge of the shelf. The pattern of distribution is unique to those of other species encountered in this study, decreasing towards the east and indicating that the source of larvae may be to the south or south west of the study area.

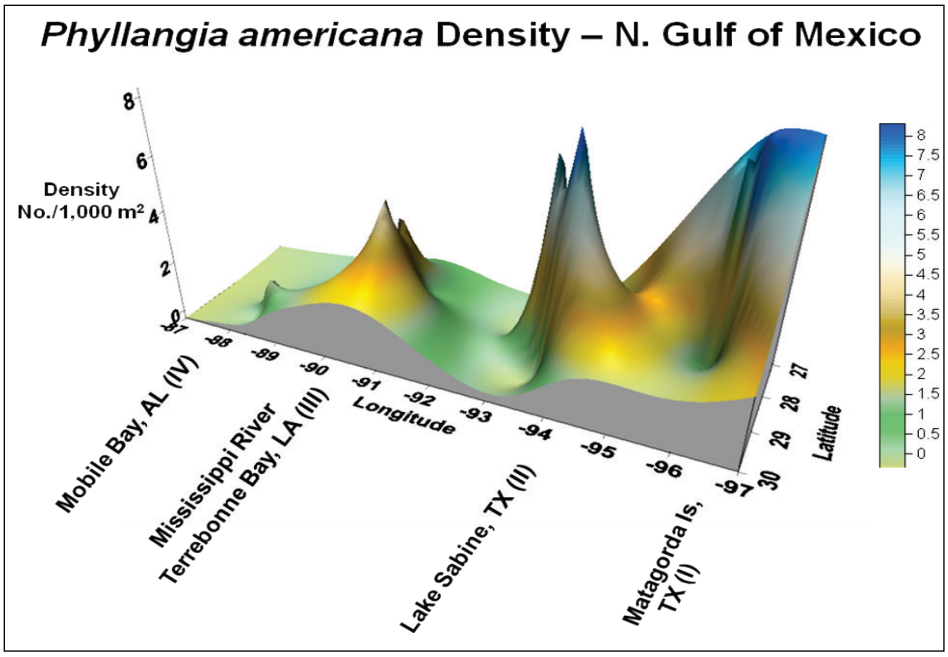
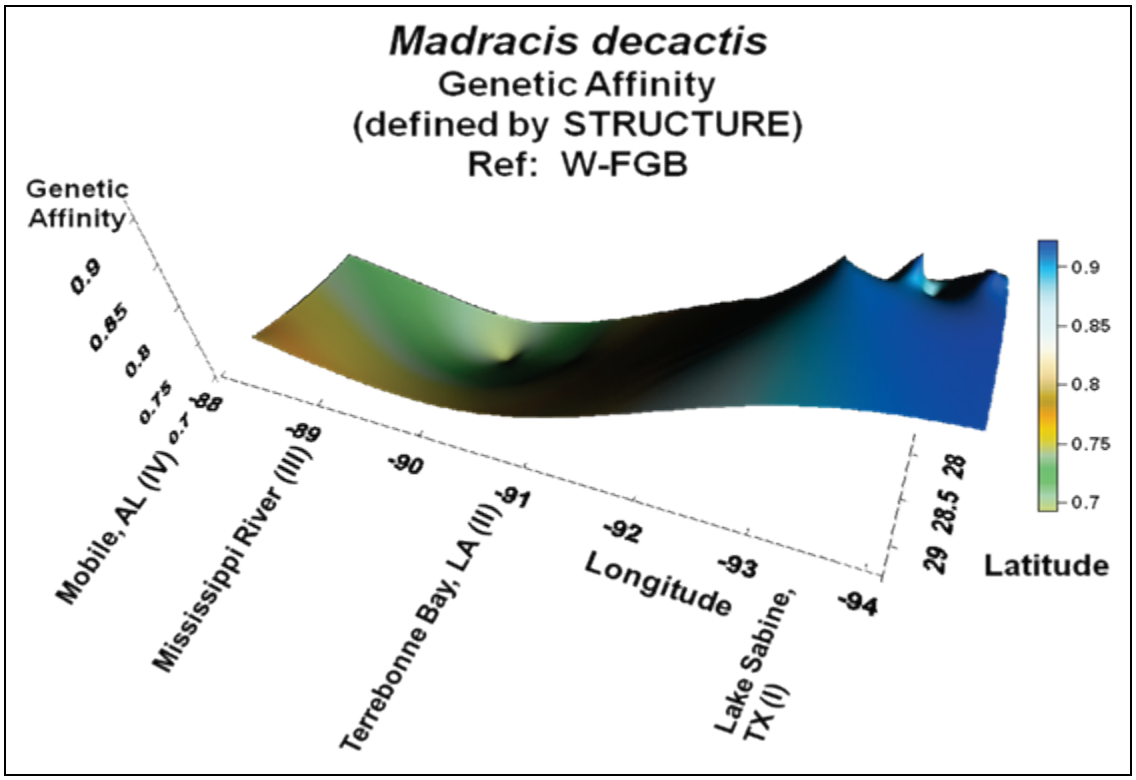


Figure 15. Density of *P. americana*, on oil and gas platforms in the northern GOM.

3.2 GENETIC CONNECTIVITY IN CORALS IN THE NORTHERN GULF OF MEXICO

3.2.1 Relationship between Genetic Distance and Geographical Distance for *Madracis decactis*, Using STRUCTURE

In examining *M. decactis* on platforms in the northern GOM, the analyses derived from STRUCTURE revealed a clear pattern. The highest levels of genetic affinity in this species occurred between those coral populations on platforms in Transect II, off of Port Arthur-Lake Sabine, Texas, and particularly on platforms around the FGB (Figure 16). (Transect I had an insufficient sample size to be included in this analysis.) Genetic affinity clearly peaked in the west (Transect II, off Lake Sabine) and then decreased steadily and smoothly to the east, to Transect III, south of Terrebonne Bay. The genetic affinity then increased slightly in Transect IV, off Mobile, Alabama. There was also an anomalous point depression in genetic affinity which occurred near the edge of the continental shelf in Transect III (off Terrebonne Bay, Louisiana). The peak in the west implies that corals on the platforms were most likely derived from the Flower Garden Banks. Population differentiation is also in the east, on either side of the Mississippi River mouth. The point-depression south of Terrebonne Bay, Louisiana may represent a population drawn from outside of the northern GOM.



Note: Population differentiation determined by STRUCTURE. Reference population was the West FGB

Figure 16. *M. decactis*: Genetic affinity in coral populations on oil and gas platforms across the continental shelf in the northern GOM. Transect I (Matagorda Island) not shown because of lack of *M. decactis* there.

3.2.2 Relationship between Genetic Distance and Geographical Distance for *Madracis decactis*, Using AFLPOP

We then focused on comparing genetic affinities of *M. decactis* populations on either side of the Mississippi River mouth (Transects III and IV), to determine whether this large-scale geographic feature could be acting as a geographic barrier to dispersal. Enough samples were collected on the east side of the Mississippi River (Transect IV) that individual platforms were analyzed. Samples were combined on the east side of the River (Transect III) to have a sample size large enough for analysis. When analyzing the genetic data using AFLPOP, with a log-likelihood threshold value of "0" (all colonies must be assigned to a population), it became clear that not only was there no recognition between the two sets of populations, but there was also little to no recognition between platform populations within a transect in this region (Table 3). When this analysis was repeated using a log-likelihood threshold value of 1.0 (a colony must be 10X more likely to belong to a given populations than another before being assigned there), a much more conservative approach, there was very little difference in the results (Table 4). Both analyses indicated minimal levels of dispersal between these two sets of populations, i.e., between transects on either side of the Mississippi River plume, and also between platforms within a transect.

Table 3

M. Decactis: Genetic affinities in populations of corals on oil and gas platforms in the northern GOM along two transects on either side of the Mississippi River

Madracis decactis
Transects III & IV
AFLPOP Analysis, Log-Likelihood = 0
Percentage (%) of Colonies

		Transect III		**Transect IV**
		W. of Miss. River		**E. of Miss. River**
Allocated to	**ST-295**	SS-277	ST-292	**MP-All**
ST-295	100	0	0.3	0
SS-277	0	100	0	0
ST-292	0.2	0	99.7	0
MP - All	0	0	0	100

Note: Platforms on the east side of the Mississippi River were combined to provide sufficient sample size for comparison. Note extraordinarily levels of high self-assignment to home populations and lack of recognition of neighboring populations. This indicates geographic isolation of these coral populations and possibly different larval sources. All of the MP populations were combined to provide sample sizes large enough to accommodate analysis.

Table 4.

M. Decactis: Genetic affinities in populations of corals on oil and gas platforms in the northern GOM along two transects on either side of the Mississippi River mouth

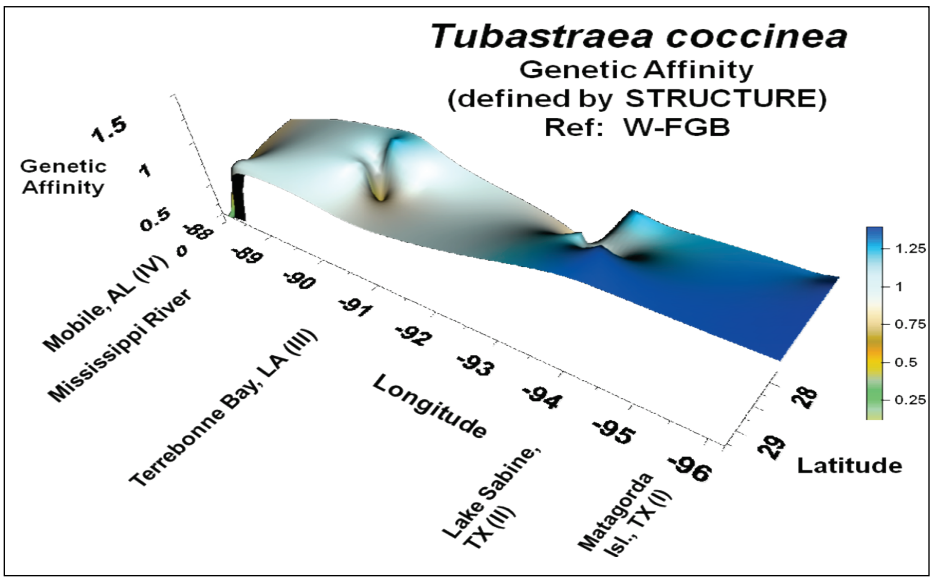
Madracis decactis **Transects III & IV** **AFLPOP Analysis, Log-Likelihood = 1** **Percentage (%) of Colonies**				
		Transect III		**Transect IV**
		W. of Miss. River		**E. of Miss. River**
Allocated to	**ST-295**	**SS-277**	**ST-292**	**MP-All**
ST-295	99	0	0	0
SS-277	0	100	0	0
ST-292	0.1	0	99.4	0
MP - All	0	0	0	100
CNM	0.6	0	0.6	0

Note: Platforms on the east side of the Mississippi River were combined to provide sufficient sample size for comparison. Data analyzed with AFLPOP, with a log-likelihood value set at 1. The resulting pattern is almost identical to analysis performed with more liberal 0 setting- See Table 3. All of the MP populations were combined to provide sample sizes large enough to accommodate analysis.

3.2.3 Relationship between Genetic Distance and Geographical Distance for *Tubastraea coccinea*, Using STRUCTURE

The analytical program STRUCTURE yielded clear results for *T. coccinea*. In general, the genetic affinity values in this species were higher across the continental shelf than those for *M. decactis* (Figure 17). Affinities exhibited more dramatic changes across the continental shelf for *T. coccinea* than for *M. decactis*. Although levels of genetic affinity generally decreased from west to east in this species, there were two substantial local variations in this pattern. First, genetic affinities dropped precipitously east of the Mississippi River. Second, an anomalous point depression in genetic affinity in *T. coccinea* occurred at the edge of the continental shelf off Terrebonne Bay, Louisiana. The relative flatness of the curve indicates no major local larval source; i.e., it is unlikely that the FGB are a source of larvae for the region for this species. The steep drop-off in the east indicates major population differences in genetic population structure between the two sides of the Mississippi River. The point depression south of Terrebonne Bay indicates a population from a very different source than the rest of the western populations.

Genetic affinity values were calculated as maximal genetic distance value minus individual genetic distance value for each point, yielding an estimate of affinity.



Note: Population differentiation determined by STRUCTURE. Reference population was the West FGB.

Figure 17. *T. coccinea:* Genetic affinity in coral populations on oil and gas platforms across the continental shelf in the northern GOM.

3.2.4 Relationship between Genetic Distance and Geographical Distance for *Tubastraea coccinea*, Using AFLPOP

The AFLPOP was used to compare genetic affinities of *T. coccinea* populations on either side of the Mississippi River. Note that the sample size was large enough to compare individual platforms east of the River, but that all samples were combined west of the River to obtain sufficient sample size for the analysis. When one makes a direct comparison of genetic affinities of populations occurring off Terrebonne Bay, Louisiana vs. off Mobile, Alabama using AFLPOP with a log-likelihood threshold value of 0.0 (forcing assignment), it becomes apparent that, once again, there was little recognition of populations across the mouth of the Mississippi River (Table 5). A slightly higher degree of recognition occurred between populations within transects for *T. coccinea* than occurred for *M. decactis*. This indicates some genetic similarities between populations on different platforms within a transect. When this analysis was repeated using a log-likelihood threshold value of 1.0 (much more conservative), self-assignment to home populations decreased and more colonies fell into the CNM (Criteria Not Met) category (Table 6). In general, these analyses indicate that dispersal is higher in *T. coccinea* than in *M. decactis*.

Table 5.

T. coccinea: Genetic affinities in populations of corals on oil and gas platforms in the northern GOM along two transects on either side of the Mississippi River mouth

Tubastraea cocceinea

Transects III & IV

AFLPOP Analysis, Log-Likelihood = 0

	Percentage (%) of Colonies on these Platforms					
	W. of Miss. River	E. of Miss. River				
	Transect III	Transect IV				
Allocated to	ST & SS pops	MP-144	MP-236	MP-265	MP-288	MP-289
ST & SS pops	100	0	0	0	0	0
MP-144	0	70	0.1	8.6	4.2	9.3
MP-236	0	0.6	99.7	0.2	0	0.5
MP-265	0	12.6	0.1	90.3	0.4	0.6
MP-288	0	4.6	0	0.3	94.8	0.8
MP-289	0	12.2	0.1	0.6	0.6	88.8

N_i = 500, 10x

Note: Platforms on the western side combined to provide sufficient sample size for comparison. Only those populations for which there were sufficient sample sizes were analyzed here.

Table 6.

T. Coccinea: Genetic affinities in populations of corals on oil and gas platforms in the northern GOM along two transects, on either side of the Mississippi River mouth

Tubastraea cocceinea

Transects III & IV

AFLPOP Analysis, Log-Likelihood = 1

	Percentage (%) of Colonies on these Platforms					
	Transect III	Transect IV				
	(W. of Miss. River)	(E. of Miss. River)				
Allocated to	ST & SS pops	MP-144	MP-236	MP-265	MP-288	MP-289
ST & SS pops	100	0	0	0	0	0
MP-144	0	21.4	0	0.8	0.2	0.4
MP-236	0	0.4	98.4	0	0	0
MP-265	0	1.6	0	58.6	0	0
MP-288	0	1	0	0	82.8	0.2
MP-289	0	2.2	0	0	0	57.8
CNM	0	73.4	1.6	40.6	17	41.6

N_i = 500, 10x

Note: Platforms on the western side combined to provide sufficient sample size for comparison.

4.0 DISCUSSION

4.1 PATTERNS IN CORAL SPECIES RICHNESS, COMPOSITION, AND ABUNDANCE ON THE NORTHERN GOM SHELF

4.1.1 Hermatypic Corals

The fact that species richness of hermatypic corals on the northern GOM shelf peaks at the FGB indicates several things. First, in accordance with MacArthur and Wilson's (1967) and Simberloff and Wilson's (1969) Theory of Island Biogeography, the platforms represent islands, although much smaller islands than the FGB. Second, they are reticulate and do not offer a substantial barrier to far-field flow. Currents flow generally through them, rather than around them. Third, they are very young communities, both in ecological and geological time. The oldest platforms sampled were < 30 years old. Even for a coral reef, this can represent a short period of time for community development (Hughes and Connell, 1999). By contrast, in their current configuration and under current sea level conditions, the FGB are estimated to be ~14,000 years old (Rezak et al., 1985), allowing a climax community to develop, even considering that some of its coral species can live for hundreds of years (Boto and Isdale, 1985; Hough-Guldberg, 1999). Fourth, because the species richness of hermatypic corals on the platforms clearly dissipates rapidly with increasing distance from the FGB, following a negative logarithmic pattern, this is the first indication in the study that the hermatypic corals on the platforms are derived primarily from the FGB, not from elsewhere in the GOM or the Caribbean. This is further supported by the pattern of *Diploria strigosa*'s density around the FGB, which mimics very closely that of hermatypic coral species richness, peaking at the FGB and dissipating rapidly with distance (to be discussed further below).

Next, the fact that there is a distinct extension of species richness and density of *D. strigosa* inshore towards Port Arthur and Lake Sabine, Texas lends support to the hypothesis proposed by Lugo-Hernandez et al. (2001). Their drifter study revealed currents that dominate during the spawning season which move east along the edge of the continental shelf, across the FGB, then flow north, follow a rapid long-shore current to the west and then move south, looping back towards the FGB again. They propose that such a current would allow coral planulae released by FGB corals to be drawn north towards land and then be brought back out to the FGB region in time for settlement. This would provide a mechanism for enhanced larval recruitment on those platforms near, or to the north of, the FGB. It would also allow for a self-seeding mechanism for the FGB, as proposed by Lugo-Hernandez et al. (2001).

As in our earlier study (Sammarco et al., 2004), the dominance of three hermatypic species on the platforms–*Madracis decactis, D. strigosa*, and *M. cavernosa*–was somewhat unexpected. First, these are the dominant, late-sere corals on the FGB. This is an anomaly. Corals which generally colonize young reef communities or substratum which has become newly available are usually pioneer species or opportunistic species. Among these for the Caribbean are the brooding species *Agaricia agaricites, Agaricia spp., Porites spp.,* and *Favia fragum*, and some other species. The species found to be dominant in the GOM platform communities are characteristic of later series in community development (Odum 1969, 1971; Smith and Smith, 1999). Also, two of them (*Diploria* and *Montastraea*) are broadcast spawners. *M. decactis*, however, is a brooder. This emphasizes the point that platform coral communities are not typical

of natural coral reefs in the region or in the Caribbean. They have their own unique character as artificial reef communities.

The fact that the density of the primary dominant hermatypic coral, *M. decactis*, was not centered on platforms around the FGB was unexpected. The peak in its density was south of Terrebonne Bay, Louisiana, implying that platforms in this region were receiving a larger supply of this species' larvae than platforms directly around the FGB. The center of this highdensity region lies east of the FGB. It falls on the edge of the continental shelf and is skirted by a westerly current which travels from the western GOM to the east. This current could carry coral larvae from the FGB to this center within their viable period. The bathymetry of the edge of the continental shelf would be important to consider here, regarding eddies and overall flow. Coral planulae released by brooding corals are nearly fully developed upon release and capable of settling in as few as four hours. They can remain competent to settle, however, for ~60–90 days, maximum. Most planulae settle, however, within two to four days (Harrison and Wallace, 1990). Thus, the window for peak settlement in this region by planulae of *M. decactis* is approximately correct to create such an abundance peak; (see discussion below regarding major currents in this region).

The density pattern of *D. strigosa* on the northern GOM, on the other hand, which was centered on platforms around the FGB, varied greatly from that of *M.* and implied a different pattern of larval dispersal. The fact that the center of distribution of *Diploria* is on platforms around the FGB implies that the fertilized eggs and larvae generally remain in that vicinity. This is consistent with our earlier findings that this species, which is a broadcaster, recruits more locally than its brooding associate, *M. decactis,* which has peak densities on platforms to the east of the FGB (south of Terrebonne Bay, Louisiana). The finding is again counter-intuitive, as spawned eggs must be fertilized in the water column, and they require 24–72 hours for development. Thus, they must spend a minimum of this amount of time in the water column before even being competent to settle, unlike larvae from the brooders. It is possible that the larvae of both species may be retained by eddies around the FGB, but that those of *M. decactis* spend a longer period of time in the water column than those of *D. strigosa*.

*M. cavernosa'*s recruitment pattern partially mimics that of *D. strigosa*, in that its peak occurs in the vicinity of the FGB. Thus, one may draw some similar inferences between them. The fact that this species also exhibits a somewhat smaller peak on the east side of the Mississippi River, however, in the Main Pass area, suggests that it may be receiving larvae from a distant source there, perhaps from the Caribbean through the Loop Current (Figure 18; Sturges and Blama, 1976; Hamilton et al., 1999; Lugo-Fernandez and Gravois, 2010) or from the southern GOM in the Alacran area off the Yucatan Peninsula. The molecular genetics portion of this study has demonstrated that adult coral populations of *M.* and *Tubastraea* on the two sides of the Mississippi River mouth are clearly distinct. It is also possible that the *Montastraea* populations on either side of the Mississippi River may are distinct as well. Lugo-Fernandez et al. (2010) has proposed that there may be a jet current that is capable of carrying larvae N-NE directly from the Caribbean to the northeastern GOM Main Pass area within a time period which encompasses the period of larval competence for the species. This has yet to be confirmed via a comparative molecular genetics study of the Yucatan coral populations.

4.1.2 Ahermatypic Corals

Although the species richness of ahermatypic corals was greatest in the western GOM, their densities were highest in the east. This density of ahermatypic corals caused the extraordinary peak of total coral density (hermatypic and ahermatypic) in the northeastern GOM. The densities of *T. coccinea* were clearly driving the total coral density pattern.

T. coccinea's densities were orders of magnitude higher than any other coral in the study. This invasive species was clearly the dominant coral on platforms throughout the northern GOM. It is believed to have entered the western Atlantic through the Panama Canal in the 1940s and spread through the Americas and the Antilles over the next 70 years. During this period of time, it has extended its biogeographic range from the Florida Keys to Brazil. The density data presented here demonstrates that the greatest coral densities occur in the eastern half of the study area and suggest that this population of *T. coccinea* may have entered through the Port of New Orleans (29°54'51" N, -90°5'26" W) or Port Fourchon (29°37'27" N, -90°11'40" W). Densities were substantially higher east of the Mississippi River, off Mobile, Alabama, than densities observed to the west of the River. However, our molecular genetics data indicate that the populations on the east compared with the west side of the Mississippi are not related. If nothing else, we may be observing the results of two independent introductions.

The molecular genetics data for *T. coccinea* also indicate that there is a gradual decrease in genetic affinity in populations from the west to the east, although it is very subtle. The populations on the eastern side of the Mississippi are totally different, however. It is possible that the western population was introduced to the GOM from Mexico and the Caribbean through the clockwise current around the GOM or through another port. It might also be possible that a separate seeding occurred at another time through direct input from the Loop Current or, indeed, through the hull or ballast water of a ship, to the eastern side of the Mississippi River. The Mississippi River discharge appears to be sufficient to keep the two populations separate. Only further molecular genetics studies will be able to shed further light on this situation.

The pattern of decreasing richness in ahermatypic coral species from west to east implies that the source of larvae for this group as a whole is derived from somewhere in the GOM. Once again, the decrease in species richness follows the clockwise current direction around the GOM, and it is likely that, on the average, the larval source is the southern GOM or the Caribbean. There is variance in this pattern, of course. For example, *Oculina diffusa* shows evidence of being derived directly from the FGB. The fact that richness peaks more on the mid-shelf than at the shelf-edge implies that this group is better adapted to more variable salinities and temperatures than its hermatypic counterparts.

4.2 Genetic Affinities of Corals in the Northern Gulf of Mexico

The high degree of genetic affinity in *M. decactis* between populations on the platforms in the west (Transect II), as determined by STRUCTURE, confirms that populations of this coral species in the northern GOM most likely originated from the FGB. Populations on those platforms show high affinity for the populations on the FGB and for those populations on other platforms around them. Also, as the populations become more distant from Transect II and the FGB, they exhibit greater isolation and less genetic affinity to each other. The slight increase in local genetic affinity in the eastern sector (Transect IV), beyond the mouth of the Mississippi

River mouth, underscores the lack of affinity between the populations on the eastern and western sides of the river. It is likely that the Mississippi River is creating a strong geographic barrier to larval dispersal via lower salinities, high sedimentation, and high nutrient discharges in this region.

The anomalous point depression in genetic affinity exhibited by *M. decactis* off Terrebonne Bay, Louisiana, raises an important question. It is possible that some *M. decactis* larvae are being introduced to this region by more than one means. In the first case, they may be introduced from the Caribbean through the Loop Current entering the GOM through the Yucatan Straits and proceeding north to the Mobile, Alabama region (Transect IV compared with Transects I, II, and III; see Figure 18).

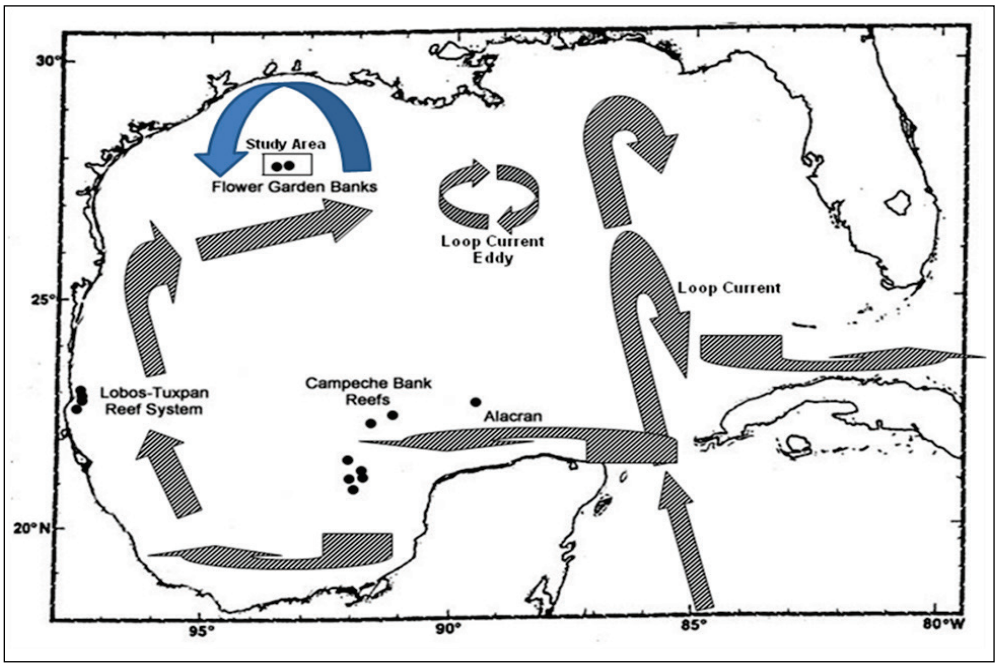


Figure 18. Map of the GOM, depicting examples of general currents known to exist. Note the general westerly current across the continental shelf in the vicinity of the FGB.

Alternatively, *M. decactis* larvae may have been introduced via a jet current from the northern portion of the Yucatan Peninsula (Lugo-Hernandez, 2006). In either case, it is clear that this *M.* population is different from all other *M. decactis* populations sampled in the northern GOM.

The geographic pattern exhibited in genetic affinity by *T. coccinea* in the northern GOM, as determined by STRUCTURE, had general similarities to that of *M. decactis*, in that there was a general decrease in affinity from west to east. The variations in this pattern that were observed in *M. decactis,* however, were much more dramatic in *T. coccinea*. Firstly, the highly precipitous drop-off in genetic affinity near the mouth of the Mississippi River indicates a sharp differentiation between the population off Mobile, Alabama, and all of those to the west of the Mississippi River. In addition, a deep point depression in genetic affinity of *T. coccinea* was noted south of Terrebonne Bay, Louisiana. It was similar to that observed in *M. decactis*, but

much more dramatic. On that platform, there was clearly a population of this invasive species which was unrelated to the others in the northern GOM. This may represent an additional introduction of this species to the northern GOM. The source might be the Caribbean, as described above; but, it is also possible that this could represent a third successful introduction to the western Atlantic from a commercial vessel from the Indo-Pacific, its native habitat. In either case, this population is unrelated to the other populations in this large region.

Judging from the data collected here, it is clear that the Mississippi River represents a formidable east-west barrier to coral larval dispersal in this region. This was evidenced through the dichotomy of, and lack of genetic affinity between, coral populations on either side. Also, this pattern was clearly evident in two coral species: *M. decactis* and *T. coccinea*.

There are two possible explanations for the differences in differential population structure on either side of the Mississippi River, and they are not mutually exclusive. The first is that the lower salinity, higher sediment content, and higher nutrient concentrations associated with the Mississippi River plume (Rabalais et al., 1996; Dagg and Breed, 2003; Lohrenz et al., 2008; Dagg et al., 2008) may decrease coral larval survivorship levels in this region preventing the larvae from successfully crossing the Mississippi River plume and promoting genetic drift (see Bassim et al., 2002; Bassim and Sammarco, 2003). The second is that larvae from corals in the Caribbean Sea may be seeding platforms to the east of the Mississippi River plume as they are carried up by the Caribbean Current into the northern GOM by the Loop Current. Eddies that break off from the Loop Current can traverse the Main Pass region (eastern sector) in the north-eastern GOM, dispersing larvae to the east of the Mississippi River plume before moving to the W-SW over the next six months or so (Oey et al., 2005). The two different sources of larvae, the FGB for the west and the Caribbean Sea for the east of the Mississippi River plume, could explain the lack of genetic affinity in *Madracis* and *Tubastraea* on either side of the Mississippi River plume.

Another point which emerged from this part of the study is that the invasive ahermatypic *T. coccinea* has higher larval dispersal and recruitment capabilities than even the most abundant and widely dispersed native hermatypic species encountered in this study: *M. decactis*. *M decactis* populations on either side of the river mouth showed almost no genetic affinity to each other. The same was true for *T. coccinea*. Population recognition was stronger in the latter, however, between transects on either side for *T. coccinea.*

The results of this study support the findings from our earlier study (Sammarco et al., 2004; Brazeau et al., 2005; Atchison et al., 2008) that the *M. decactis* are highly isolated on these platforms and that their variation from each other most likely resulted from Founder Effect (also see Hellberg, 2007 for a discussion of similar patterns in deep-sea corals). That is, the local population was the product of the arrival of a small group of larvae from the mother FGB population to the west or another source to the east, which then expanded to create a sub-population of that mother population with a different genetic signature characteristic of only a portion of the mother population. It was originally a sample-size effect. This is consistent with the Island Model of gene flow (Futuyma, 1998; Gold et al., 2001), as explained above, whereby small islands are seeded by a large mother population and then can also seed each other.

Another conclusion may be drawn from comparisons between *M. decactis* and *T. coccinea*. The higher dispersal rates exhibited by the latter species may be the reason it has been so successful in its distribution throughout the Greater Caribbean region over the past 70 years. Its reproductive, larval dispersal and recruitment capabilities are simply very good, better than the dominant native species in this study. Its dispersal capabilities are also better than those of one of the only other successfully introduced coral species, *Fungia scutaria* (P.W. Sammarco, pers. obs., 1973; J.C. Lang, pers. obs., 1972; LaJeunesse et al., 2005). Indeed, with reproductive characteristics like these (including rapid asexual reproduction and growth), the only reason that this species has not over-run our natural coral reefs is that it apparently does not compete well in natural systems, only in artificial habitats (breakwaters, platforms, bridge pilings, etc.).

It is possible that some other Indo-Pacific species may be similarly better adapted to reproduce and disperse than our native species, and that all precautions should be taken to eliminate them should they be successfully introduced in our waters. Sammarco et al. (2010) recently reported the new introduction of a closely related species–*Tubastraea micranthus*–into the northern GOM in the Grand Isle lease area, S-SW of the mouth of the Mississippi River. Once again, this area is close to the commercial shipping lanes (safety fairways) for the Mississippi River and Port Fourchon. We are currently attempting to determine the extent of the invasion. Nonetheless, a rapid eradication would be fitting for such species because of a) the possibility of success of such an invasion (Fitzhugh and Rouse, 1999), b) the decreasing probability of success of eradication if such is delayed (Simberloff, 2000; Hewitt et al., 2005), and c) major problems that can arise if one waits too long to proceed with eradication (Bergstrom et al., 2009; Casey, 2009).

5.0 CONCLUSIONS

5.1 ADULT CORAL COMMUNITIES ON PLATFORMS THROUGHOUT THE NORTHERN GULF OF MEXICO

- The peak in hermatypic coral species richness in the northern GOM occurs on the FGB. The number of species observed there is approximately three times higher than the maximum observed on any individual oil and gas platform. Coral species richness is very low inshore.
- The three dominant hermatypic/zooxanthellate coral species observed on the platforms were, in order of abundance, *Madracis decactis, Diploria strigosa,* and *Montastraea cavernosa*.
- The other hermatypic/zooxanthellate species observed on platforms were *Porites astreoides*, *Madracis formosa*, *Colpophyllia natans*, *Stephanocoenia intercepta, Stephanocoenia michelinii, and Millepora alcicornis.*
- The dominant ahermatypic/azooxanthellate coral species on platforms in the northern GOM was *Tubastraea coccinea*.
- The other two species of ahermatypic corals on platforms were, in order of abundance, *Oculina diffusa* and *Phyllangia americana*.
- Total density of hermatypic/zooxanthellate corals peaked on the oil and gas platforms in the north-central GOM in Transect III, south of Terrebonne Bay, Louisiana. There was an extension of higher densities to the north, towards shore, in this region. Slight peaks in density were also noted around the FGB, south of Lake Sabine-Port Arthur, Texas, in Transect II. Densities dropped to low levels outside of these regions. In no case were corals observed within ~50km of shore.
- Densities of *M. decactis*, a brooder, peaked on platforms in the north central GOM at the edge of the continental shelf, south of Terrebonne Bay, Louisiana, in Transect III. Densities of this coral were primarily driving patterns of overall hermatypic coral density.
- Densities of *D. strigosa*, a broadcaster, the second dominant hermatypic in the platform coral community, peaked on platforms around the FGB, generally mimicking the pattern observed in coral species richness, with an extension of higher densities northward towards Port Arthur-Lake Sabine (Transect II).
- Densities of the third dominant hermatypic coral on the platforms–*M. cavernosa*, a broadcaster–was bimodal, with its highest peak around the FGB (Transect II) and a second somewhat lower peak on east side of the Mississippi River mouth off Mobile, Alabama in Transect IV.
- Density of all corals, including hermatypic/zooxanthellate and ahermatypic/azooxanthellate types, was four orders of magnitude higher than hermatypes alone and peaked in the central and eastern regions of the northern GOM. These peaks of tens of thousands of colonies occurred south of Terrebonne Bay, Louisiana and Mobile, Alabama (Transects III and IV).
- The density pattern of total corals in the northern GOM was driven entirely by the density of ahermatypic/azooxanthellate corals, which far surpassed the densities of hermatypic corals.
- The pattern of total ahermatypic/azooxanthellate corals in the northern GOM was driven entirely by the densities of *T. coccinea*, whose densities were in the tens of thousands per 1,000 m^2.
- Species richness of ahermatypic corals was highest in the western region of the northern GOM, south of Matagorda Island, Texas, in Transect I. It peaked in each of the transect

areas, in mid-shelf and inshore areas. In general, ahermatypic coral richness decreased from west to east. The peak in Transect I indicated that the FGB were most likely not the source of ahermatypic corals in the northern Gulf and that they most likely are derived from the southern GOM off Mexico or the Caribbean.

5.2 GENETIC AFFINITIES OF CORALS IN THE NORTHERN GULF OF MEXICO

- Using STRUCTURE, it was determined that genetic affinity between *M. decactis* populations on the platforms was highest south of Port Arthur-Lake Sabine, Texas in Transect II and decreased with distance to the east. A slight increase in genetic affinity in the eastern region indicated some isolation between the populations on either side of the Mississippi River (Transects III and IV). A point-drop in genetic affinity at the shelf edge south of Terrebonne Bay, Louisiana indicated a population differing from all others in the northern GOM, most likely derived from elsewhere.
- Using STRUCTURE analyses, genetic affinity between populations of *T. coccinea* was also found to be highest in the west off Matagorda Island, Texas (Transect I) and generally decrease to the east. A precipitous drop in genetic affinity off of Mobile, Alabama indicated a dramatic difference in populations between that area and the others to the west of the Mississippi River mouth, indicating that this hydrographic feature represents a formidable barrier to coral larval dispersal in this region.
- STRUCTURE also identified a point drop in genetic affinity offshore from Terrebonne Bay, Louisiana similar but more pronounced than that observed in *M. decactis* also indicates that a population very different from the others in the northern Gulf exists here. Either of these populations could have been seeded by the Loop Current derived from the Caribbean Current, or a jet current originating from the southern GOM.
- In a geographically-focused, high-resolution study of *M. decactis* populations, AFLPOP analyses revealed that the populations off of Terrebonne Bay, Louisiana and those off of Mobile, Alabama were almost 100% distinct from each other, showing almost no cross-population recognition. Home population recognition was extremely high but cross-site recognition was extremely low. These results indicated that larval dispersal across the river mouth and even between populations on platforms within a transect on either side of the river was highly limited.
- This same trend of no population recognition across the river mouth was even stronger in *Tuabastraea coccinea*. Self-allocation to home sites, however, was highly variable, and between-platform population recognition was higher than in *M. decactis*. This indicated that *T. coccinea* has higher larval dispersal and recruitment capabilities and gene flow than *M. decactis*. The fact that both species are brooders makes them directly comparable.
- The Mississippi River plume appears to be forming a barrier for coral larvae, inhibiting gene flow from either side of the plume to the other.

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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.