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Corals on Oil and Gas Platforms Near the Flower Garden Banks: Population Characteristics, Recruitment, and Genetic Affinity

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Coastal Marine Institute
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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	NOAA Flower Garden Banks National Marine Sanctuary
GOM	Gulf of Mexico
hrs	hours
km	kilometers
m	meters
min	minutes
ft	feet
no.	number
pg	picograms
s	second(s)
x g	times gravity

EXECUTIVE SUMMARY

ADULT CORAL COMMUNITY STUDY

There are approximately 3,200 oil and gas platforms in the northern Gulf of Mexico (GOM). These platforms provide hard substratum that extends throughout the euphotic zone, in a region where such has been rare in recent geological time. Major exceptions to this are the coral reefs of the Flower Garden Banks (FGB), ~180 km S-SE of Galveston, Texas, which rise up to within 17 m of the sea surface. In this study, we attempted to determine whether extensive scleractinian coral populations have colonized these platforms, quantify them, and determine their population and community characteristics. We also examined the relationship between these variables and distance from the FGB, platform age, and depth. Surveys were performed on 13 oil or gas production platforms down to 33 m depth, encompassing an ellipse around the FGB. Corals occurred in abundance on most of the platforms. Eleven species were found: eight hermatypic scleractinians, two ahermatypic scleractinians, and one hydrozoan coral. The most abundant corals were *Madracis decactis*, *Diploria strigosa,* and *Tubastraea coccinea*. Distance from the FGB was not related to the coral community variables measured, including total coral abundances of the dominant three species in shallow water ($\leq$ 14 m.), deep water (14-33 m), or both depths combined. Total coral abundance increased significantly with platform age, and the community was best developed on platforms $\geq$ 12-15 years in age. Abundance of *M. decactis* increased significantly with platform age in the deeper zone and both depths combined, as did coral species diversity (S). This was not the case with *D. strigosa*, indicating that it may not be associated with any particular successional sere. Neither was *T. coccinea* abundance associated with platform age, except in shallow water, where it decreased in abundance with age, indicating that this species may be an opportunistic pioneer species. All corals exhibited a significantly non-uniform depth distribution, with total coral abundance peaking at ~20 m and 28 m depths. The bimodal depth distribution of *M. decactis* exhibited a disproportionately high peak at depths $\geq$ 27 m. *D. strigosa* exhibited peaks at depths of ~10 m and 23 m and was not found at depths $\geq$ 27 m. *T. coccinea* exhibited a near-normal distribution, with a single mode at ~17 m depth. Platforms have facilitated expansion of coral populations in the GOM. Such platforms have intrinsic environmental value through the presence of coral populations and this may influence future decisions about their decommissioning (removal).

CORAL SETTLEMENT STUDY

The FGB are two of the very few true coral reefs in the northern GOM. There are other recognized coral reefs in the southern GOM, such as at Tampico, Mexico and the eastern GOM in the Florida Keys. There are also a couple of mesophotic reefs in the northern GOM that boast significant amounts of hermatypic corals and may be considered to be true coral reefs; these include corals at Pulley Ridge in the eastern GOM and McGrail Bank near the shelf edge in the central GOM. Numerous other banks in the northern GOM support significant coral communities that include a variety of corals, sponges, and other reef invertebrates but these are not actively accreting coral reefs. The offshore oil and gas platforms deployed in the northern GOM were the first set of structures in shallow-water in this region since the Holocene, providing substratum for colonization for corals. Because scleractinian corals are sessile epibenthic organisms, the only means of dispersal for them is by larval dispersal and settlement.

To assess coral recruitment rates on oil and gas platforms around the FGB, terracotta settlement plates were mounted on racks, deployed on, and retrieved from six platforms at depths of 15 and 27 m for a period of one to two years. Plates were analyzed in the laboratory with a dissecting microscope for taxonomic identification, distribution, and abundance.

Density of coral spat settling on plates on the platforms was extraordinarily low when compared with other Caribbean sites or the Great Barrier Reef-averaging < 1/450 cm^2 -over a period of 10-12 months. This emphasizes the uniqueness and fragility of these artificial reef sites in comparison to natural sites. There was no significant difference between platforms with respect to spat density, suggesting that the distance between the platforms and the E-FGB-their potential larval source, was large enough (> 0.6-1.2 km, as determined by Sammarco and Andrews, 1988) to allow diffusion of larvae, suppressing larval densities. There was a significant difference between coral spat densities on the platforms compared with those directly on the E-FGB (derived from a sister experiment). Only three species of coral spat were found: *T. coccinea*, *Montastraea* sp. (most likely *Montastraea cavernosa*), and *Madracis* sp. (most likely *M. decactis*), in order of abundance. This species composition varied substantially from the dominant genera of spat observed on the E-FGB: *Agaricia* and *Porites*. The observed recruitment was also unusual in that the dominant recruits matched the dominant adults in the community. *Tubastraea* and *Montastrea* spat densities did not vary significantly between platforms or between racks. The platforms in the northern GOM generally exhibit very low levels of coral recruitment for the tropical western Atlantic. Nonetheless, this recruitment has permitted the development of adult coral communities on these platforms and their associated benthic, demersal, and pelagic biota over the past ~30 years. These communities should be considered fragile because of their slow development rate. Mass coral mortality on these platforms would require decades for recovery.

MOLECULAR GENETICS STUDY

At the time of this study, the northern GOM held ~3,600 offshore oil and gas structures. These structures serve as artificial reefs on the continental shelf, where, until their introduction, shallow hard substrata were rare. This newly available substrate has helped to expand scleractinian coral populations in the GOM. Here, we conduct molecular genetic analyses on adult scleractinian corals on the FGB coral reefs (~180 km S-SE of Galveston, Texas [TX]) and on surrounding oil and gas platforms. We have attempted to determine the degree of genetic affinity among the natural populations and those on the surrounding platforms. The three species collected were the most abundant hermatypic scleractinians: *M. decactis*, *D. strigosa*, and *M. cavernosa*. Tissue samples were collected from the E-FGB and W-FGB, and seven platforms within a 65 km radius, at a depth range of 5-37 m. Genetic variation was assessed using Amplified Fragment Length Polymorphisms (AFLPs). The large number of polymorphic markers generated by AFLPs allowed for the use of standard genetic analysis tools (AMOVA) as well as population allocation techniques (AFLPOP). The AMOVA analyses indicated that the E- and W-FGB were genetically homogeneous for *M. decactis* and *D. strigosa* populations. *M. cavernosa* populations, however, were significantly different between banks. In all species, genetic distance (Φ_{ST}) increased significantly with geographic distance between populations. In the brooding species *M. decactis*, this pattern was even stronger when one considered the shortest distance between platforms and the nearest perimeter of the FGB, particularly the nearest FGB, suggesting that the FGB may be a source of larvae for platform populations. The

AFLPOP analyses showed that the degree of self-allocation to home sites also increased with inter-site distance. Cross allocations between sites dropped significantly and exponentially in all species within only one to several kilometers of the FGB. *M. decactis,* a brooder with extended larval release periods and near-immediate settlement competence, shows greater affinity to the FGB with distance than *D. strigosa*, a broadcaster. This brooder appears to be more effective at colonizing small, nearby target sites and expanding its geographic range at the meso-scale. The low degree of genetic affinity exhibited by all species on the platforms may be attributed to genetic drift/founder effect or relatively small population sizes, although total populations were sampled. In general, genetic affinity decreased with inter-site distance. Young coral populations are highly differentiated at the meso-scale during early stages of community succession, implying that much time and repeated colonization of patchy habitats around larger potential larval sources will be required before genetic equilibrium or homogeneity is reached.

1.0 INTRODUCTION

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

1.1.1 Background: Geological, Biological and Regulatory Framework

Approximately 40,000 oil and gas wells have been drilled in the northern Gulf of Mexico (GOM) since the 1940s (Francois, 1993). There were ~3,200 platforms servicing these wells in 2011 (USDOI, BOEM, 2012). These platforms act as hard substratum for many reef organisms to settle on and grow (Gallaway and Lewbel, 1981; Driessen, 1989, Bright et al., 1991; Adams, 1996; Boland, 2002; K. Deslarzes, pers. comm.). The continental shelf in the northern GOM is a region where very little hard substratum either exists now or has existed in recent geological time (Curray, 1965a,b; Blum et al., 2001; also see Frost, 1977; Schroeder et al., 1995; Blum et al., 1998). The Flower Garden Banks (FGB), which rise to within 18 m of the surface, are the most remarkable exceptions for the Gulf and support thriving coral populations (Rezak et al., 1985; Bright et al., 1992; Gittings 1992, 1998).

There are 37 named banks protected by the Bureau of Ocean Energy Management (BOEM) in the northern GOM including the two FGB, which developed on top of two salt diapirs (Gross & Gross 1995) at the edge of the continental shelf. Those banks that occur offshore in "blue water" (e.g., Rankin-1, Rankin-2, Bright, Geyer, Elvers, Claypile, etc; Rezak et al., 1985; Lugo-Fernandez et al., 2001; Boland, pers. obs.), which might be able to support substantial coral reefs, are too deep or lack other appropriate environmental conditions to do so. A number of banks do have limited populations of reef-building corals but are not sufficiently developed to be considered true coral reefs – reefs built entirely of calcium-carbonate, particularly secreted by hermatypic corals. Examples include Stetson, Bright, Sonnier and MacNeil Banks, the last of which has recently been shown to support a sizeable coral community at the depth limits of these organisms (Schmahl, 2003). The FGB represent the only banks that possess thriving coral reefs in the northern Gulf (Rezak et al., 1985; Sammarco et al., 2002; Sammarco and Atchison, 2003) and are considered to be among the most isolated coral reefs in the western Atlantic (Bright, 1981; Rezak et al., 1985; Snell et al., 1998) and the healthiest (Bright et al., 1992; Gittings, 1992; Gittings et al., 1992 a,b; Sammarco et al., submitted) coral reefs in the western Atlantic. The sister banks of the FGB could potentially act as a source of larvae for the platforms, but it is more likely that the FGB represent the primary larval source, simply because of the magnitude of their resident coral populations.

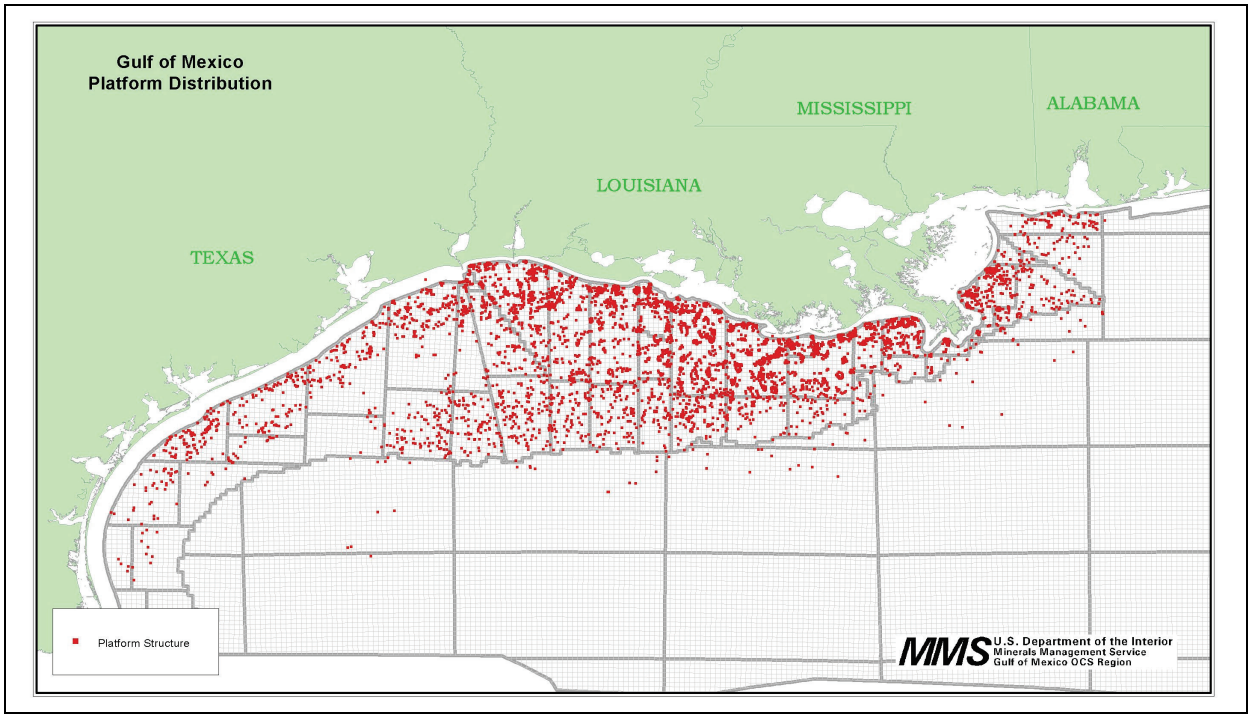

Figure 1. Map of the northern GOM, indicating location of oil and gas platforms present in 2003.

The GOM has experienced several sea level changes in recent geological history (Curray, 1965a, b; Blum et al., 2001; also see Frost, 1977; Schroeder et al., 1995; Blum et al., 1998). During stands of 30 m below present sea level, deeper banks would have been at shallow enough depths to support coral reefs. Provided that seawater temperatures were high enough, it is likely that the northern GOM supported dozens of coral reefs during this period, judging by the distribution of these banks, at the edge of the continental shelf (Rezak et al., 1985). The relatively short distances between them most likely allowed exchange of coral larvae relatively easily through the Island Model of gene flow (Futuyma, 1998). As sea level rose, however, over the past 6,000-10,000 years, the reefs drowned, and the FGB now represent the only coral reefs in the northern GOM. "Drowned" coral reefs are those that could not accrete calcium carbonate layers fast enough to keep pace with sea level rise. Eventually the corals were starved of the light necessary to support the symbiotic algae (zooxanthellae) that live in their tissues, supply a large part of their diet, and facilitate the precipitation of calcium carbonate. The nearest shallow reefs to the FGB are off the northern coast of Yucatan peninsula (Alacran and associated reefs-650 km, Tampico, Mexico (700 km), and the Florida Keys (1,089 km). External sources for seeding the FGB are unknown at present. From what is known about current regimes in the region, sources of larvae may include the above north Mexican areas (Salas-de-Leon et al., 1998). These larvae would be transported by the Western Boundary Current (Vidal et al., 1999) or larvae may be drawn from the Cozumel and Cancun regions and these larvae would be transported north by the Caribbean Current into the Gulf and then west via the Loop Current (Sturges and Blama, 1976; Hamilton et al., 1999). Recent data suggest that currents may be able to transport biological material 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. Data on the molecular genetics of coral spat at the FGB, however, suggest that corals are not being seeded

from the eastern Gulf. The coral spat there show no genetic affinity to adult populations in the Bahamas and Florida Keys (Brazeau et al., 2005), and these data suggest that the FGB are self-seeded, at least with respect to the brooding species *Agaricia agaricites*. Recent physical oceanographic research using drifters deployed during nights of broadcaster spawning supports these findings. Lugo-Fernandez (1998; Lugo-Fernandez et al., 2001) has demonstrated meso-scale patterns of circulation in the vicinity of the FGB, which could drive self-seeding there (Sammarco and Heron, 1994 for a general discussion). Work continues on affinities between adults and spat in this region.

When oil and gas platforms were introduced into the GOM in the 1940s (Francois, 1993), they represented the only substratum other than the FGB and a few other banks in shallow water capable of supporting coral communities. In the absence of these structures, survivorship of coral larvae derived from the FGB or other reefs in the northern GOM would clearly have been much lower due to mortality in the water column after extensive dispersal, attempts to settle on soft bottom, or being transported into nearshore habitats unsuitable for settlement (low salinity, low temperatures, high turbidity, etc.). Earlier studies have shown that a single platform in 33 m of water exposes ~8,100 m^2 of hard surface to the surrounding waters (Shinn 1974).

Before this study was done, the presence of scleractinian corals on the platforms had not been extensively investigated. Some observations had been made of corals on the platforms, along with some documentation (Bright et al., 1991; Boland, 2002; K. Deslarzes, pers. comm., pers. obs. all authors), but no quantitative studies had been performed. The expansion of organisms, both terrestrial and marine, via "leap-frogging" or "stepping stone" mechanisms, has been well documented (Elton, 1977; Futuyma, 1998). In the case of reef fish, such expansions of distributions have been afforded anthropogenically by introducing new suitable habitat, such as oil and gas platforms (Shinn, 1973; Winfield, 1973; Sonnier, et al., 1976; Boland et al., 1983; Shinn and Wicklund, 1989; Pattengill et al., 1997; Rooker et al., 1997; Childs, 1998; Love et al., 2000; but see Schroeder et al., 2000). At a time when coral reefs at the global level are experiencing a severe decline in health and mass coral mortalities because of bleaching, poor fishing techniques, nutrient enrichment, etc. (Sammarco, 1996; Souter and Linden, 2000; Hughes et al., 2003; McClanahan et al., 2008), it is important to determine whether systems exist where coral populations are expanding their distributions.

According to federal legislation, all oil and gas platforms introduced into U.S. waters within a lease block (usually ~4.8 x 4.8 km) must be removed within one year after the end of all production activities within a lease block (BSEE Regulation 30 CFR 250.1718). Some platforms are used by the states bordering the GOM in their Rigs-to-Reefs Programs (e.g., Louisiana, Texas, Alabama, Florida; Dauterive, 2000). These programs are administered in cooperation with the U.S. Department of the Interior, BOEM. Through these programs, the platforms are permitted to either remain on site or are brought to a State-approved location and are used as artificial reefs. Scleractinian corals occurring on natural substratum are protected from harvest and take by federal legislation (Magnuson-Stevens Fisheries Conservation Management Act, 1975, amended Oct. 11, 1996; Public Law 94-265) and are protected from trade by international treaty. These laws may have implications for coral populations present on platforms. If corals are present on them, the structures may have environmental value and may be benefitting the

environment as artificial reefs. Here, for the first time the extent to which corals have colonized these platforms is being elucidated.

1.1.2 Survey of Adult Corals on Platforms around the Flower Garden Banks: Questions Posed

Here, we pose several questions regarding these platforms:

1. Being situated in sub-tropical waters, do they harbor any coral populations?
2. If so, which species?
3. How does coral density and species diversity relate to platform age?
4. How do these variables relate to distance or bearing of a platform from the FGB, indicating that the FGB may be a possible source of larvae for the platforms?
5. How does density and species distribution relate to depth?
6. What is the average colony size on the platforms?
7. How does colony size relate to platform age and distance from the FGB, respectively?

1.2 Coral Larval Dispersal and Recruitment on Oil and Gas Platforms in the Northern Gulf of Mexico

1.2.1 Background

Most of the 3,600 production platforms currently in the Gulf are located in the coastal shelf waters of Louisiana and Texas (Francois, 1993) where the bottom is characterized almost entirely by soft sediment (Rezak et al., 1985). Before the advent of production platforms, hard substratum was limited to relatively scarce, scattered banks and shoals, often in deep water (mesophotic or depths having low light) (Rezak et al., 1985), as were the organisms requiring this type of habitat. The advent of these platforms provided thousands of artificial islands that have introduced suitable substratum from the seabed to the surface for settlement over a large geographic area where otherwise little or none has existed in recent geological history.

Coral reefs of the FGB are considered to be among the most isolated in the western Atlantic (Bright, 1981; Snell et al., 1998; Sammarco et al., 2004; Precht et al., 2008). Corals are sessile, epibenthic organisms and colonization of new habitats such as the FGB is achieved via larval dispersal. The FGB are isolated by hundreds to thousands of kilometers from well-developed neighboring true coral reefs (Rezak et al., 1985; Sammarco et al., 2004), which could potentially serve as sources of coral larvae for colonization there. Coral larvae can potentially travel such distances to successfully settle on remote reefs (Richmond, 1982, 1987). There are submerged banks possessing coral communities near the FGB and elsewhere on the northern shelf. The coral populations there are relatively limited, compared to the FGB, and the banks are not true coral reefs because they are not geologically biogenic in origin. The FGB represent a healthy coral community with a well-developed adult coral community (Gittings, 1992), mass coral spawning (Bright et al., 1992; Gittings et al., 1992a,b), and high recruitment levels (Brazeau et al., 2008, 2011). Gittings (1992) suggested that the reefs were self-sustaining, primarily because of self-seeding of coral larvae within the Bank system.

A high degree of self-seeding is not necessarily a sign of long-term ecosystem stability. Self-seeding in an isolated system can be risky, because the system is almost entirely dependent upon

itself for producing viable larvae and having them recruit locally (Sammarco, 1996; Gold et al., 2001; Palumbi, 2003; Faunce, 2005; Froukh and Kochzius, 2007). For example, in the late 1970s and early 1980s, the highly isolated reefs of the Pacific coast of Panama suffered mass coral mortality due to coral bleaching caused by El Niño and associated high seawater temperatures, producing local coral species extinctions (Glynn, 1983). Two hydrocoral species were driven locally extinct (Glynn and de Weerdt, 1991). Isolation by distance and associated low recruitment levels can place a site at high risk of local extinction (Sammarco,, 1994; Hawkins et al., 2000; Graham et al., 2006). Re-seeding of these communities must come from neighboring communities and, if distant, may require long periods of time (MacArthur and Wilson, 1967). Generally, the more remote a site is, the longer the recovery time. This is because the probability of a particle encountering a site after being released from another site is a function of the inverse of the square of the distance between the two sites (Okubo, 1980, 1994; Okubo and Levin, 1989). Time required for population regeneration is also determined in large part by the density of adults and the balance between cross-seeding (connectedness between coral communities) and self-seeding (where larvae are derived from within the same community).

Prior to this study, it was not known to what degree the platforms in the vicinity of the FGB experience coral recruitment, i.e., the rates of settlement of corals. In fact, little is known about coral recruitment in the GOM. In the first experiment in this region on this topic, Baggett and Bright (1985) found that recruitment on a platform was very low if not absent, even at close distances to the FGB. They examined coral recruitment on the East Flower Garden Bank and the nearby platform HI-A-389. They determined that coral recruitment was absent on this platform, despite the fact that it was located directly to the east of the E-FGB, 2.1 km from the 30 m isobath of the reef cap. All platforms considered in this study are located at greater distances than this from the FGB.

It is possible that platforms at distances up to ~50 km are being seeded by larvae derived from coral populations on the FGB. If recruitment is high across many of the platforms, then the presence of adult coral populations and their recruits on the platforms could be contributing to the stability of the coral community on the FGB or other banks (Lugo-Fernandez et al., 1998, 2001; also see Deslarzes, 1998). The process of successful colonization and possible "island-hopping" by larvae (Futuyma, 1998) as a dispersal mechanism may be operating in this system of patchily distributed habitats (Bright et al., 1991; Holland et al., 1992; G. Boland, pers. obs., pers. comm., unpub. data; K. Deslarzes, pers. comm.). Before any of these questions can be addressed, basic data need to be collected regarding coral recruitment on oil and gas platforms surrounding the FGB.

1.2.2 Coral Reproduction, and Dispersal of Coral Larvae among Reefs and Platforms

Currently, our understanding of factors affecting the genetic diversity of scleractinian coral populations, either within a reef system or among them, is limited. Gene flow is one of the most important processes determining the genetic structure and diversity of populations (Mayr, 1970). Since coral adults are sessile, dispersal of coral planulae is largely responsible for gene flow among populations (Sammarco, 1986). Thus, defining the sources and sinks of their larvae is

critical to understanding factors influencing coral genetic diversity, stability, and the role which individual reefs or structures play in maintaining that diversity.

Corals exhibit two primary modes of sexual reproduction. Brooders have internal fertilization of sperm and egg and develop their planula larvae internally (Harrison and Wallace, 1990). Corals with external fertilization (broadcast spawners) have larvae that spend more time in the plankton and have potential for wider dispersal and a lower self-seeding capacity (Sammarco and Andrews, 1989; Sammarco, 1994). Corals that brood their larvae may have more of a tendency to self-seed their own (natal) reefs or structures of origin (in this case, platforms) (Szmant, 1984, 1986; Sammarco and Andrews, 1988, 1989; Grosberg, 1991).

It is important to understand whether recruits arriving at a platform are derived from brooding or broadcasting corals. This information can provide insight into the ability of certain platforms to seed neighboring areas and reciprocally seed nearby banks, such as the FGB (Sammarco, 1996).

1.2.3 Objectives

The questions raised in this portion of the study are:

a) What are the densities of coral recruitment on oil and gas platforms surrounding the FGB, within a maximum radius of 45 km?

b) What is the species distribution and abundance of those recruits?

c) Do coral recruit density, distribution, and abundance vary among the platforms and the FGB?

d) Does recruitment vary significantly among platforms?

e) Does recruitment vary significantly among replicate settlement racks within platforms?

f) Are recruitment rates similar to other known rates in the Caribbean?

This information will help provide new information on the environmental value of the platforms as artificial reefs in the GOM. It will also provide information to assist in the decision-making process regarding whether individual platforms should be retrieved, left in place, toppled, or dismantled at the end of their useful lifespan.

1.3 Genetic Connectivity in Corals on the Flower Garden Banks and Surrounding Oil and Gas Platforms, Gulf of Mexico

1.3.1 Background

Offshore oil and gas platforms in the northern GOM, numbering as many as 3,600 at the time of writing (Dauterive, 2000; Sammarco et al., 2004; G. Boland, pers. comm.), have served as substrate for the colonization of numerous marine organisms since the 1940s. This region is generally characterized by terrigenous sandy and siltymuds (silt-clay muds) with little habitat diversity (Rezak et al., 1983, Scarborough-Bull, 1989). The platforms extend up through the euphotic zone, providing hard substrate in open water (Shinn, 1974) that would otherwise be

unavailable to such marine organisms. A 200-ft-tall platform jacket can provide thousands of square meters of hard substrate which can support algae, barnacles, bivalves, and other sessile, epibenthic invertebrates (Driessen, 1989, Scarborough-Bull, 1989). Scleractinian corals, including *Diploria* spp., *Porites astreoides*, *Madracis decactis*, *M. asperula*, and *Millepora alcicornis*, have been found on various platforms in the GOM (Bright et al., 1991; Sammarco et al., 2004).

The NOAA Flower Garden Banks National Marine Sanctuary (Dokken et al., 2002) is located among these platforms in the northern GOM (~180 km S-SE of Galveston, TX). There are two banks: the East Bank (27º54'32" N, 93º36' W) and West Bank (27º52'27" N, 93º48'47" W; Bright et al., 1984; Rezak et al., 1983; Figure 2). Coral reefs have developed on their caps (Bright et al., 1984; Dokken et al., 1999), rising to within 18 m of the sea surface (Lugo-Fernandez et al., 2001). They are productive (Rezak et al., 1985), healthy reefs, characterized by 24 species of hermatypic corals (Bright et al., 1984; Dokken et al., 2002), including *M. decactis*, *Diploria strigosa*, *Montastraea cavernosa*, and other species (Gittings et al., 1992; Lugo-Fernandez et al., 2001). These are the only two major coral reefs in the northern GOM. The FGB are separated by $\geq$ 640 km of open ocean from other well-developed coral reefs (Hagman et al., 1998a; Sammarco et al., 2004); the closest reef system is Lobos-Tuxpan, located 13 km off Cabo Rojo, Mexico (Dokken et al., 2002; Figure 2). There are other banks on the northwestern GOM shelf, including Stetson, Sonnier, 32 Fathom, etc., but they are not true coral reefs; that is, the benthic substratum is not biogenic (composed of calcium carbonate that has been accreted by corals). Corals are present there, but cover is generally low (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 these banks could be a source of larvae for platform colonization, but the densities of corals are low. The level of their impact on recruitment is unknown.

We studied three hermatypic scleractinian coral species on oil and gas platforms near the FGB and on the FGB themselves, to assess the degree of genetic connectedness among the natural and platform populations. Three species were chosen based on their abundance and different reproductive strategies (Atchison et al., 2006). These were *M. decactis* (Lyman, 1859; Pocilloporidae), a brooder, and two broadcasters, *D. strigosa* (Dana, 1846; Faviidae) and *M. cavernosa* (Linnaeus, 1767; Faviidae). *M. decactis* is a simultaneous hermaphrodite that releases planulae from March to December, with maximum release occurring from September to November (Vermeij et al., 2003).

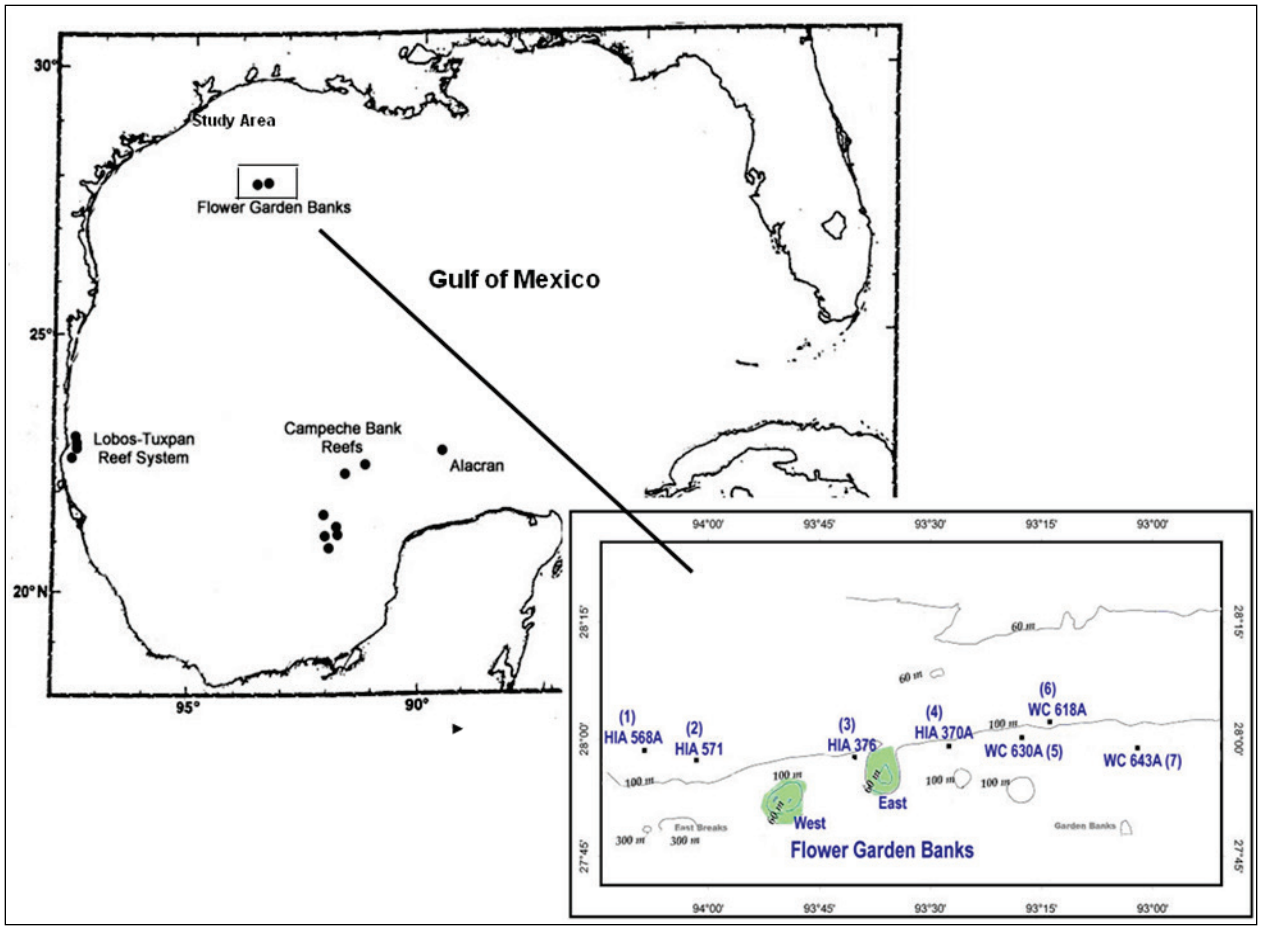

Figure 2. Map of the GOM depicting the location of the FGB and the nearest neighboring reefs (e.g., the Lobos-Tuxpan reef system and Campeche Bank reefs). Inset: Map depicting the study sites, including the FGB and seven of the thirteen offshore platforms sampled in this study. Only the FGB and seven platforms possessed coral populations of the target species: (1) HI-A-568A; (2) HI-A-571A; (3) HI-A-376A; (4) HI-A-370A; (5) WC-630A; (6) WC-618; and (7) WC-643A.

There is an abundant literature regarding brooding compared with broadcasting in numerous marine species (Hellberg et al., 2002; Taylor and Hellberg, 2003; Jones et al., 2005), but we will limit our comments here to corals. The fully-developed larvae of brooding corals are competent to settle in ≥ 4 hrs (Harrison and Wallace, 1990). These species typically become reproductive at younger ages (1-2 years) than broadcast spawners (≥ 4 years). Brooders can also planulate monthly, releasing larvae 8-10 times each year (McGuire, 1998) for a period of days before and after their peak release date. Broadcast coral spawning is usually seasonal, occurring over only one to several days during the summer, being synchronized with a lunar phase and occurring during a single month (Harrison and Wallace, 1990). The resultant embryos require 4-7 days for development. Mass spawning in corals occurs on the FGB (Gittings et al., 1992, Hagman et al,. 1998a,b) as it does elsewhere in the Atlantic (de Graaf et al., 1999) and the Pacific. Spawning in *D. strigosa*, *M. cavernosa,* and other broadcasting species on the FGB (Bright et al., 1991,Gittings et al., 1992; Hagman et al., 1998a,b) is synchronous with other Caribbean reefs (Lugo-Fernandez et al., 2001).

Some coral studies suggest that brooders are effective at short-distance dispersal, while broadcast spawners are adapted for longer-distance dispersal on and between reefs (Baums et al., 2005). After planulae are fully developed, however, the potential for long-range dispersal is most likely comparable between brooders and broadcasters (Sammarco and Andrews, 1989; Sammarco, 1994).

1.3.2 Objectives

Here we will do the following with respect to molecular genetics of corals in the study region.

- Examine genetic affinities among populations of the scleractinian corals *M. decactis, D. strigosa,* and *M. cavernosa*, respectively–one brooder and two broadcasters–on the FGB and on a set of offshore platforms surrounding them in the first phase of this ongoing study. These platforms represent the proximal platforms around the FGB.
- Examine the degree of connectedness between coral populations on the natural reefs and the surrounding platforms, the degree of self-allocation, and the degree of connectivity among neighboring platforms themselves.
- Examine effectiveness of colonization of the platforms by brooding compared with broadcasting species, as it pertains to an island-hopping strategy of colonization (MacArthur and Wilson, 1967; Maltagliati et al., 2002; Atchison, 2005; Baums et al., 2005).
- Data regarding *M. decactis* and *D. strigosa* were preliminarily analyzed by Atchison et al., (2006). We will expand those analyses to include *M. cavernosa* and apply a more conservative statistical analytical approach to examine the data, based on the results of extensive simulations, and examine the data from a more detailed geographic perspective.

1.4 DURATION

This initial phase of the study ran for four years, from 2000 through 2003. A variety of circumstances, such as hurricanes, caused in cruise delays and extended the study two years beyond the projected original anticipated date of completion. The first and second years were spent surveying the platforms, sampling coral populations on the selected platforms, and deploying coral settlement racks. We also conducted preliminary statistical analyses. Plates deployed during the first and second years of the study were retrieved during the second and third years and processed for coral spat. Analysis of adult samples continued, adults and spat were genetically finger-printed, and statistical analyses of the data were initiated during the fourth year. Several 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 regarding adult coral populations on platforms surrounding the FGB, we initiated a set of field surveys and experiments, followed by laboratory analyses. To determine whether platforms support substantial coral communities, we chartered a dive vessel (M/V *Fling*, Freeport, Texas) and surveyed 13 oil and gas platforms over a period of two years (Table 1). Surveys were conducted with teams of SCUBA divers during the summer and fall of 2001 and the 2002. The sample platforms fell within a narrow ellipse ranging from 10 to 15 km west of the FGB to 50 km east of the FGB and 10 to 15 km north (Figure 2). Divers examined the platform jackets from the surface down to a depth of 33 m. Data were collected on the following variables: 1) numbers of scleractinian and hydrozoan corals; 2) depth of occurrence; and 3) species identification.

Data were standardized to density by estimating the area surveyed. In this report, "density" refers to no./unit area; "abundance" refers to general numbers of organisms. Architectural structural drawings of the platform jackets were obtained from the oil and gas companies concerned. Total surface area was estimated for each platform, for each 3 m interval of depth. Areas were standardized to compensate for horizontal support structures, which occurred at 10-15 m and 24-27 m. The number of colonies added at a given depth by these structures were divided by area at that depth and included in analyses as a single sample.

Data on coral colony size was also collected. Because of time restrictions at depth, however, only a limited amount of data could be collected and only the most abundant species received attention. Size was estimated by measuring the length of the longest axis of the colony and the widest width (Sammarco, 1980, 1982). Area was estimated by calculating elliptical area.

Data were also gathered about the platforms themselves. The date of installation was determined from BOEM records (Table 1). Distance of the platforms from the nearest reef perimeter, and their bearing from the FGB, was determined by nautical charts, also provided by BOEM.

Standard parametric univariate statistical analyses were performed on the data. Data were transformed by square-root (Y+0.5) where necessary for purposes of normalization (Sokal and Rohlf, 1981). Kolmogorov-Smirnov Frequency Tests of Independence were performed on the coral depth distribution data to test for variation from a uniform distribution. (The bins, or depth categories, are chosen on the basis of frequencies of corals within each. The analyses cannot be performed on bins with less than a certain number of corals in them.) A multivariate pattern-seeking analysis entitled PATN (Belbin, 1995) was performed on coral community data derived from experimental platforms, using square-root transformations where necessary. This analysis used the Bray-Curtis metric (Bray and Curtis, 1957) and classified the samples by the progressive fusion strategy variously known as the "error sum of squares" (Ward, 1963) or "incremental sum of squares" (Burr, 1970) technique. Details of statistical tests will be presented in the figure and table legends. Only significant results will be discussed.

Table 1.

Details of Oil and Gas Platforms Studied

Platform	MMS No.	Owner	Lat.	Long.	Date of Deployment	Age at Time of Sampling (years)	Distance from FGB perim. (km)	Bearing from FGB (degrees)
EC-317B	23361	Merit Energy	28.20839	92.95187	1989	12	52.30	65
HI-A-330A	10067	El Paso/Coastal Oil & Gas	28.09624	93.47840	1975	26	14.08	46
HI-A-349B	10096	El Paso/Coastal Oil & Gas	28.07030	93.46913	1977	24	12.87	51
HI-A-370A	10060	Kerr-McGee	27.98545	93.45840	1976	25	10.86	68
HI-A-376A	10175	Anadarko	27.96197	93.67089	1981	20	2.01	44
HI-A-382	10300	Apache Oil; UNOCAL	27.91319	93.93510	1986	15	6.44	276
HI-A-385C	28001	Kerr-McGee	27.91682	93.91682	1994	7	3.22	314
HI-A-368B	463	El Paso/Coastal Oil & Gas	27.97170	93.51782	1999	2	5.23	66
HI-A-568A	10133	Samedan	27.97627	94.14394	1979	22	24.46	283
HI-A-571A	10116	W&T Offshore	27.95564	94.02712	1978	23	15.05	283
WC-618	23286	Newfield	28.03671	93.23121	1986	15	30.18	71
WC-630A	22031	Forcenergy	28.00344	93.29414	1977	24	24.14	74
WC-643A	21757	Texaco	27.98137	93.03419	1975	26	48.68	81

2.2 ASSESSMENT OF CORAL SETTLEMENT ON THE PLATFORMS

2.2.1 Experimental and Technical Designs, and Field Activities

The experimental design to assess coral settlement on the platforms followed a one-way, nested replicated design (Sokal and Rohlf, 1981). The primary factor was the study platforms. Racks were deployed on 13 platforms (see Table 2 for complete details). The original design was to expose settlement plates for a period of one year, retrieve the settlement racks, and re-deploy a replacement set of racks at the same sites for a second year. This would allow sufficient time for growth of spat into a size suitable for visual recognition with a dissecting microscope in the laboratory, taxonomic identification, and sampling of tissue for molecular genetic analysis. The original design called for placement of three racks at 15 and 27 m, respectively. Five replicate plates were attached to each rack for a total of 30 racks.

Ceramic terracotta tiles (Versatile®, Canton, OH; unglazed, vitreous - partially glass, ceramic quarry tiles) were used as settling substratum. Each plate was 15 x 15 cm or 225 cm^2 for one side, for a total of 450 cm^2 for top and bottom (minus the small center area covered by mounting washers). Data will be reported as no./450 cm^2. These tiles have been demonstrated experimentally to be well-suited for this type of study (Baggett and Bright, 1985; Harriott and Banks, 1995; Maida et al., 1995a,b; Gleason, 1996). McGuire (1995) has demonstrated that survival and growth of coral spat was higher on ceramic tiles than on other artificial substrata tested, such as glass, PVC, concrete, and coral/limestone blocks.

Tiles were center-drilled, mounted on stainless steel all-thread rods, and secured with plastic and steel lock-washers and nuts (Sammarco and Andrews, 1988, 1989; Sammarco, 1991). The all-thread was mounted on galvanized steel racks (Figure 3). The rugose sides of the tiles were oriented downward when mounted on the platform to provide planulae with their preferred surface irregularity and positioned at an angle of 37°-45° from the horizontal (Carleton and Sammarco, 1987; also see Bak and Engel, 1979; Oakley, 1988; Mundy, 2000). Racks were pre-assembled in the laboratory and deployed by SCUBA divers. We used the M/V *Fling* (Freeport, Texas) to access the study sites and as a base for offshore dive operations. Racks and tools were transported underwater to the platform using a buoyancy device and hung beneath the horizontal support struts. The racks were secured using several 2 m long heavy-duty stainless steel hose clamps with the aid of hand wrenches and a pneumatic drill, adapted for underwater use. Upon retrieval, plates were put in Ziploc® freezer bags filled partially with SEM salt buffer to preserve the coral tissue of the spat for later molecular genetics analysis. The bags were then stored in small ice chests and kept frozen at -20°C on shipboard and in the laboratory for processing later.

Plates–tops, bottoms, and all sides-were processed visually in the laboratory using a dissecting microscope. Spat were identified via their skeletons, with the assistance of specimens archived from earlier coral recruitment studies in Jamaica, West Indies; light and scanning electron micrographs from the same and other collections were also used (Sammarco, 1977, 1980, 1982, unpub. micrographic collection; Budd et al., 2006). All taxa reported to recruit onto the FGB by Baggett and Bright (1985) are also known to recruit in Jamaica. Information was gathered on the distribution and abundance of coral spat species on the experimental settlement plates and how they relate to the distribution of platform and FGB adult coral populations.

Table 2.

List of Northern GOM Oil and Gas Platforms on which Coral Settlement Racks Were Deployed, 2001-2003

Platform Code	Year 1			Year 2		
	Deployment	Retrieval	Months of Exposure	Deployment	Retrieval	Months of Exposure
HI-A 330A*	5/01	5/02	12			
HI-A-349B*	5/01	5/02	12			
HI-A-382*	5/01	5/02	12			
HI-A-376A*	10/01	5/02	7			
HI-A-382F	5/01	5/02	12	5/02	5/03	12
HI-A-368-B*	5/01	5/02	12	5/02	5/03	12
HI-A-376-A	5/01	5/02	12	5/02	5/03	12
HI-A-568A				5/02	5/03	12
HI-A-571A*				5/02	5/03	12
EC-317A/B	10/01				6/03	18
WC-643A	10/01				6/03	18
HI-A-370A	5/01				6/03	25
WC-618A	10/01					**

* = Platforms from which plates were processed for this study.

** = Racks lost, most likely from storms

Figure 3. Coral spat settlement rack. Galvanized steel angle iron supporting stainless steel all-thread pins. Terracotta tiles (15 x 15 cm) were used for settlement plates. Plates and pins attached with stainless steel flat washers, lock-washers, and nuts. Settlement surfaces of plates insulated from steel via Teflon washers. Racks were hung from horizontal struts hanging downward (opposite orientation of that shown).

2.2.2 Statistical Analyses

Standard univariate parametric and non-parametric statistical analyses were performed on the data (Sokal and Rohlf, 1981) using BIOMStat V3.2 and V3.3. These included multi-way and/or nested ANOVAs, a posteriori SS-STP tests, Kruskal-Wallis tests, least-square linear regressions, etc. Data were compared between platforms, racks, and plates. They were also compared between the platforms and the E-FGB, where recruitment data had been collected in a parallel study. Data were transformed by square-root (Y+0.5) where necessary for normalization purposes.

2.2.3 Technical Considerations and Alteration of Original Plan

Several factors caused us to alter our plans. First, poor or severe weather conditions frequently caused the cancellation or premature abortion of cruises, in the interests of safety of the scientific and ship's crew. Second, we encountered technical and safety issues with the deployment and retrieval of racks and sometimes threats to divers (sharks) during these activities. These factors resulted in the alteration of dates of deployment and retrieval, and a reduction in the numbers of racks deployed per platform, particularly at the deeper stations. Third, because of the paucity of spat on the settlement plates, and the inordinate amount of time required to process the plates with a dissecting scope, it was decided to stop plate-processing after the sixth platform. For these reasons, racks were treated as nested within platforms; depth effects will not be considered here. Plates from the following platforms were analyzed: HI-A-330, HI-A-349B, HI-A-368B, HI-A-376A, HI-A-571, and HI-A-382 (Table 2).

2.3 Determining Genetic Connectivity in Corals on the Flower Garden Banks and Surrounding Oil and Gas Platforms, Gulf of Mexico

2.3.1 Study Site

Thirteen oil and gas platforms off the Louisiana and Texas coasts were surveyed for hermatypic scleractinian corals. The target species–*Madracis decactis, Diploria strigosa,* and *Montastraea cavernosa*-were found on seven of these, which will from herein be referred to as Platforms #1 thru #7 going west to east (Figure 2). All platforms considered here had been in place for 15-26 years, a platform age range known to be associated with the development of substantial adult coral populations (Sammarco et al., 2004).

2.3.2 Sample Collection

Tissue was collected from all coral colonies present on the platforms, i.e., total populations between 5 and 37 m depth. At the E- and W-FGB, samples of the larger populations were collected haphazardly within a diameter of 100 m by teams of divers. The platforms fell within an elongated ellipse, inclusive of the FGB, extending from 10 to 15 km west of the W-FGB to 50 km east of EFGB and 10-15 km north. The sampling regime was skewed to the east because of the known prevailing westerly currents in the region (Sturges, 1993; Oey, 1995; Lugo-Fernandez, 1998; Lugo-Fernandez et al., 2001; Figure 4). Because of problems associated with transfer of samples over international borders, it was not possible to sample corals from other potential source populations including those in Mexico (Tampico, Bay of Campeche, Alacran Reef, etc.).

Using small hammers and chisels, teams of SCUBA divers collected tissue samples, each two cm^2 in size, from the growing edge of adult colonies of the three target species. Total population sizes on the platforms were small. For this reason, sample sizes (provided in tables) represent all corals on each platform within the depth range sampled. That is, populations assessed within this depth-range were not sub-sampled. Once on shipboard, the samples were sealed in small plastic freezer bags containing SED buffer (saturated NaCl, 250 mM EDTA, pH 7.5, 20% DMSO) to preserve the DNA. This allowed the samples to be stored at room temperature, eliminating the need for storage in liquid nitrogen. Bags were then put in ice chests containing additional SED buffer and returned to the laboratory.

2.3.3 Technique Used to Determine Genetic Affinity - Amplified Fragment Length Polymorphism (AFLP)

The AFLP technique was used to conduct molecular genetic analyses. It is a DNA-fingerprinting technique (Sunnucks, 2000) that detects polymorphisms based upon the selective PCR amplification of a subset of the massive population of restriction fragments generated using two different restriction enzymes (Vos et al., 1995; Mueller and Wolfenbarger, 1999). The AFLPs tend to be highly polymorphic but are not co-dominantly expressed. Bensch and Åkesson (2005) have noted that AFLPs are commonly used in studies of crop species and economically important species but have had only a modest impact in animal studies. This is surprising, since many studies are limited by the availability of polymorphic markers, something AFLPs can provide. The AFLPs have been used successfully to determine migration rates (He et al., 2004), species boundaries (Lopez et al., 1999; Fukami et al., 2004), and parental contributions to populations (VanToai et al., 1997). Though AFLPs are less than ideal for many population genetic applications (Sunnucks, 2000), they are well suited for population assignment or allocation studies (Blears et al., 1998; Mueller and Wolfenbarger, 1999; Sammarco et al., 2001, 2012) where the number of polymorphic loci is more important than allelic diversity (Bernatchez and Duchesne, 2000).

One weakness of AFLPs is that some variation detected may not be derived from the target organism (Sunnucks, 2000). In corals, the major concern is with symbiotic zooxanthellae. Here we use zooxanthella-specific PCR primers to confirm for each sample that zooxanthellar DNA contamination are at levels far below those necessary for AFLP (5-10 pg of zooxanthellar DNA in a background of coral DNA; Brazeau et al., 2005). In an earlier work, we assessed the consequences of zooxanthellar DNA contamination on coral AFLPs (Brazeau et al., 2005). Using zooxanthellar DNA spiked into coral DNA preparations the lower limit of zooxanthellar DNA detected by PCR primers specific for zooxanthellae was five to six orders of magnitude (4.8 pg) less than the amount of coral DNA present in each sample (minimally 50-100 ng). Attempts to generate AFLP bands using pure zooxanthella DNA at amounts ranging from 0.48 to 480 pg were unsuccessful. Thus, coral samples that show no detectable zooxanthellae PCR product will have too little zooxanthella DNA to contribute any substantial numbers of AFLP bands.

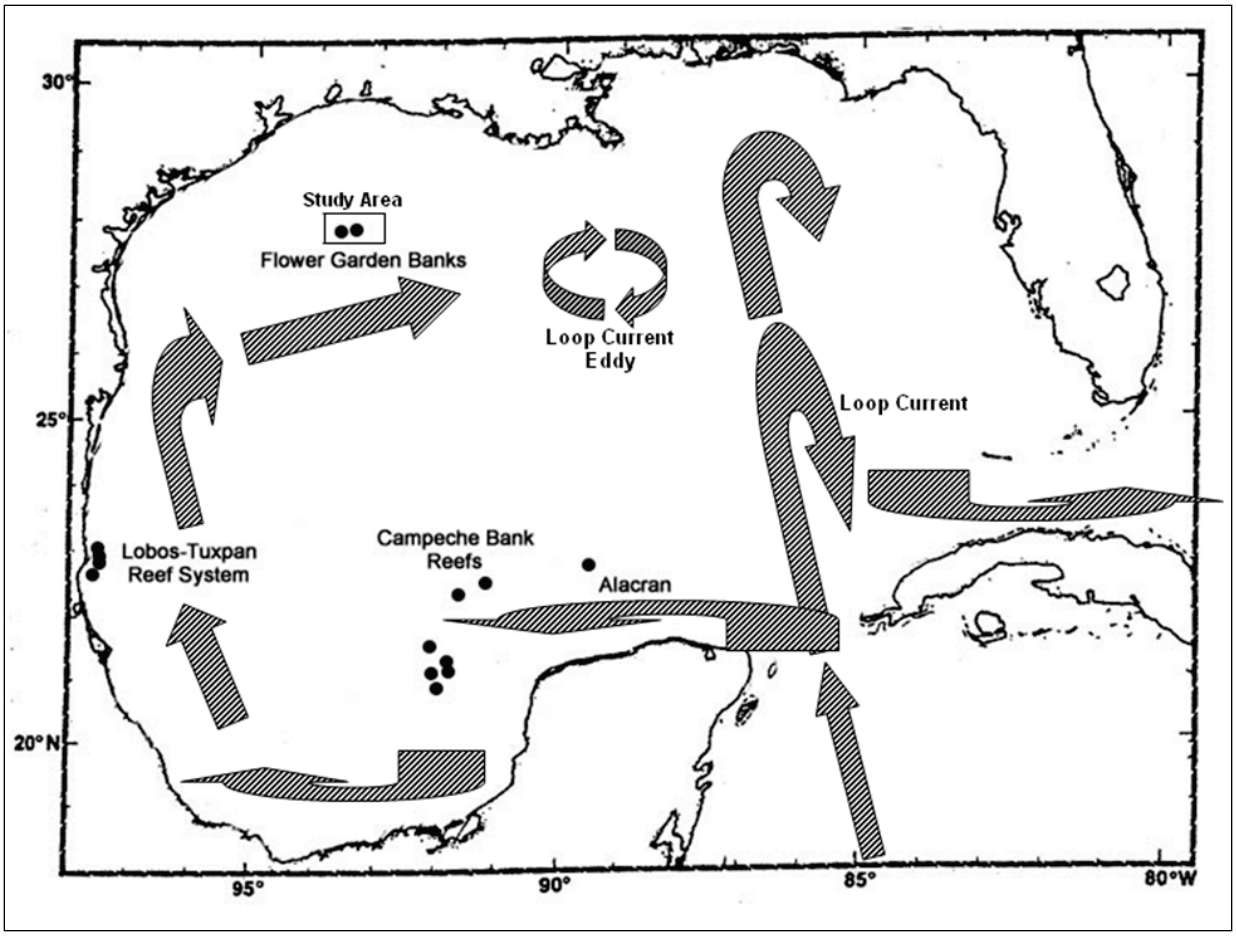

Figure 4. Map of the GOM, depicting examples of general currents known to exist. Note the general westerly current across the continental shelf in the vicinity of the FGB and the northerly jet extending from Alacran to the FGB, indicating potential larval dispersal.

2.3.4 Preparation of Coral Tissue Lysates for Genetic Analysis

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

The 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 to uniformly distribute any error potentially introduced by reaction conditions 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, Beverly, MA), 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 3. 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 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. To each 0.5 ml tube, 15 µl of the pre-selective amplification master mix was added, 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 ss denaturation at 94ºC, 30 s annealing at 56ºC, and 2 min extension at 72ºC. The 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.

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 nine 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, 30 s 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 on 20 banding pattern 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.

Table 3.

Sequences of the Adapters and Primers Used in the AFLP Protocol. Pre-Selective and Selective Nucleotides are Indicated in Bold.

	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**

2.3.5 Statistical Analyses

With respect to the molecular genetics section of the study, two statistical analyses were used to assess population differentiation: Analysis of Molecular Variance (AMOVA; Excoffier et al., 1992), and AFLPOP population allocation analysis (v. 1.0; Duchesne and Bernatchez 2002). AMOVA estimated population differentiation based upon presence-absence data and generated Φ_{ST} values for all possible pair-wise comparisons between populations by species. A bootstrap of 1000 iterations was performed to estimate p values for each species for population statistics. Significance levels (p-values) were corrected using a Bonferroni correction for multiple tests (Bonferroni, 1936). No clones were encountered during the study; thus, adjustments for clonality were unnecessary.

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. 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 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) found that this may yield potentially misleading results, because there may be more than one population with nearly equal likelihood values. Here, we 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, meaning the individual was not assigned to any population 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 which case it could have been derived from an outside populationas discussed in a preliminary report (Atchison et al., 2006). In this study, we focus primarily on those cases where clear assignments have been made including self-allocations to sites of origin and cross-population allocations.

The genetic variables derived above were further analyzed via additional parametric and non-parametric statistical techniques, as mentioned above. The software used for such was BIOMStat V. 3.2 and SigmaPlot V. 10.0. For normalization purposes, data were transformed before analysis.

3.0 RESULTS

Data generated by this report are available upon request from the senior author.

3.1 ADULT CORAL COMMUNITIES ON PLATFORMS SURROUNDING THE FLOWER GARDEN BANKS

The diver surveys revealed a total of 11 species of corals on the platform jackets, occurring between 0- and 33 m depth. Eight of these species were hermatypic scleractinians, two were ahermatypic scleractinian corals, and one was a hydrozoan (Table 4). The dominant hermatypic scleractinian corals were *Madracis decactis* and *Diploria strigosa.*

3.1.1 The Effect of Distance from the Flower Garden Banks on Corals Located on Platforms.

A number of correlation and regression analyses–both parametric and non-parametric–were performed on the adult coral data *versus* distance from the FGB. The independent variables regarding the adult coral populations were as follows: 1) total coral abundance per platform; 2) *M. decactis* abundance per platform; 3) *D. strigosa* abundance per platform; 4) coral species diversity per platform (H', J', and S; Pielou, 1969, 1975); and 5) abundance of *Tubastraea coccinea* per platform. Each of these variables was analyzed with respect to distance to nearest FGB reef perimeter. In all cases, there was no significant relationship between any of these variables and distance from the FGB. The only case in which there was a tendency towards a significant trend was in the abundance of *T. coccinea*, which appeared to decrease with distance from the FGB. This trend was not significant, however, as shown by both parametric (regression analysis) and non-parametric (Kendall's Rank Correlation analysis) tests.

Table 4

List of Coral Species, with Authorities, Found on the Oil and Gas Platforms in this Study. Mode of Reproduction Also Shown, with Approximate Spawning or Larval Release Times and Bibliographic Sources from which those Data were Drawn.

			Reproduction		
				Times*	
Order	Coral Spp	Authority	Mode	(Months**)	Source
Scleractinia - hermatypic	*Colpophyllia natans*	Houttuyn, 1772	spawner	8,9	1,3
	Diploria strigosa	Dana, 1846	spawner	8,9	1,3,4,5,8,9,11
	Madracis decactis	Lyman, 1859	brooder	3 to 12	2
	Madracis formosa	Wells, 1973	brooder		
	Montastraea cavernosa	Linnaeus, 1767	spawner	7,8,9,10	1,3,6,7,8,9,10,11
	Porites astreoides	Lamarck, 1816	brooder	6-9,1-12	8,12,13,14,15
	Stephanocoenia intersepta	Lamarck, 1816	spawner	8,9	1
	Stephanocoenia michelinii	Edwards & Haime, 1848	spawner	7,8	7
Scleractinia - ahermatypic	*Phyllangia americana*	Edwards & Haime, 1849			
	Tubastraea coccinea	Lesson, 1829	brooder		16,17
Hydrozoa	*Millepora alcicornis*	Linnaeus, 1758			(see 18)
* Caribbean-wide					
** 1=Jan, 2=Feb, etc.					
1 Hagman et al. 1998	6 Acosta & Zea 1997	11 Wyers et al. 1989		16 Ayre & Resing 1986	
2 Vermeij et al. 2003	7 Gittings et al. 1994	12 Gleason et al. 1999		17 Hebbinghaus 2001	
3 Steiner 1995	8 Soong 1993	13 McGuire 1998		18 Soong & Cho 1998	
4 Bassim & Sammarco 2003	9 Gittings et al 1992	14 McGuire 1995			
5 Bassim et al. 2002	10 Szmant 1991	15 Chornesky & Peters 1987			

3.1.2 Abundance of Hermatypic Corals on Platforms.

Abundance of shallow hermatypic corals (≤ 14 m depth) increased significantly with the age of the platforms, as indicated by linear regression analysis and non-parametric correlation analysis (Figure 5a). This pattern of increasing abundance as a function of platform age was also significant for corals found in deeper water (> 14 m to 33 m), indicated by both linear regression and correlation analyses. The pattern was as strong or stronger when data from both depths were combined. One clear relationship was a marked increase in coral abundance after ~12-15 years; prior to this, coral growth visible to the naked eye was nominal or absent.

M. decactis, the most abundant coral found on the platforms, showed no significant relationship between abundance and platform age in shallow water (Figure 6). However, a clear positive relationship was found between these variables in deeper water, and for both sets of depths combined.

D. strigosa was the second ranking dominant hermatypic coral found on the platforms. However, in this species, no significant relationship was found between abundance and platform

age, in shallow water, at deeper depths, or with both sets of depths combined ($p > 0.05$, least squares linear regression analyses, Pearson's product-moment correlation analyses, and Kendall's rank correlation analyses).

A significant relationship was found between coral abundance and platform age in *T.coccinea* in shallow water, but, unlike *M. decactis*, that correlation was negative (correlation, $r = -0.544$, $p = 0.05$; Figure 7). No similar significant relationship was found at deeper depths or for all depths combined ($p > 0.05$ for linear regression analyses, correlation analysis, and Kendall's rank correlation analysis).

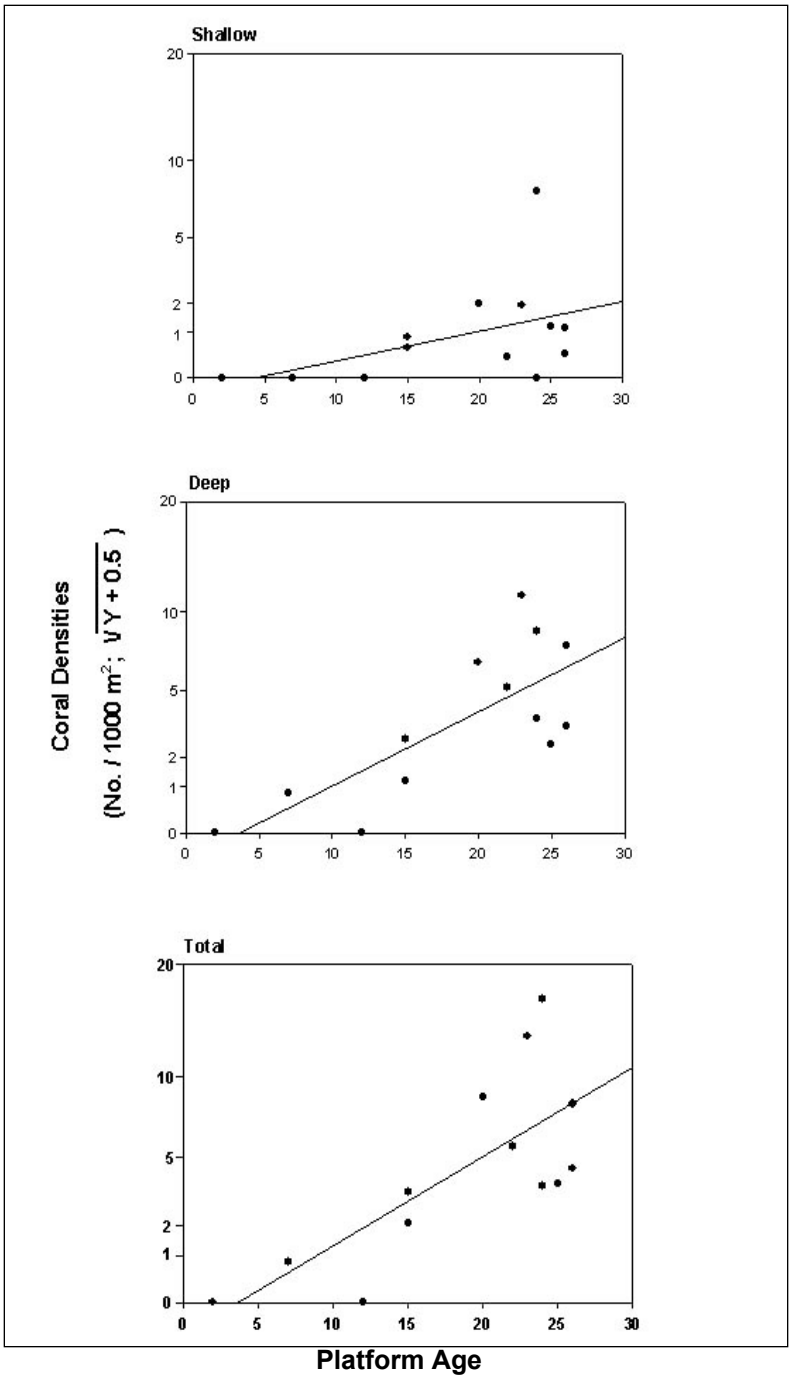

Figure 5. Relative abundances for all spat of different coral genera found on six oil and gas platforms in the northern GOM in the vicinity of the FGB. Data derived from coral settlement on terracotta plates mounted on steel racks and deployed at depths of 15 and 27 m for one year during 2001-2003. Data combined for platforms, racks, depths, and plates. Proportion and 95% confidence limits shown. Data transformed arcsine for normalization purposes.

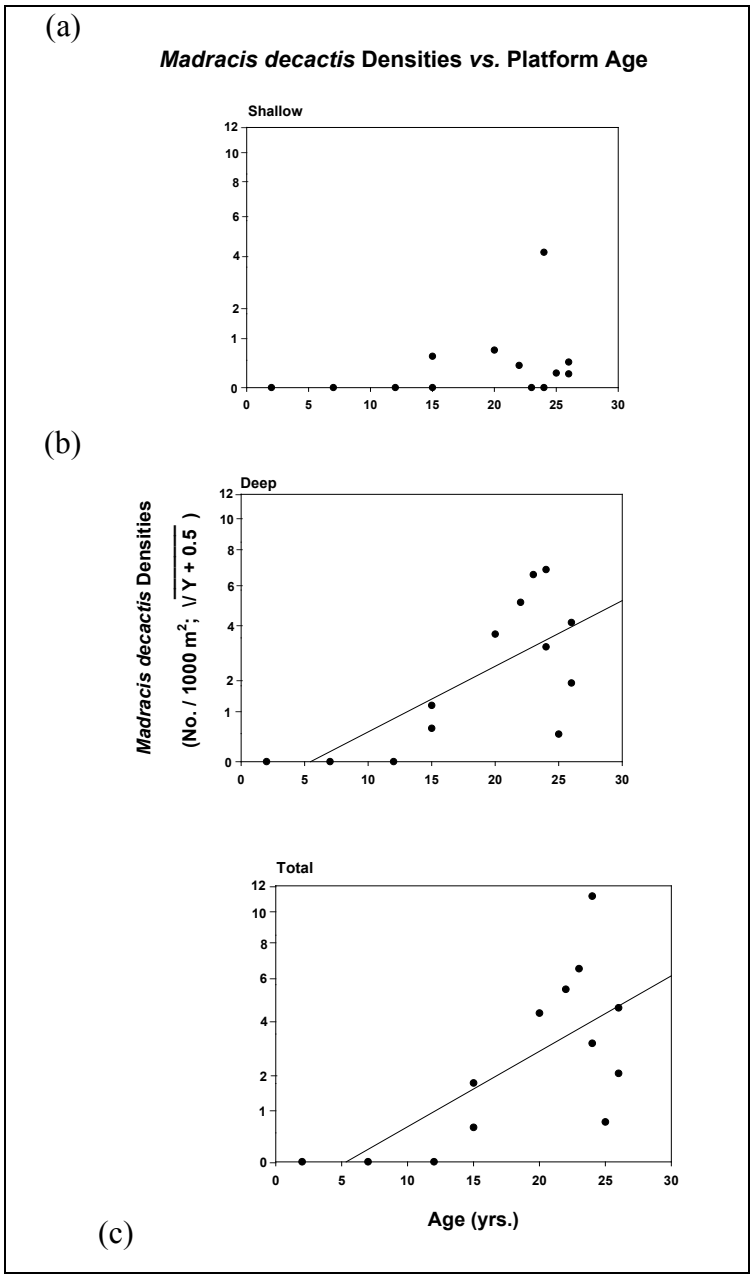

Figure 6. (a) Graph depicting the relationship between total abundance of the coral *M. decactis* in shallow water (0-14 m,) on the platforms studied *versus* age of those platforms. See Figure 3 legend for details of abundance calculations. No significant relationship found ($p > 0.05$, least squares linear regression analysis; Pearson's Product-Moment Correlation Coefficient, $r = 0.335$, $p > 0.05$; Kendall's Rank Correlation Coefficient, $T = 0.2910$, $p > 0.05$). (b) Graph depicting same, but in deeper water (< 14 m – 27 m,; max. 33 m). Significant positive relationship found here (regression, $Y = 0.069 X + 0.332$, $p = 0.01$; correlation, $r = 0.711$, $p < 0.01$). (c) Graph depicting same, but for shallow and deep water data combined.

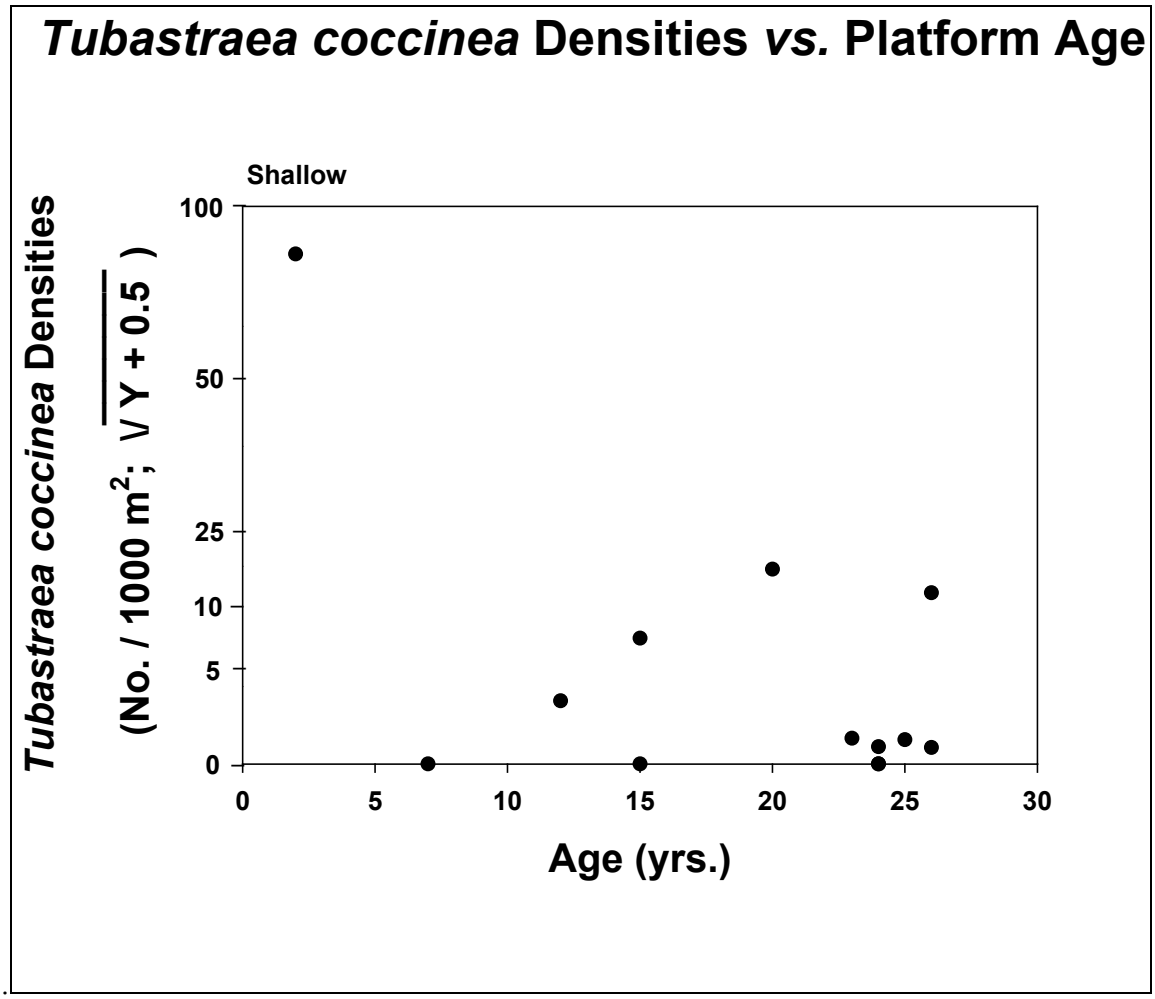

Figure. 7. Graph depicting the relationship between total abundance of the coral *T. coccinea* in shallow water (0-14 m) on the platforms studied *versus* age of those platforms. See Figure 3 legend for details of abundance calculations. Significant relationship found (Pearson's Product-Moment Correlation Coefficient, r = -0.544, p = 0.05). No significant relationship found between *T. coccinea* abundance and platform age in deep water or in both depths combined (p > 0.05, regression, correlation, and Kendall's rank correlation).

3.1.3 Species Diversity of Corals on Platforms.

A highly significant relationship was found between coral species diversity, as measured simply by number of species (S), and platform age. The relationship was strong in shallow water (Figure 8a), even more pronounced in deep water (Figure 8b), and was highly significant when data from both sets of depths were combined (Figure 8c).

A similar significant pattern was found for all corals when species diversity ($H' = - \Sigma p_i \log p_i$; Figure 9a) and equitability ($J' = H'/\log S$); Figure 9b) were used as species diversity measures.

3.1.4 Depth Distribution of Corals on Platforms.

None of the corals considered here were distributed uniformly with respect to depth. This occurred regardless of the distribution of available substrate, even after standardization for available area, which varied greatly with depth because of the presence of horizontal support structures. Total coral abundance exhibited a bimodal distribution, with peaks at depths of ~20 m and 28 m, and with little representation at 0-6 m (Figure 10a). The abundance of *M. decactis* peaked at the same depths (Figure 10b). Unlike *M. decactis*, *D. strigosa* exhibited peaks in abundance at ~10 m and 23 m (Figure 11). *T. coccinea*, unlike these other species, exhibited high abundances at 12 to 21 m depth (Figure 12). Average coral abundance was compared between depth categories above and below 27 m. Average abundances were standardized by number of depth categories above and below that level (i.e., 9 depth intervals *versus* 2 depth intervals). Total coral and *M. decactis* abundances showed no significant difference above *versus* below 27 m depth (Figure 10). No *D. strigosa* were found below 27 m depth on any of the platforms surveyed. *T. coccinea* occurred in much greater numbers at depths of < 27 m than below this; this difference was highly significant (see figure legends for statistical details).

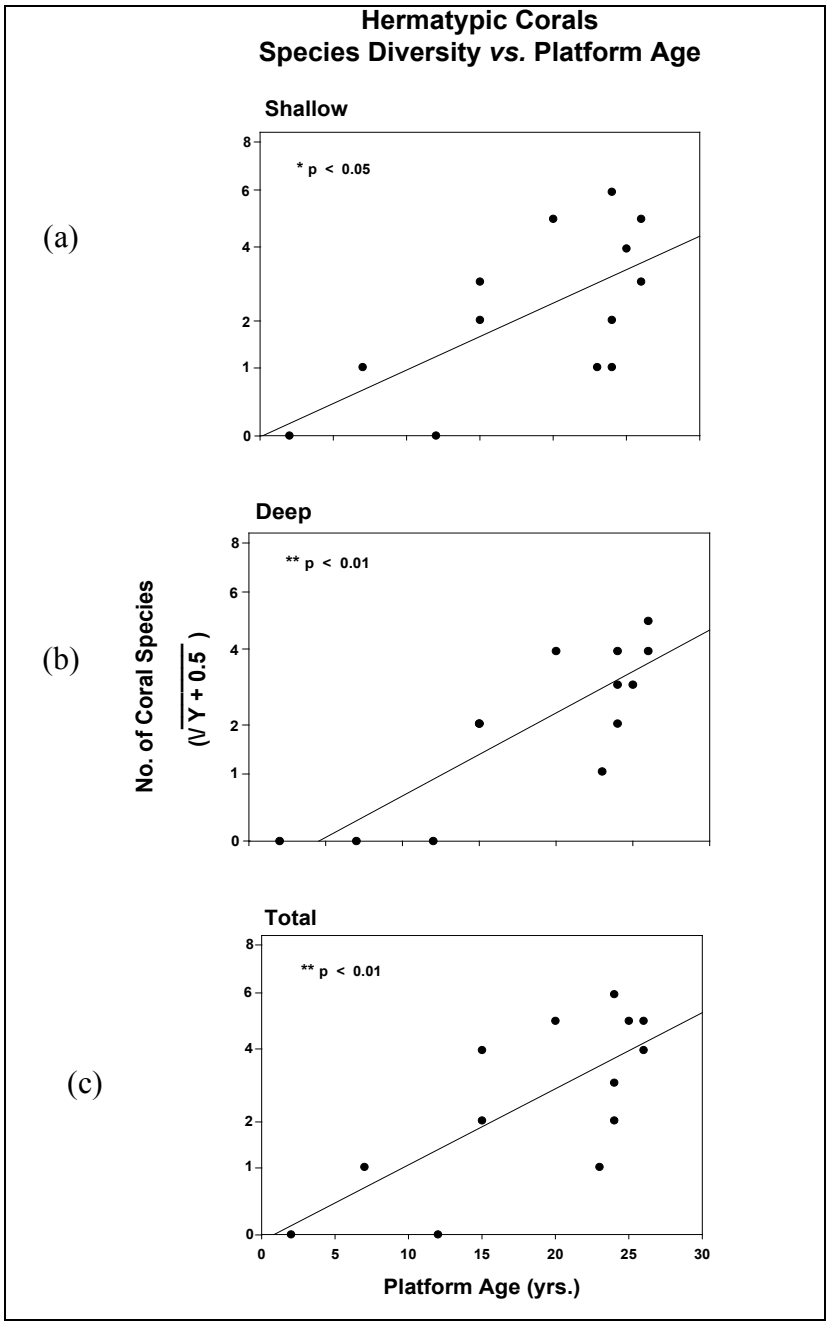

Figure 8. (a) Graph depicting the relationship between coral species diversity as measured by number of species (S) in shallow water (0-14 m,) on the platforms studied *versus* age of those platforms. Significant positive relationship found ($p < 0.01$, least squares linear regression analysis, $Y = 047\ X - 0.519$; correlation, $r = 0.590$, $p < 0.05$). (b) Graph depicting same, but in deeper water (< 14 – 27 m; max. 36 m). Significant positive relationship also found here (regression, $p < 0.01$, $Y = 0.062\ X - 0.508$, $p < 0.01$; correlation, $r = 0.822$, $p < 0.001$). (c) Graph depicting same, but for shallow and deep water combined. Significant positive relationship found here as well (regression, $Y = 0.064\ X - 0.569$, $p < 0.01$; correlation, $r = 0.795$, $p < 0.01$).

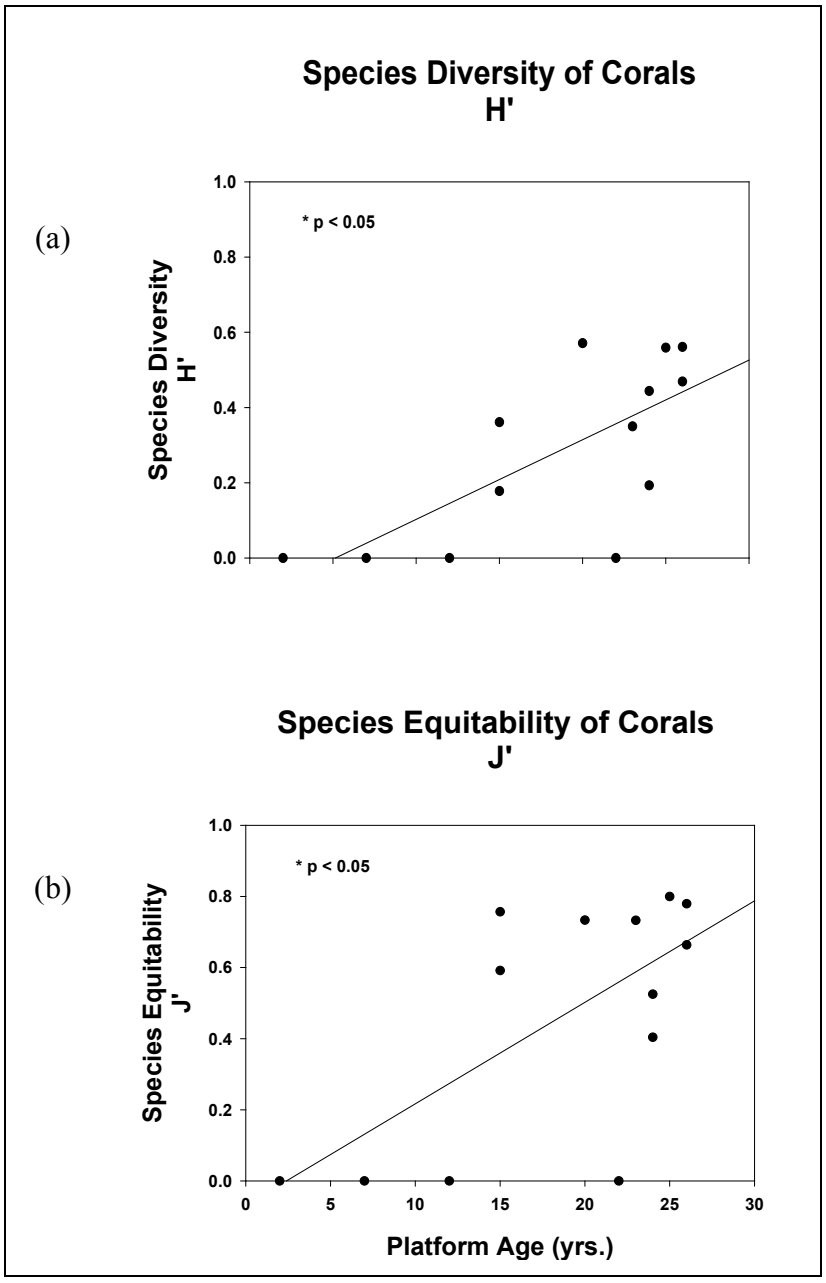

Figure 9. (a) Graph depicting the relationship between coral species diversity as measured by H' on the platforms studied *versus* age of those platforms. Significant positive relationship found (least squares linear regression analysis, Y = 0.021 X – 0.109, $p < 0.05$; correlation, $r = 0.707$, $p < 0.01$). (b) Graph depicting the relationship between coral species equitability as measured by J' on the platforms studied *versus* age of those platforms. Significant positive relationship found (regression, Y = 0.028 X – 0.068, $p < 0.05$; correlation, $r = 0.655$, $p < 0.05$).

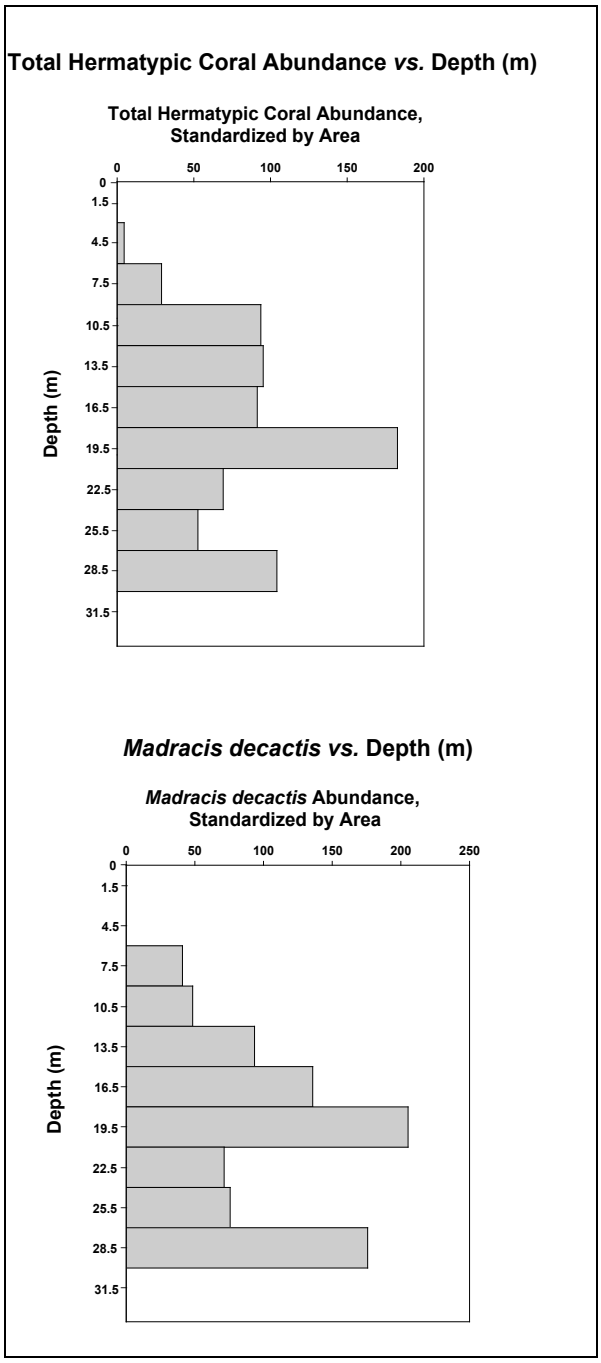

Figure 10. (a) Depth distribution of all corals on the study platforms ranging from 0 to 33m. This distribution was significantly different from uniform distribution ($p < 0.01$, Kolmogorov-Smirnov Frequency Test). There was no significant difference in average total coral abundance above *versus* below 27 m depth ($p > 0.05$, Komolgorov-Smirnov Frequency Analysis). (b) Depth distribution of the coral *M. decactis*. This distribution was significantly different from uniform distribution ($p < 0.01$, Kolmogorov-Smirnov Frequency Test). There was no significant difference in average *M. decactis* abundance above versus below 27 m depth ($p > 0.05$, Komolgorov-Smirnov Frequency Analysis).

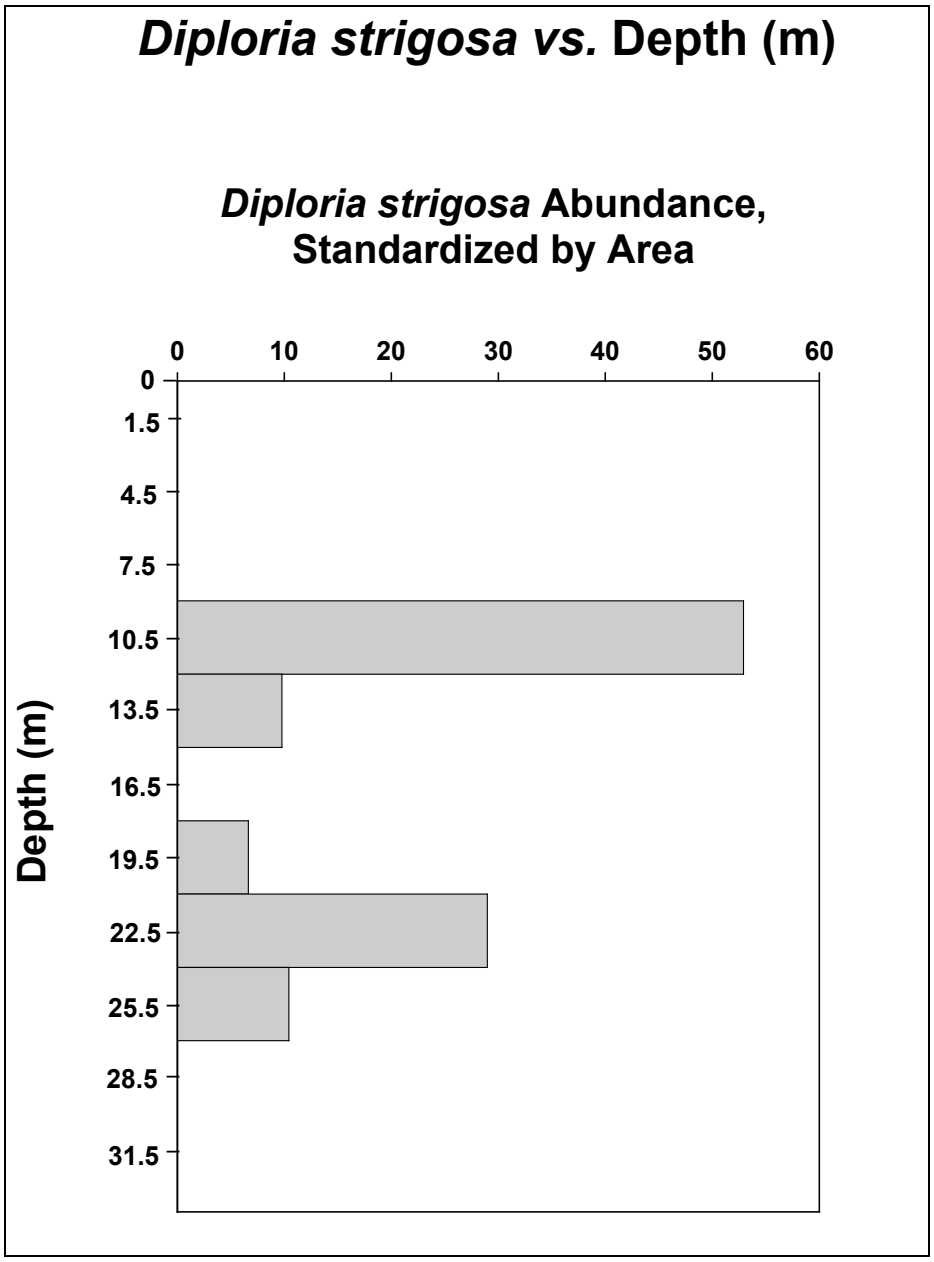

Figure 11. Depth distribution of the coral *D. strigosa* on the study platforms, ranging from 0 to 33 m. This distribution was significantly different from uniform distribution ($p < 0.01$, Kolmogorov-Smirnov Frequency Test).

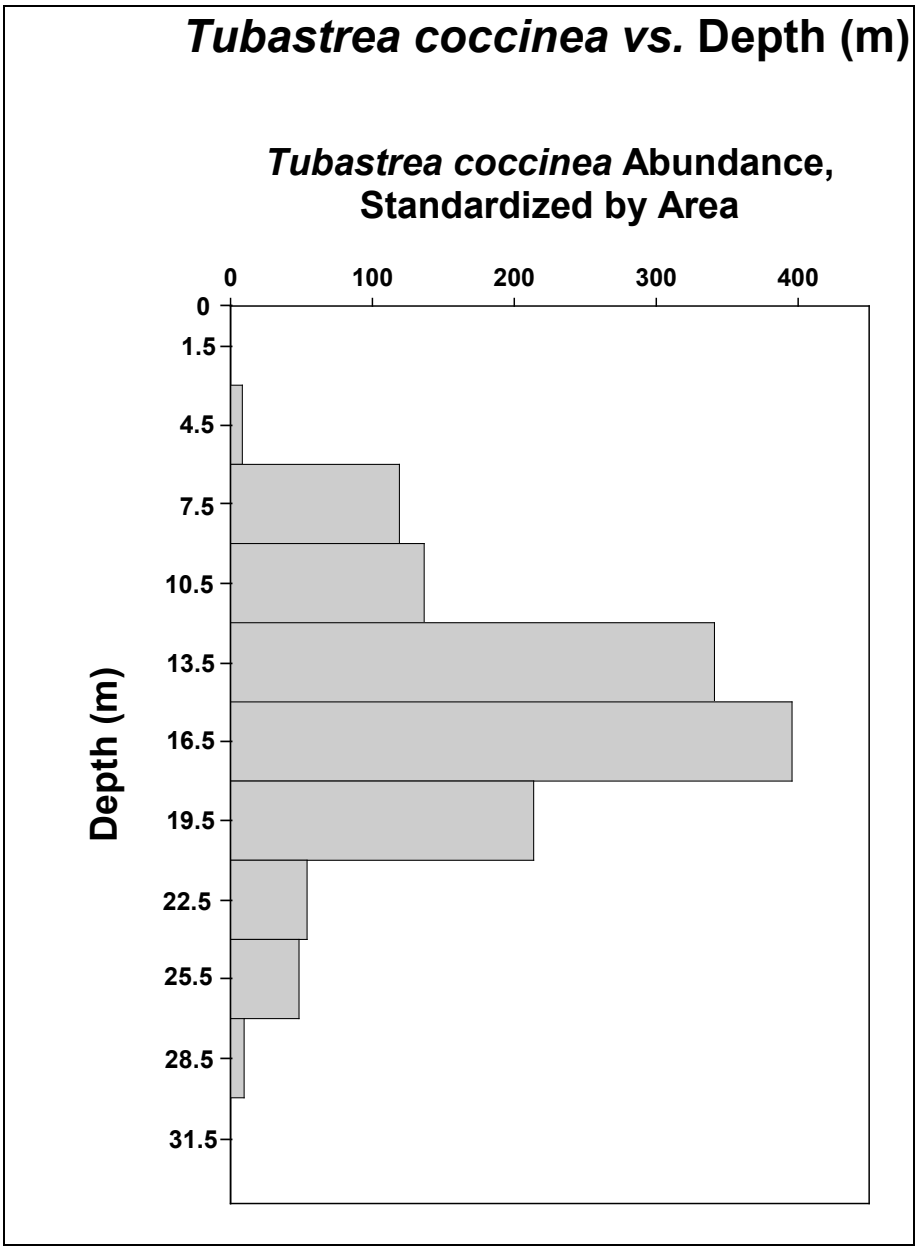

Figure 12. Depth distribution of the ahermatypic coral *T. coccinea* on the study platforms, ranging from 0 to 33 m. Significantly different from a uniform distribution ($p < 0.01$, Kolmogorov-Smirnov frequency test). Significant difference in average abudnace above versus below 27 m depth, with much higher numbers in shallow water ($p < 0.001$, Komolgorov-Smirnov frequency analysis).

3.1.5 Pattern-Seeking Analysis of Adult Coral Communities on Platforms.

A multivariate analysis of all of the coral community data performed simultaneously on all platforms revealed a relatively simple pattern of grouping among platforms. The platforms ranged from 2 to 26 years in age. The pattern-seeking analysis identified a major split in the similarity index between the communities at fusion values below 0.79 (Figure 13). It placed the platforms into two age groups: one large group of platforms that possessed coral communities between 14 and 26 years old, namely HI-A-382, HI-A-370, HI-A-330, HI-A-571, WC-630, HI-A-568, WC-618, HI-A-376, WC-643, and HI-A-349; and a second group that was smaller in number and consisted of platforms of the lower age range (0-13 years), namely HI-A-385, HI-A-368, and EC-317.

3.1.6 Coral Colony Size.

For statistical comparison, a sufficient number of samples of colony size was available only for *M. decactis* (see Materials and Methods above). It was clear that large colonies of this species occurred on platforms ranging from 14 to 26 years of age. There were significant differences between the mean colony size on different platforms, although no particular pattern emerged (Table 5). In addition, a variety of a posteriori tests revealed no significant differences between platforms. Colony size did not vary significantly with platform age within this platform age group or with distance from the FGB within the spatial scale used in this study.

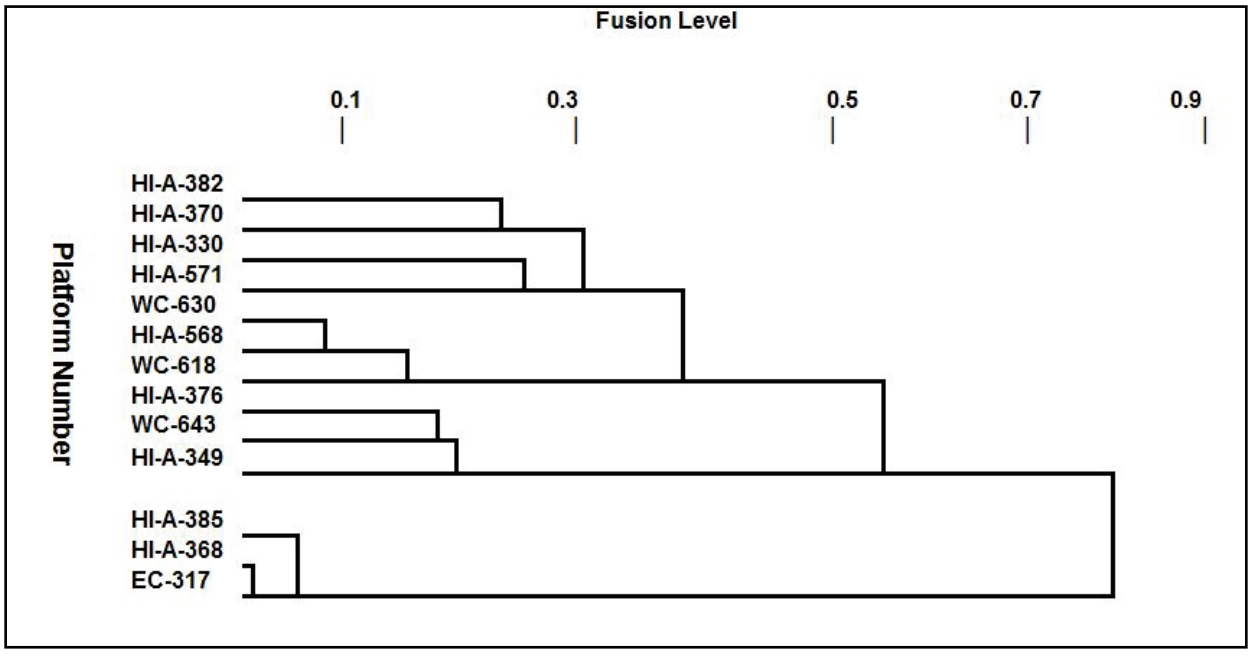

Figure 13. Results of pattern-seeking analysis (PATN), examining the relatedness of coral community structure found on the individual study platforms. Data used were coral abundance by species. Two major groups were identified–one characterized by older platforms and one by those generally < 12 years of age. See text for discussion of pattern.

3.2 RECRUITMENT OF CORALS ON PLATFORMS

The abundance of coral spat collected from the settlement plates placed on the platforms was very low and could be considered rare. Average spat densities on the platforms varied between 0 and < 1 per 450 cm^2 (both plate sides summed; Figure 14). Spat densities on the platforms were significantly ($p < 0.05$; for the a posteriori tests GT2, T', and Tukey-Kramer) lower than recruitment levels observed to occur on the E-FGB in a parallel study (Sammarco and Brazeau, 2001; Sammarco, 2002, 2003, 2005; Brazeau et al., 2005, 2008, in press). On the E-FGB, average total spat densities were ~6 per 450 cm^2. Coral densities were not significantly different between platforms ($p > 0.05$; one-way nested ANOVA), but they were significantly different between racks ($p < 0.001$; Figure 15).

Two of the dominant scleractinian species observed as adults on platforms in this study were *T. coccinea* and *M. cavernosa*. These were also the most common corals observed as spat on settling plates placed on the platforms. *T. coccinea* was the most abundant spat, and *M. cavernosa* was the second most abundant (Figure 16). Only one newly settled spat of *M.* sp. (most likely *M. decactis,* although because of the small size of the spat, this could not be confirmed) was found on the plates. With respect to reproductive modes (Fadlallah, 1983; Harrison and Wallace, 1990; Richmond and Hunter, 1990; Moulding, 2009 for reviews), *Tubastraea* and *Madracis* are brooders; all *Montastraea* species are broadcasters.

With respect to *T. coccinea*, there was no significant difference in density of coral settlement between platforms ($p > 0.05$, nested ANOVA; Figure 17). The only larval recruitment observed in this species occurred on the platforms. This species did not recruit at all to the E-FGB, despite overall high levels of recruitment by other species there. There was also no significant difference between racks with respect to *T. coccinea* spat densities ($p > 0.05$; Figure 18).

Montastraea cavernosa also recruited to the platforms. Settlement in this species, however, was homogeneous between all platforms and all racks ($p > 0.05$, nested ANOVA; Figures 19 and 20). In fact 100% of the variance was found to be associated with difference between plates. Coral recruitment levels were not sufficiently high on the platforms to permit meaningful molecular population genetic analyses to be performed and examine their genetic affinities between populations at different sites.

Table 5

Colony Size in *M. decactis* on Several Oil and Gas Platforms in the Northern GOM Near the FGB

Table 5. Colony Size of *Madracis decactis*						
			Platform			
	WC-643A	**HI-A-376A**	**HI-A-330**	**HI-A-571A**	**HI-A-349B**	**HI-A-568A**
$\bar{Y}$ colony size (cm^2)	873.6	1,813.80	2,396.10	3,146.80	3,369.20	3,770.10
$\bar{Y}_t$	2.72	3.19	3.13	3.4	3.16	3.45
lower 95% conf. limit	2.18	2.07	2.61	3.21	2.52	3.16
upper 95% conf. limit	3.25	4.31	3.66	3.59	3.8	3.74
s_t	0.531	0.314	0.466	0.314	0.804	0.428
n	8	3	7	17	11	14
Platform Age (yrs)	26	20	26	23	24	22
Distance from FGB (km)	48.7	2	14.1	15	8	24.5

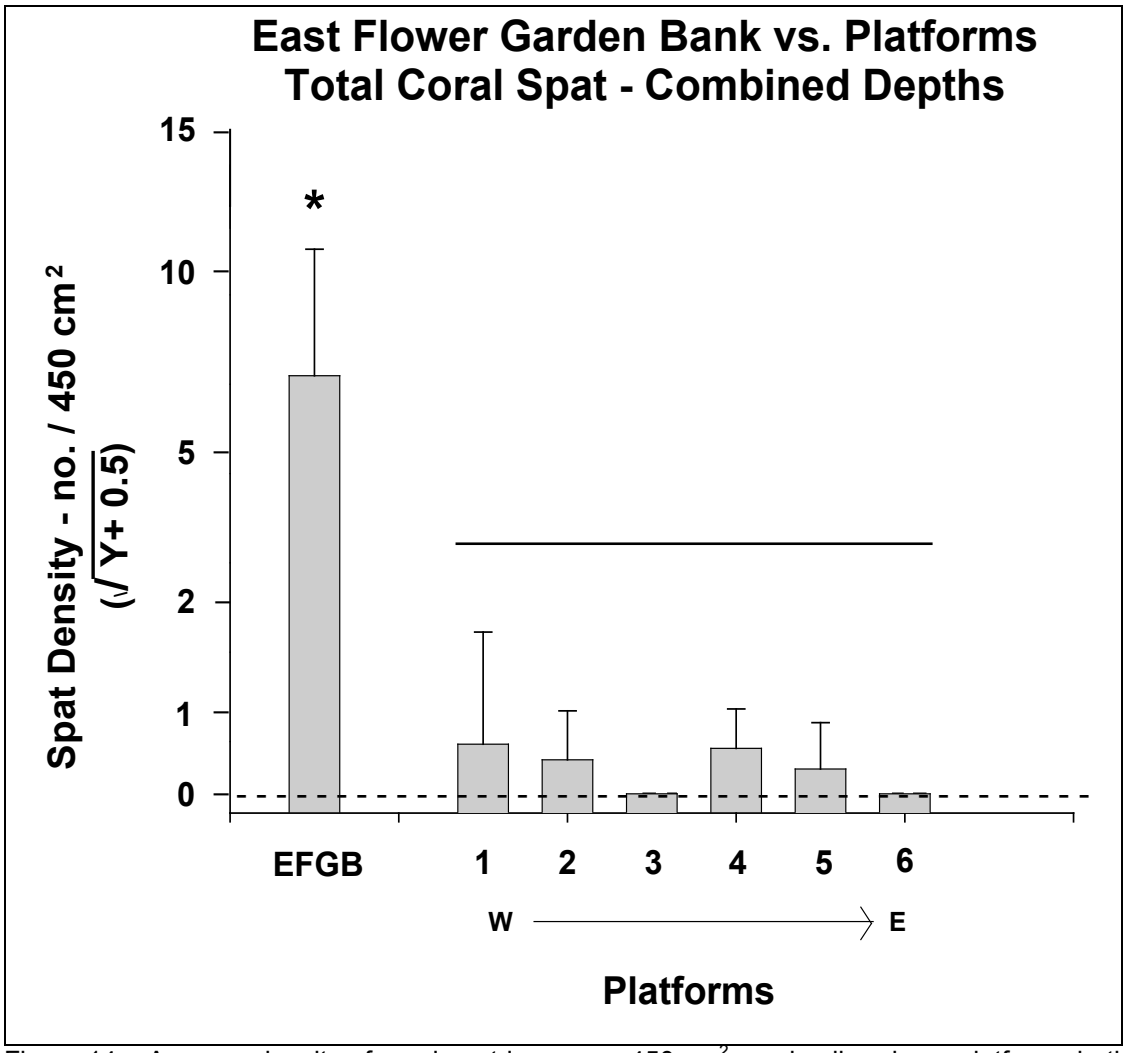

Figure 14. Average density of coral spat in no. per 450 cm^2 on six oil and gas platforms in the northern GOM in the vicinity of the NOAA FGB National Marine Sanctuary, by platform. The platforms, listed east to west, are HI-A-330, HI-A-349B, HI-A-368B, HI-A-376A, HI-A-571A and HI-A-382, and are labeled 1-6, respectively. Data derived from coral settlement on terracotta plates mounted on steel racks and deployed at depths of 15 and 27 m for one year during 2001-2002 or 2002-2003*. Data combined for depths (see text for explanation). Comparative data is also shown from a similar experiment performed on the E-FGB (Sammarco and Brazeau, 2001; Sammarco, 2002, 2003, and 2005; Brazeau et al., 2005, 2008; Brazeau and Sammarco, in prep.). Mean and 95% confidence limits shown. Data transformed by square-root (Y + 0.5) for normalization purposes. No significant difference between coral densities on platforms ($p > 0.05$, one-way nested ANOVA). The * indicates a significant difference between platforms and the E-FGB ($p < 0.05$; for the a posteriori tests GT2, T', and Tukey-Kramer).

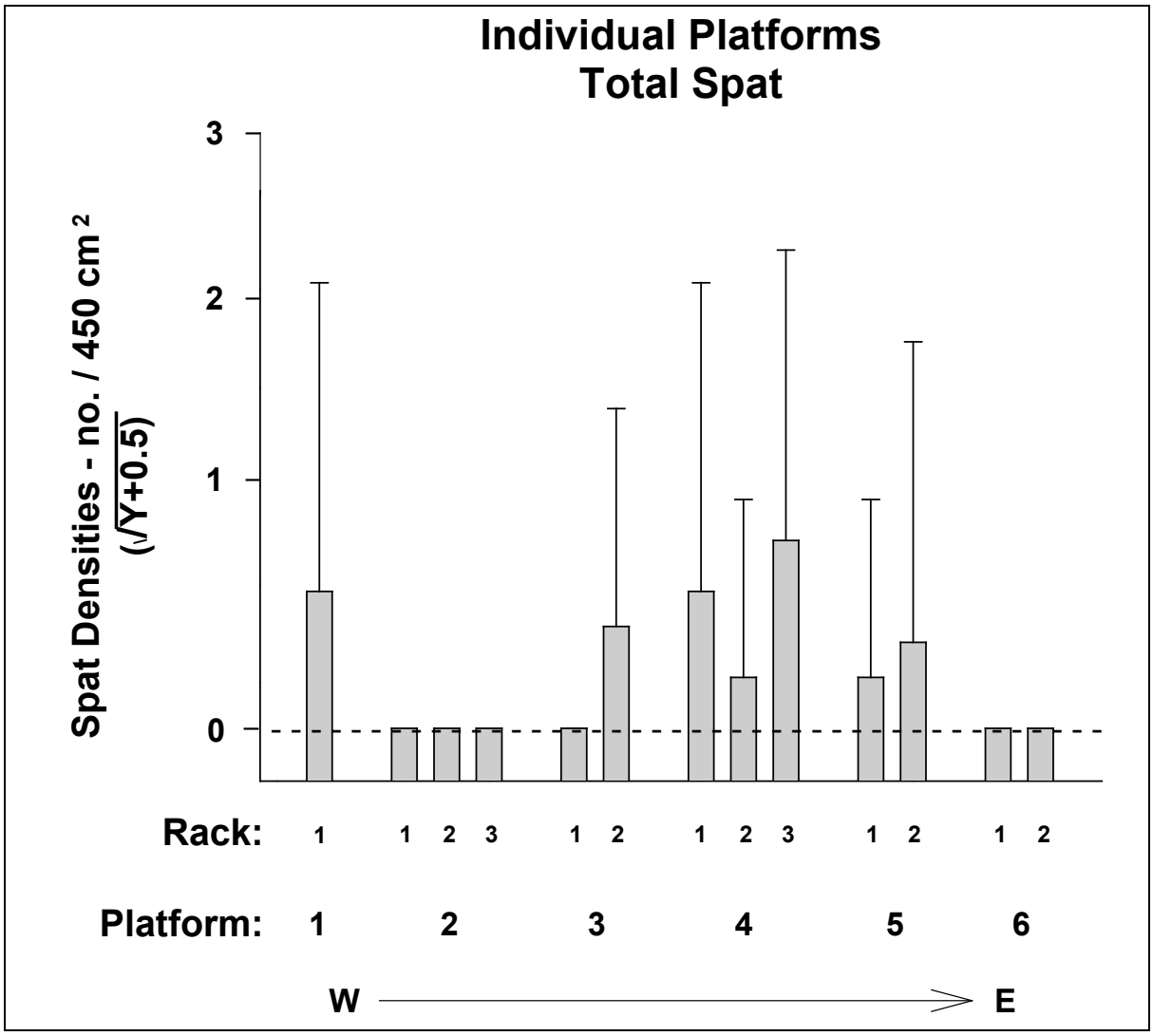

Figure 15. Average density of coral spat in no. per 450 cm^2 on six oil and gas platforms in the northern GOM in the vicinity of the FGB. Platforms presented in longitudinal sequence from west to east as they occur in the GOM: (1) HI-A-330, (2) HI-A-349B, (3) HI-A-368B, (4) HI-A-376A, (5) HI-A-571A, and (6) HI-A-382. Data derived from coral settlement on terracotta plates mounted on steel racks and deployed at depths of 15 and 27 m for one year during 2001-2002 or 2002-2003. Data shown for individual settlement racks within platforms. Data combined for depths (see text for explanation). Mean and 95% confidence limits shown. Raw data transformed by square-root (Y + 0.5) for normalization purposes. Significant difference between coral densities on racks ($p < 0.05$, one-way nested ANOVA).

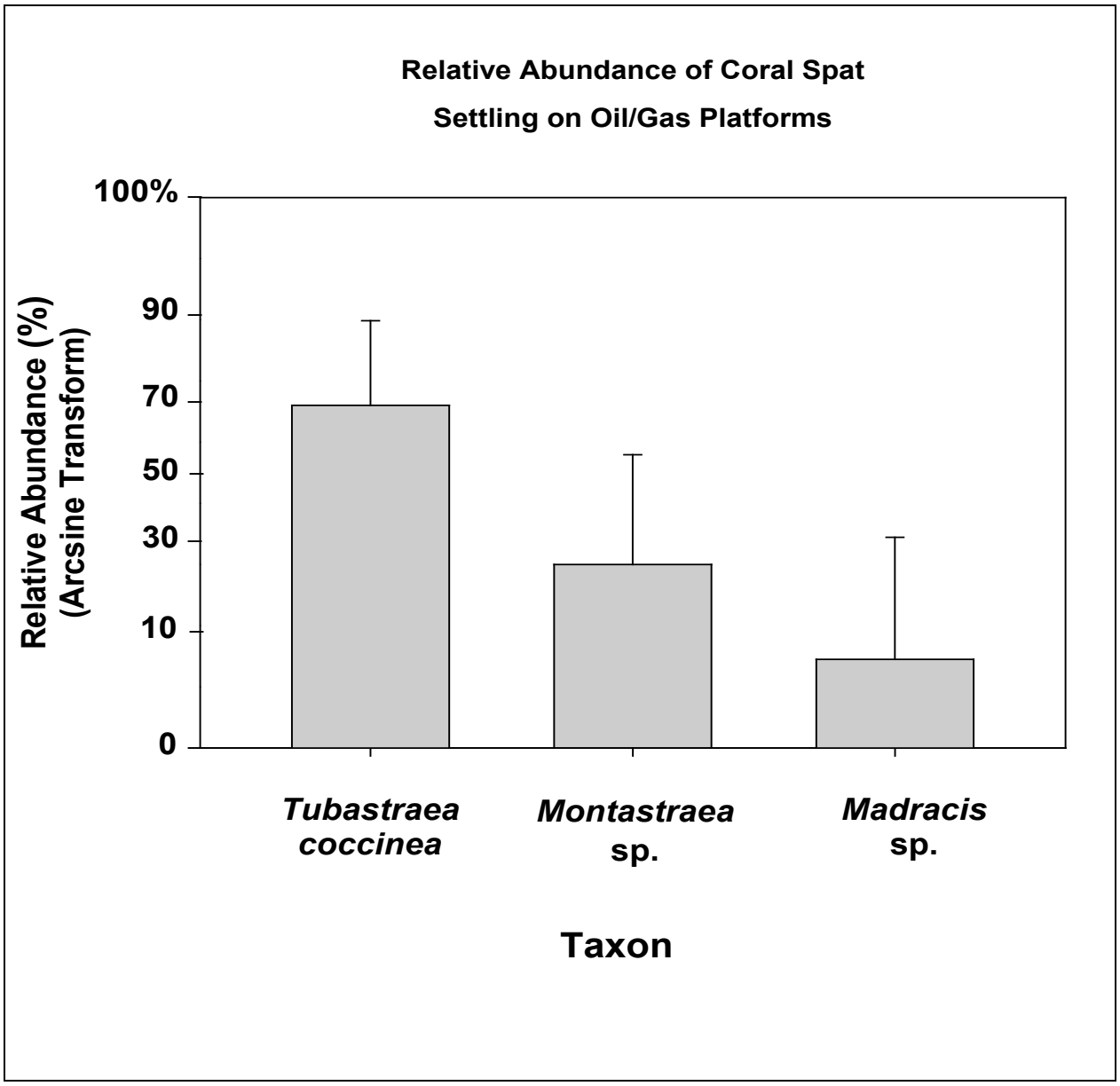

Figure 16. Relative abundances for all spat of different coral genera found on six oil and gas platforms in the northern GOM in the vicinity of the FGB. Data derived from coral settlement on terracotta plates mounted on steel racks and deployed at depths of 15 and 27 m for one year during 2001-2003. Data combined for platforms, racks, depths, and plates. Proportion and 95% confidence limits shown. Data transformed arcsine for normalization purposes.

3.3 GENETIC CONNECTIVITY IN CORALS ON THE FLOWER GARDEN BANKS AND SURROUNDING OIL AND GAS PLATFORMS, GULF OF MEXICO

A total of 291 tissue samples from three scleractinian species was examined. Two AFLP primer sets were used in the analysis. For *M. decactis*, 167 colonies produced 57 polymorphic markers. In *D. strigosa,* 64 colonies produced a total of 31 polymorphic markers and in *M. cavernosa*, tissue from 60 colonies yielded a total of 40 polymorphic markers. In some cases, only a small number of colonies per species was found on individual platforms. We have included all of the populations in the analytical results, however, because low sample sizes on some of the platforms are directly representative of low population sizes at these sites, not decreased sampling effort; we sampled the entire population at the depths concerned. Nonetheless, we have noted instances where small population sizes may constrain interpretation of the results.

3.3.1 *Madracis decactis* (brooder)

M. decactis was found on all seven study platforms plus the E- and W-FGB. Because this species was the most abundant encountered, it provided the most information regarding genetic affinities. Genetic differentiation values (Φ_{ST}) generated by the AMOVA analyses for *M. decactis* revealed that the two FGB populations were homogeneous, yielding the lowest Φ_{ST} values among all populations in this comparison (Table 6a). Several populations on the platforms exhibited consistent significant genetic differentiation, despite the small population sizes involved. These were the western-most Platform #1 and a far eastern platform, Platform #6. In fact, these platforms plus Platform #7, which are the most distant from the FGB, exhibited the highest levels of significance and most consistent genetic differentiation from the other sites. Among the populations with larger sample sizes, the highest Φ_{ST} values were observed between two of the most geographically separated populations – Platform #2 and Platform #7.

In *M. decactis*, Φ_{ST} increased with inter-site distance, being described by a significant 2° polynomial regression (Figure 21). Most populations being considered in a pair-wise manner were significantly different from each other by AMOVA; but it was also clear that all those populations that were not significantly different had Φ_{ST} values of ≤ 0.02 and were clustered at distances of ≤ 55 km from each other (Figure 21; Table 6a).

We also examined genetic differentiation patterns using the FGB as a reference point for *M. decactis*. The Φ_{ST} was significantly positively associated with distance to the W-FGB (Figure 22) and even more clearly with distance from the E-FGB as a reference point, as well as with distance to the nearest FGB perimeter. When comparing not significantly different populations, all populations with homogenous Φ_{ST} values occurred generally at ≤ 30 km from either FGB perimeter, but up to 55 km in the case of the W-FGB (Figure 22).

Using the requirement of a minimum log-1 (10-fold difference) threshold for population allocation, most of the AFLPOP assignments in *M. decactis* were allocated back to their population of origin (self-assignment; Table 6b). Populations from most platforms and the FGBs showed cross-assignments to many other populations, but the proportions of cross-assignments involving platforms were generally two orders of magnitude smaller than the self-assignments. The western-most Platform #1 and one of the eastern-most platforms Platform #6, yielded high

levels of self-assignment (94% and 97%, respectively); population sizes here were small (Table 6b). These results were consistent with the above AMOVA results.

The AFLPOP analytical results supported the concept that the genetic uniqueness of the *M. decactis* populations became increasingly distinct with increased remoteness from the FGBs (Figure 23; Table 6b). These results paralleled those yielded by AMOVA and patterns derived in Φ_{ST}. Levels of self-allocation of colonies at a given site increased significantly with distance from the E-FGB (Figure 23a), and the strength of this relationship was stronger when considering distance to the nearest FGB perimeter (Figure 23b). No relationship emerged between self-allocation of colonies to sites and distance from the W-FGB when used as a reference point.

The lowest percentages of self-allocation (26% and 32%) occurred in the E- and W-FGB *M. decactis* populations (respectively). In the center of the study region, cross-assignments were least common between the FGB and some of those platforms at the furthest sites (Table 6b). Allocation from the E- to the W-FGB was higher than to any platform. In most cases, most colonies from the FGB were identified as "CANM" (Criteria for Allocation Not Met). There was no correlation between platform age and level of self-allocation in *M. decactis* (correlation, $r = -0.654$, $p > 0.05$).

The AFLPOP analyses also yielded information on cross-allocation between *M. decactis* populations at all sites. When all possible pair-wise comparisons were made between sites, including self- and cross-allocations, a clear pattern of high self-allocation emerged but with a very low level of cross-site allocation, particularly on the platforms around the FGB, irrespective of distance from them (Figure 24a; Figure 25). As distance between sites increased, the level of cross-allocation to a site dropped significantly and highly dramatically and this was observed even at distances as low as 1 km. The pattern of this decrease followed a sharp hyperbolic decay curve and was mimicked in the other two species examined (Figures 24 b,c; see below). When the self-allocation data were excluded from the analysis, the degree of cross-allocation between populations decreased significantly in a linear fashion with distance between sites (Figure 25), again indicating an increasing amount of genetic isolation between populations with distance.

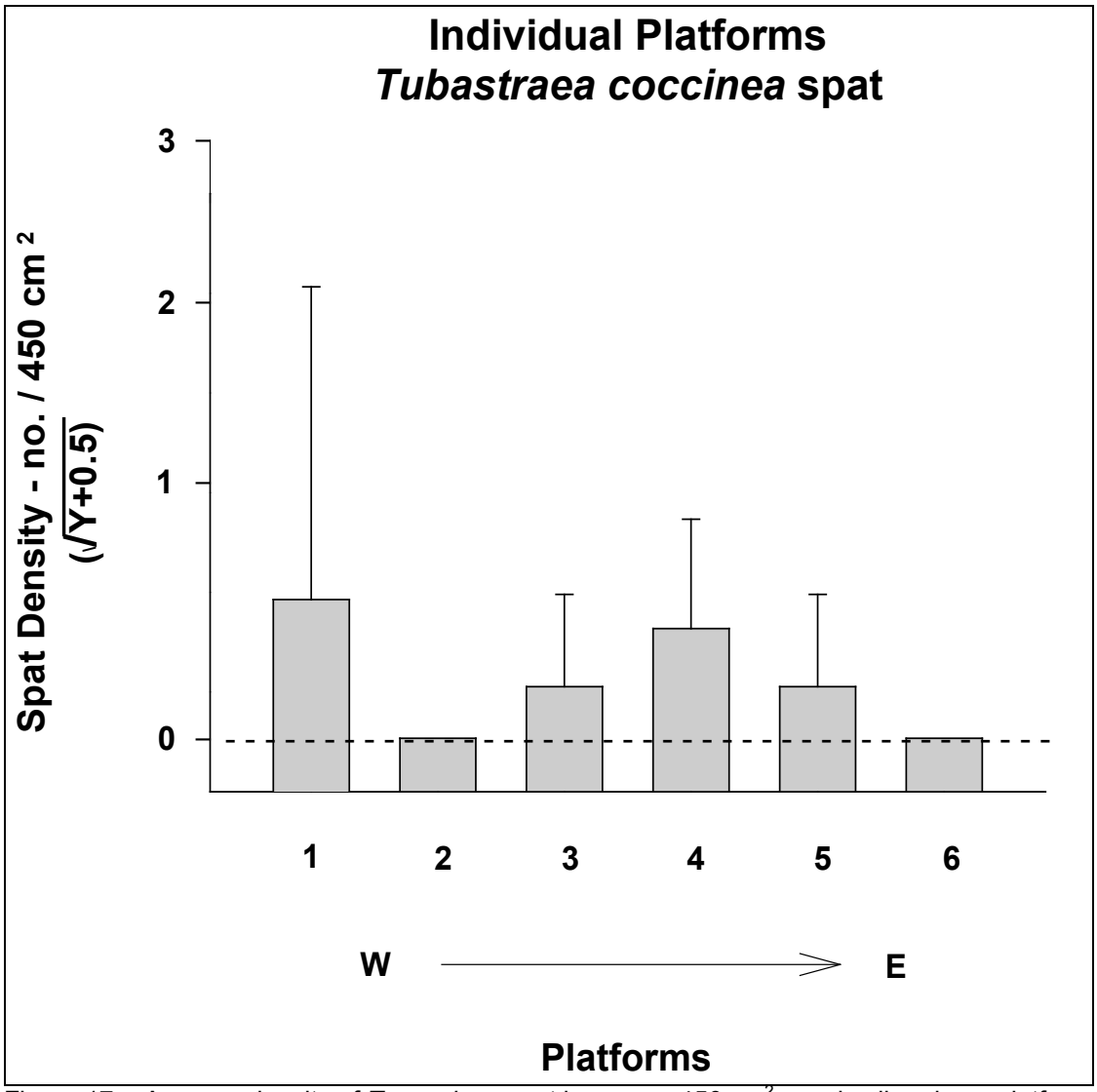

Figure 17. Average density of *T. coccinea* spat in no. per 450 cm^2 on six oil and gas platforms in the northern GOM in the vicinity of the NOAA FGB National Marine Sanctuary, by platform. Platforms presented in longitudinal sequence from west to east as they occur in the GOM: (1) HI-A-330, (2) HI-A-349B, (3) HI-A-368B*, (4) HI-A-376A, (5) HI-A-571A*, and (6) HI-A-382. Data derived from coral settlement on terracotta plates mounted on steel racks and deployed at depths of 15 and 27 m for one year during 2001-2002 or 2002-2003*. Data combined for depths (see text for explanation). Mean and 95% confidence limits shown. Raw data transformed by square-root (Y + 0.5) before calculation of means for normalization purposes. No significant difference in spat densities of *T. coccinea* between platforms ($p > 0.05$, one-way nested ANOVA).

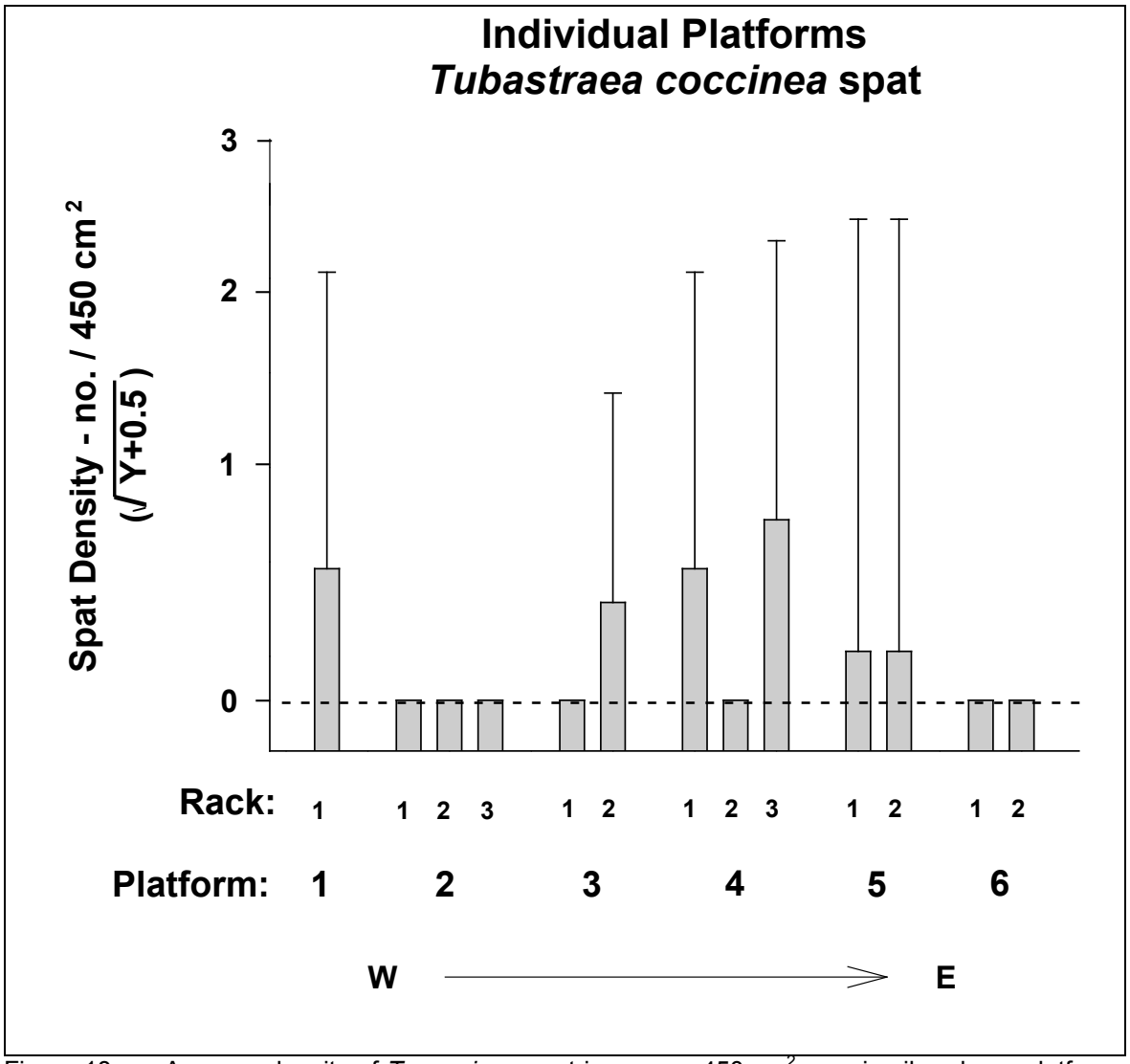

Figure 18. Average density of *T. coccinea* spat in no. per 450 cm^2 on six oil and gas platforms in the northern GOM in the vicinity of the NOAA FGB National Marine Sanctuary. Platforms presented in longitudinal sequence from west to east as they occur in the GOM: 1) HI-A-330, (2) HI-A-349B, (3) HI-A-368B*, (4) HI-A-376A, (5) HI-A-571A*, and (6) HI-A-382. Data shown for individual settlement racks within platforms. Data derived from coral settlement on terracotta plates mounted on steel racks and deployed at depths of 15 and 27 m for one year during 2001-2002 or 2002-2003*. Data combined for depths. Mean and 95% confidence limits shown. Data transformed by square-root (Y + 0.5) for normalization purposes. No significant difference between coral densities on racks ($p > 0.05$, one-way nested ANOVA). See legend of Figure 12 for additional details.

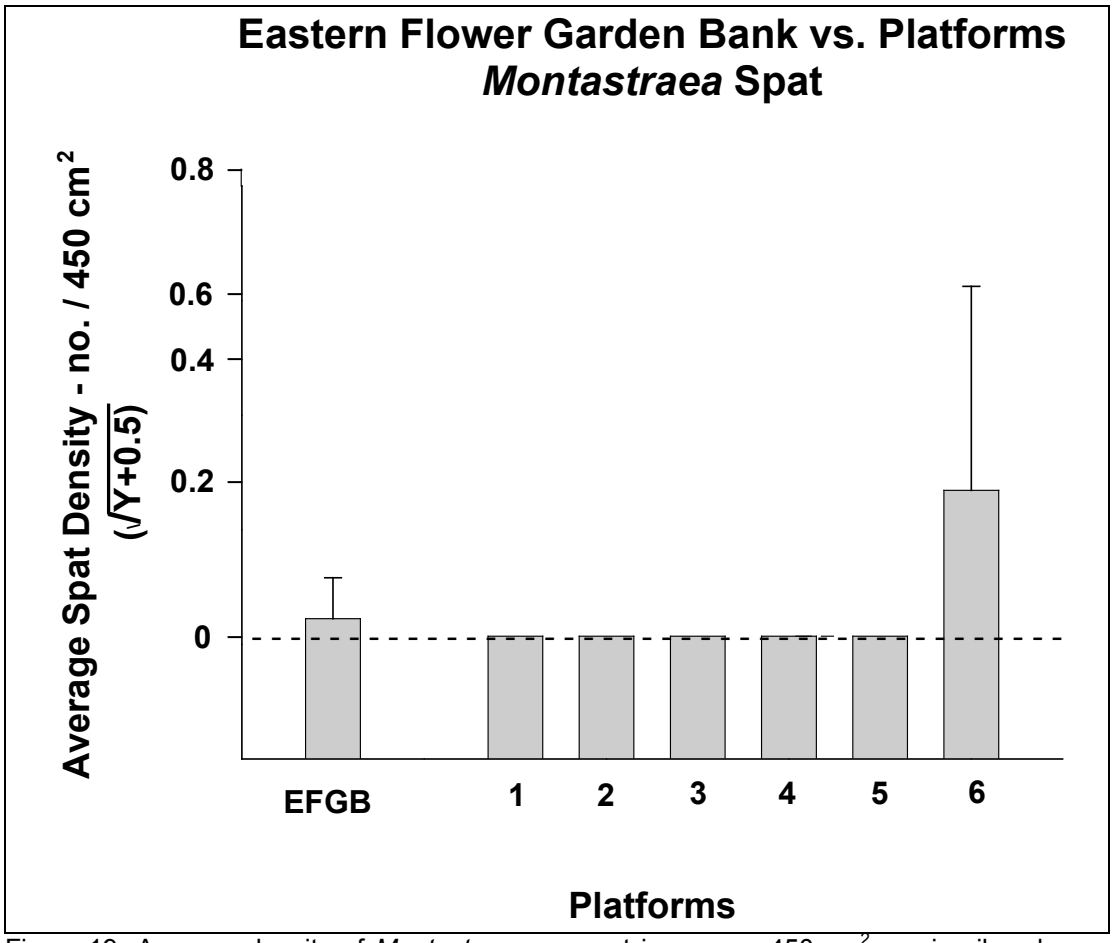

Figure 19. Average density of *Montastraea* sp. spat in no. per 450 cm^2 on six oil and gas platforms in the northern GOM, in the vicinity of the NOAA FGB National Marine Sanctuary. The platforms, listed east to west, are HI-A-330, HI-A-349B, HI-A-368B*, HI-A-376A, HI-A-571A*, and HI-A-382. Data shown for platforms. Data derived from coral settlement on terracotta plates mounted on steel racks and deployed at depths of 15 and 27 m for one year during 2001-2002 or 2002-2003*. Data combined for depths. Mean and 95% confidence limits shown. Data transformed by square-root (Y + 0.5) for normalization purposes. No significant difference between coral densities on racks ($p > 0.05$, one-way nested ANOVA). See legend of Figure 12 for additional details.

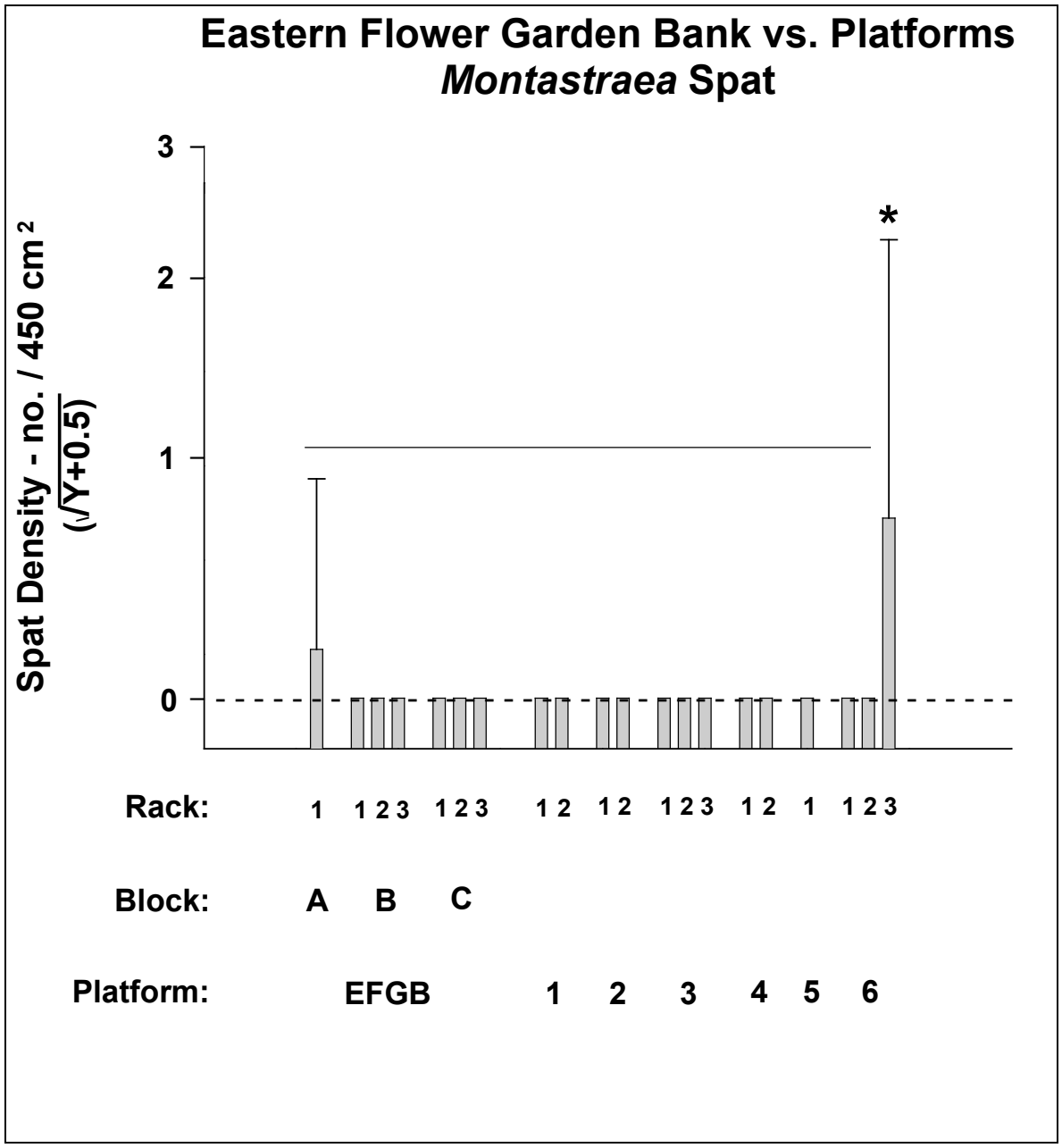

Figure 20. Average density of *Montastraea* sp. spat in no. per 450 cm^2 on six oil and gas platforms in the northern GOM, in the vicinity of the NOAA FGB National Marine Sanctuary. Platforms presented in longitudinal sequence from west to east as they occur in the GOM: (1) HI-A-330, (2) HI-A-349B, (3) HI-A-368B*, (4) HI-A-376A, (5) HI-A-571A*, and (6) HI-A-382. Data is shown for individual settlement racks within platforms. Data derived from coral settlement on terracotta plates mounted on steel racks and deployed at depths of 15 and 27 m for one year during 2001-2002 or 2002-2003*. Data combined for depths. Mean and 95% confidence limits shown. Data transformed by square-root (Y + 0.5) for normalization purposes. The * indicates a significant difference in coral density between Rack #3, Platform #6 and all other racks ($p < 0.05$, one-way nested ANOVA); no significant difference between coral densities on all other racks ($p > 0.05$).)

Table 6

Assessment of Genetic Differentiation among Populations of the Coral *M. decactis* Using Analysis of Molecular Variance (AMOVA); AFLPOP Assignment of Samples to Their Reference Home Population Compared with Other Sites

			Reference Population						
Platform/Site	1	2	W-FGB	3	E-FGB	4	5	6	7
n	8	15	25	20	18	19	28	7	27
(a) AMOVA									
Compared to									
↓									
1		**P < 0.001**	**P < 0.001**	**P < 0.001**	**P < 0.001**	**P < 0.001**	**P < 0.001**	**P < 0.001**	**P < 0.001**
2	0.1285		**P < 0.05**	**P < 0.001**	**P < 0.05**	0.3640	**P < 0.001**	**P < 0.001**	**P < 0.001**
W-FGB	0.0763	0.0421		**P < 0.05**	0.5560	**P < 0.05**	0.1440	**P < 0.05**	**P < 0.05**
3	0.0740	0.0730	0.0129		0.2440	**P < 0.001**	0.1070	**P < 0.001**	**P < 0.05**
E-FGB	0.0828	0.0250	-0.0057	0.0116		0.3030	0.4360	**P < 0.001**	**P < 0.001**
4	0.1133	0.0035	0.0189	0.0348	0.0059		0.1170	**P < 0.001**	**P < 0.001**
5	0.0674	0.0392	0.0176	0.0198	0.0012	0.0178		**P < 0.001**	**P < 0.05**
6	0.0650	0.1140	0.0771	0.0967	0.1060	0.0951	0.1097		**P < 0.001**
7	0.0987	0.1266	0.0476	0.0148	0.0485	0.0858	0.0300	0.1385	
Overall Φ_{ST} =	0.0730								
(b) AFLPOP									
Allocated To									
↓									
1	**94.3%**	0.0%	0.0%	0.2%	0.0%	0.0%	0.0%	0.0%	0.1%
2	0.0%	**62.4%**	0.2%	0.1%	0.2%	1.2%	0.3%	0.0%	0.0%
W-FGB	0.0%	0.3%	**32.2%**	0.3%	0.3%	0.4%	0.6%	0.0%	0.3%
3	0.0%	0.1%	0.4%	**38.5%**	0.3%	0.4%	0.4%	0.0%	0.4%
E-FGB	0.0%	0.2%	0.8%	0.3%	**26.2%**	0.5%	0.5%	0.0%	0.1%
4	0.0%	0.5%	0.6%	0.4%	0.4%	**37.8%**	0.6%	0.0%	0.0%
5	0.0%	0.2%	0.3%	0.2%	0.4%	0.4%	**30.9%**	0.0%	0.2%
6	0.0%	0.0%	0.2%	0.1%	0.2%	0.0%	0.0%	**97.1%**	0.0%
7	0.1%	0.0%	0.3%	1.2%	0.4%	0.2%	1.0%	0.0%	50.4%
CANM	5.6%	36.3%	65.0%	58.7%	71.8%	59.1%	65.7%	2.9%	**48.5%**
Totals	100.0%	100.0%	100.0%	100.0%	100.0%	100.0%	100.0%	100.0%	100.0%

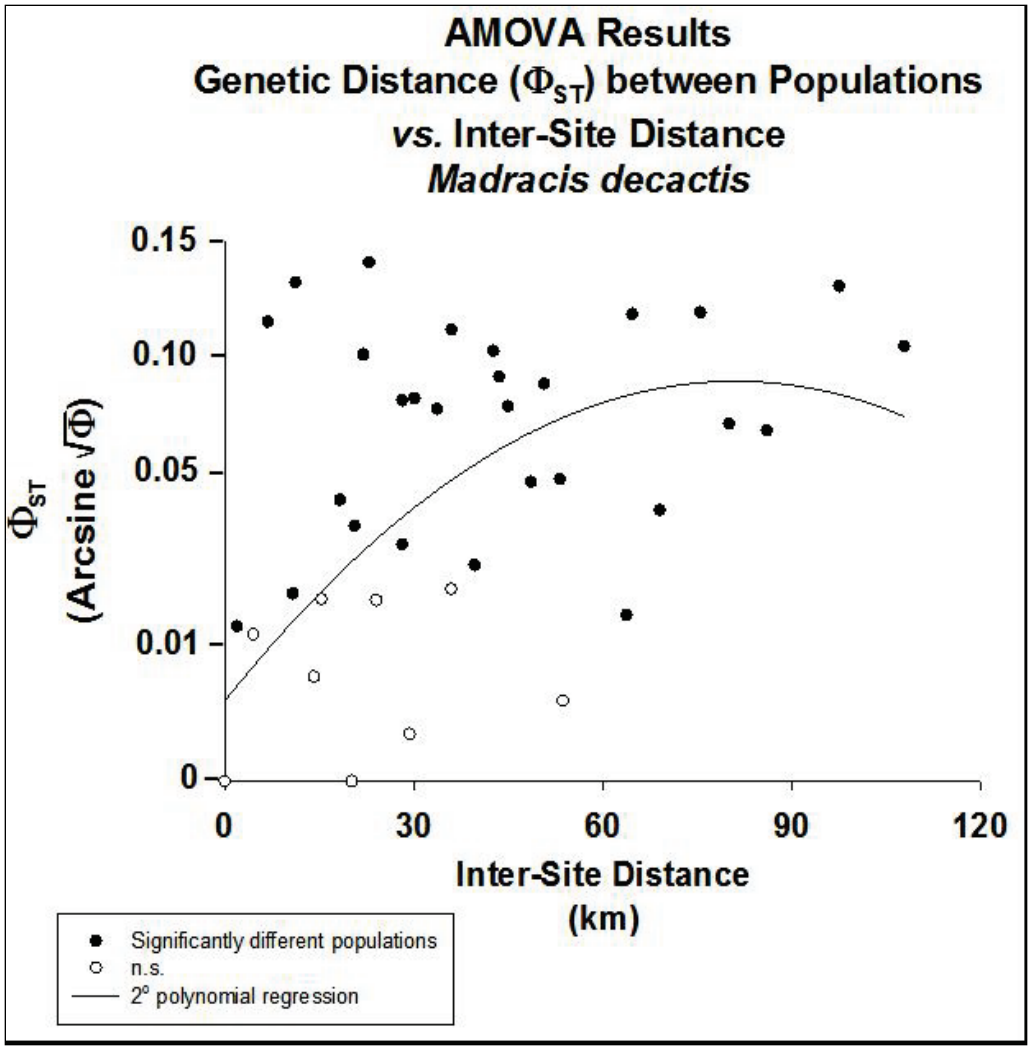

Figure 21. The Φ_{ST} or genetic differentiation between populations of the coral *M. decactis* found on all sites considered here–offshore oil and gas platforms and the E-FGB and W-FGB. Presented as a function of distance between the sites. Data analyzed by AMOVA. • = significantly different populations; ○ = not significantly different. $p < 0.001$, 2^{o} polynomial regression, $Y = 3.409 + 0.332\ X - 0.002\ X2$. Data transformed by arcsine for normalization purposes.

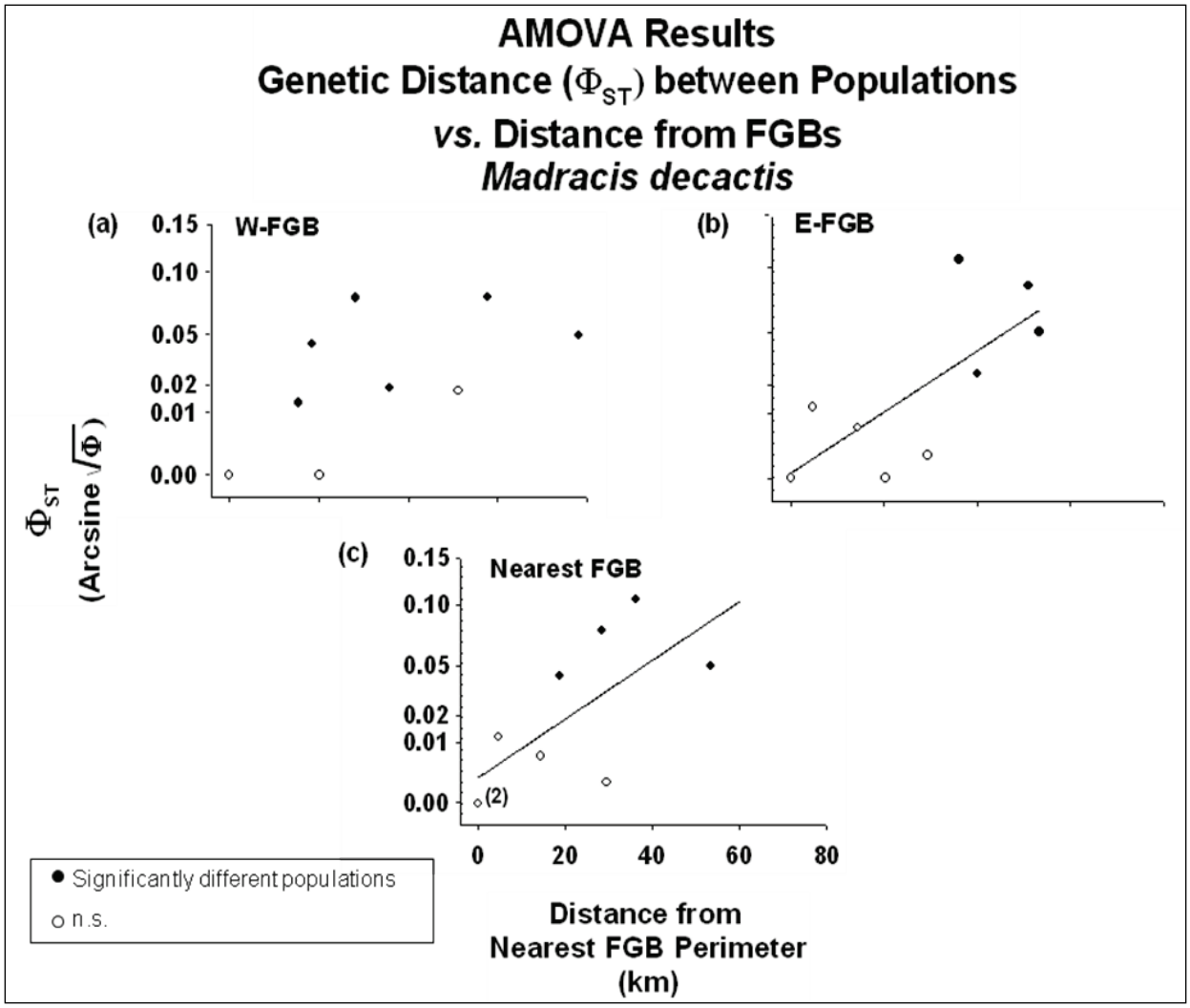

Figure 22. The Φ_{ST} or genetic differentiation between populations of the coral *M. decactis* found on sites considered in this study, using the perimeter of the FGB as a geographic reference point. Presented as a function of distance between the site and the perimeter of (a) E-FGB, (b) W-FGB, and (c) nearest FGB. Data transformed by arcsine for normalization purposes and analyzed by AMOVA. Number of multiple/over-plotted points shown in parentheses. • = significantly different populations; ○ = not significantly different. (a) $p < 0.05$, Kendall's rank correlation analysis, □ = not significantly different. (a) $p < 0.05$, Kendall's rank correlation analysis, on sites considered in this study, using the perimeter of the FGB as a geographic reference point. Presented as a function of distance between the station analysis, $r = 0.692$.

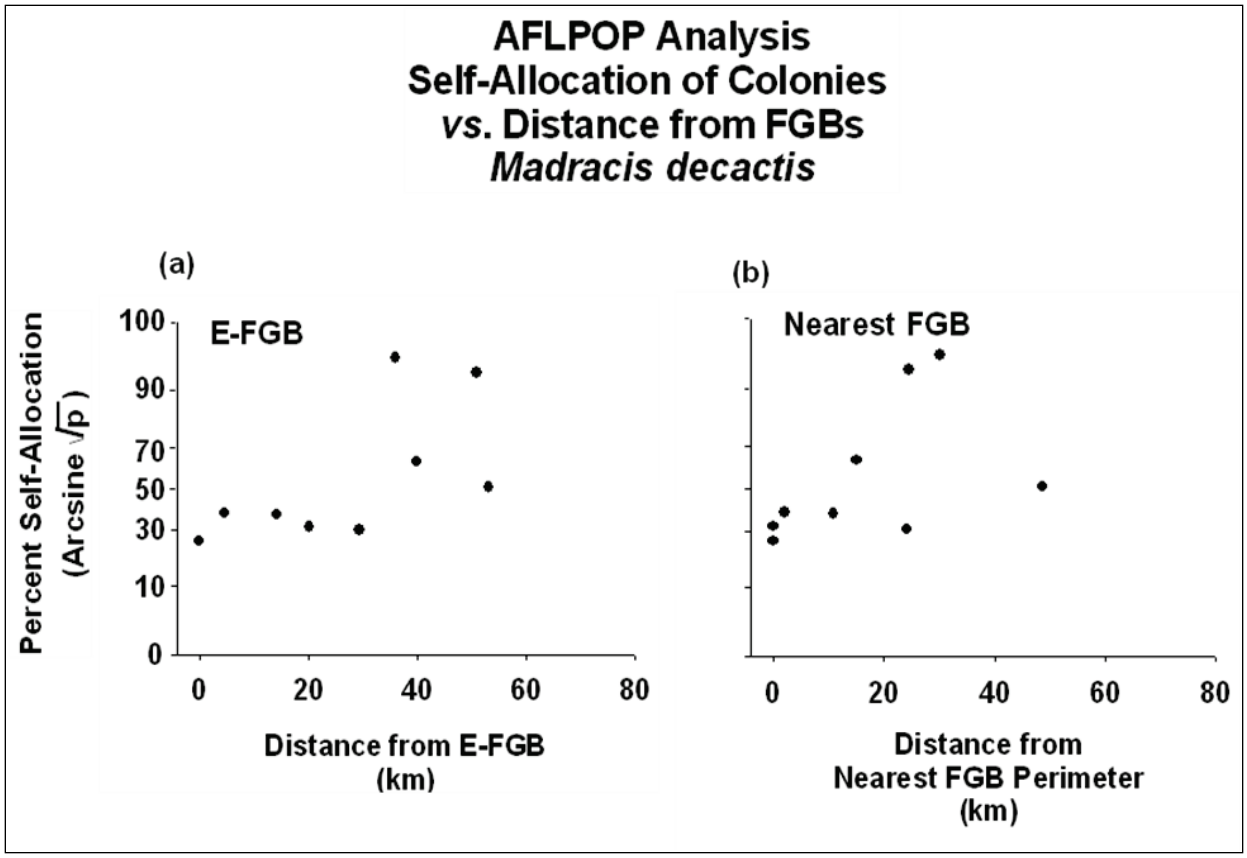

Figure 23. Self-allocation in *M. decactis* colonies; proportion assigned back to their original sites when analyzed by AFLPOP, using an assignment level with a log-likelihood threshold of 1.0. Proportions plotted against distance between the site and perimeter of the (a) E-FGB and (b) nearest FGB. Data transformed by arcsine for normalization purposes. Self-allocation increases significantly with distance from the E-FGB and nearest FGB perimeter. (a) $p < 0.05$, Spearman's rank correlation coefficient, $r = 0.683$; $p < 0.05$, Sum of squared difference in ranks. (b) $p < 0.05$, Kendall's Rank Correlation Analysis, $T = 0.535$; $p < 0.05$, Spearman's Rank Correlation Analysis, $r = 0.686$; $p < 0.05$, Sum of squared difference in ranks.

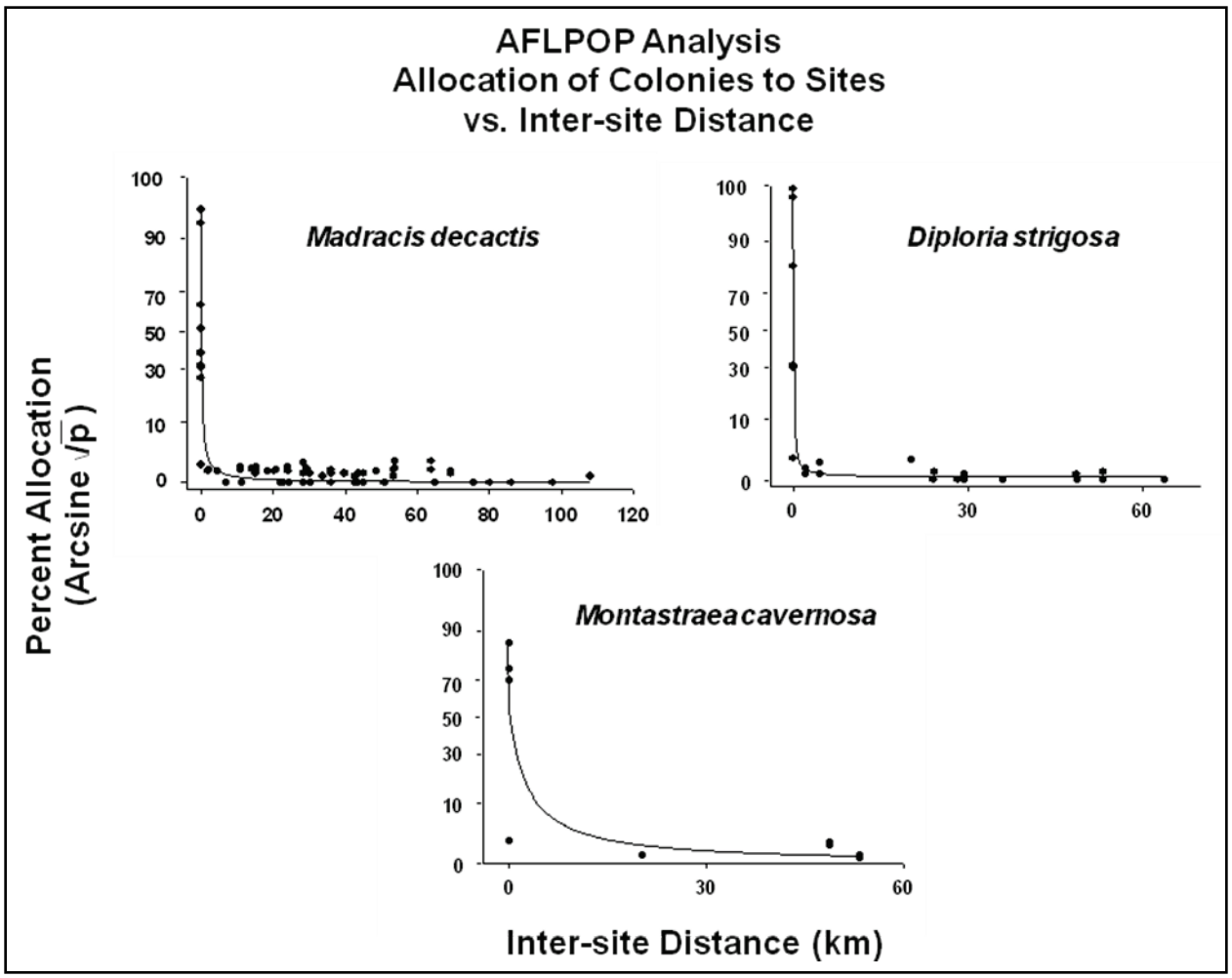

Figure 24. (a) Allocation of *M. decactis* colonies between populations at all study sites, as determined by AFLPOP. A log-linear threshold of 1.0 (highly conservative) used for analysis. Allocation of colonies to populations at other sites versus inter-site distance. All populations are included, included self-assignments to sites of origin. Significant hyperbolic decay; $p < 0.001$, 2-parameter hyperbolic regression analysis, $Y = (43.417 * 0.382) / (0.382 + X)$. (b) Same, but in *D. strigosa*. Significant hyperbolic decay; $p < 0.001$, 3-parameter hyperbolic decay regression analysis, $Y = 0.946 + (52.507 * 0.103)/ (0.103 + X)$. (c) Same, but in *M. cavernosa*. Significant hyperbolic decay; $p < 0.01$, 2-parameter hyperbolic decay regression analysis, $Y = (47.383 * 2.740)/(2.740 + X)$.

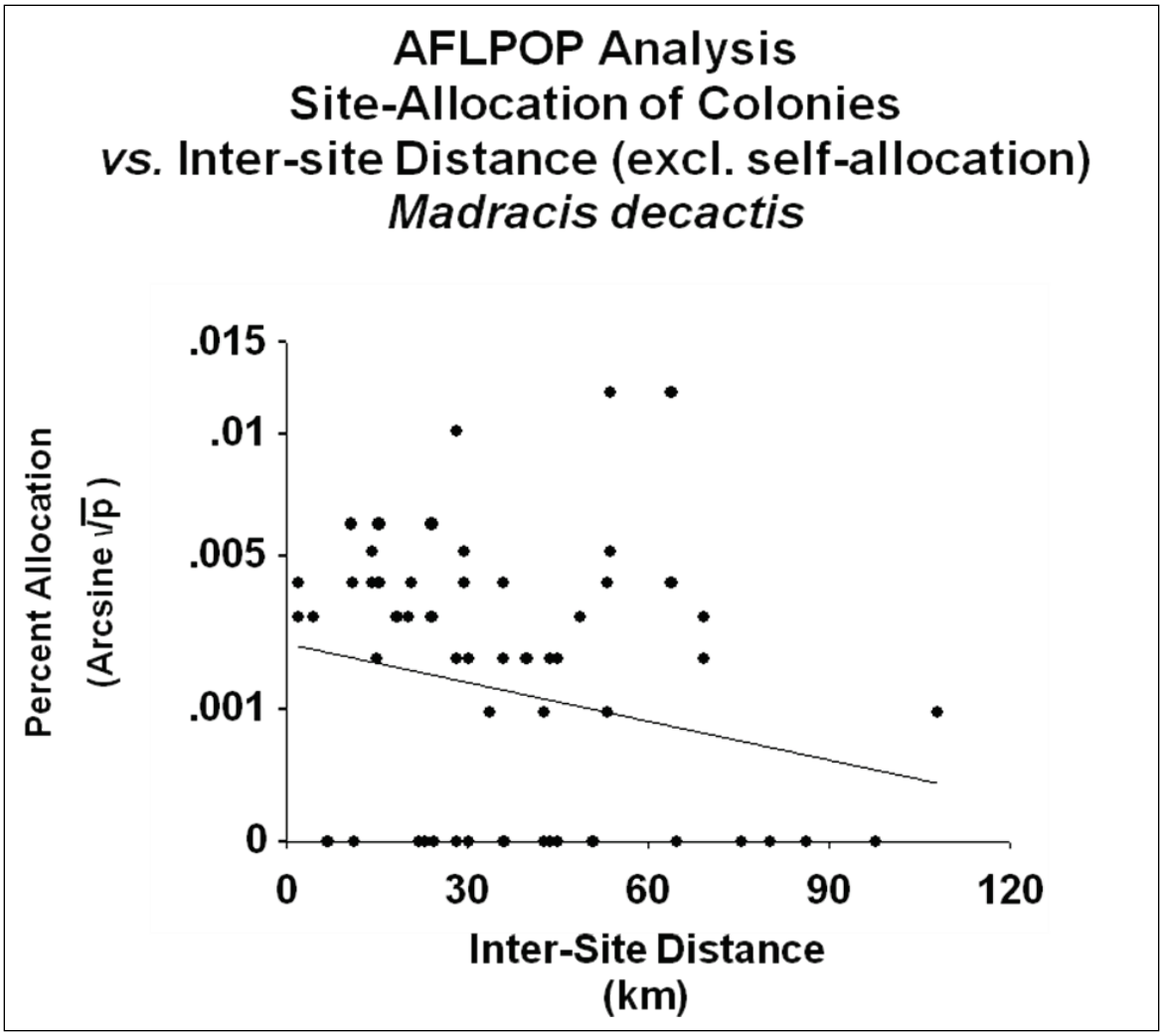

Figure 25. Allocation of *M. decactis* colonies between populations at study sites, as determined by AFLPOP. A log-linear threshold of 1.0 (highly conservative) used for analysis. Allocation of colonies to populations at other sites versus inter-site distance. Self-allocation data have been excluded. Significant negative correlation, $p < 0.05$, correlation analysis, $r = 0.266$; $p < 0.05$, Model-II linear regression analysis, $Y = 2.768 – 0.018\ X$.

3.3.2 *Diploria strigosa* (broadcaster)

D. strigosa, a broadcaster, occurred on both the E- and W-FGB, and Platforms #3, #5, and #7. AMOVA analyses identified variable genetic differentiation among populations, with Φ_{ST} ranging from 0.012 to 0.198. The two FGB populations were not significantly different from each other (Table 7a). The E-FGB population was homogeneous with all other small platform populations. The small population of Platform #3 was significantly different from the W-FGB.

In comparison to *M. decactis, D. strigosa* exhibited quite a different relationship between Φ_{ST} and inter-site distance between platforms. The Φ_{ST} was low at very small inter-site distances (Table 7a). As geographic distance increased, however, Φ_{ST} increased, peaking at an inter-site distance of 25-35 km. Beyond that, it decreased significantly out to a distance of ~65 km in a significant curvilinear manner ($p < 0.01$, 2° polynomial regression, $Y = 3.144 + 0.869\ X - 0.013\ X^2$). The Φ_{ST} in *D. strigosa* exhibited no significant trends when considered with respect to distance from the E-FGB.

For platform populations, AFLPOP analyses assigned $\geq$ 83% of the *D. strigosa* colonies back to their original reference sites, with proportions reaching almost 100% on the two platforms furthest east (Table 7b). The E- and W-FGB had the highest number of colonies not readily assignable to a single site. Similar to *M. decactis*, the central populations (E-FGB, W-FGB, and Platform #3) had the largest number of assignments to neighboring populations. There was also no correlation between platform age and level of self-allocation in *D. strigosa* (Pearson's product-moment correlation analysis, $r = 0.909$, $p > 0.05$).

Using AFLPOP, we made all possible pair-wise comparisons regarding the allocation of *D. strigosa* colonies to sites versus inter-site distance. The resulting pattern was very similar to that derived for *M. decactis* (Figure 24a). That is, populations had highly variable self-allocation levels, but, in all cases, levels of cross-allocation fell off significantly and exponentially, even at distances of one to several kilometers (Figure 24b), suggesting that the populations are highly dissimilar at even short distances. One of the differences between *D. strigosa* and *M. decactis* was that cross-allocation levels at short inter-site distances were higher in *Madracis* than in *Diploria*.

Table 7

Assessment of Genetic Differentiation among Populations of the Coral *D. Strigosa*

Reference Population					
	W-FGB	**Platform 3**	**E-FGB**	**Platform 5**	**Platform 7**
n	29	5	23	4	3
(a)AMOVA					
Compared to ↓					
W-FGB		**P<0.001**	0.1119	0.3407	0.46
Platform 3	0.0629		0.1249	**P<0.001**	0.3926
E-FGB	0.0127	0.0508		0.03846	0.3956
Platform 5	0.0222	0.1657	0.0183		**P<0.001**
Platform 7	0.0686	0.0121	0.038	0.1975	
Overall Φ_{ST} =	0.073				
(b) AFLPOP					
Allocated to ↓					
W-FGB	**34.10%**	0.10%	1.20%	0.00%	0.00%
Platform 3	0.40%	**83.30%**	0.90%	0.00%	0.00%
E-FGB	1.40%	0.10%	**32.70%**	0.00%	0.00%
Platform 5	0.20%	0.00%	0.10%	**100.00%**	0.00%
Platform 7	0.10%	0.00%	0.20%	0.00%	**99.80%**
CANM	63.80%	16.50%	64.90%	0.00%	0.20%
Totals	100.00%	100.00%	100.00%	100.00%	100.00%

3.3.3 *Montastraea cavernosa* (broadcaster)

M. cavernosa was the least abundant coral on the platforms, yielding low sample numbers. *M. cavernosa* occurred only on the E- and W-FGB and Platform #7. Nonetheless, patterns in genetic affinities were still discernible. Unlike the other two species, AMOVA identified the two FGB populations as being significantly different from each other (Table 8a). Like *M. decactis*, however, the small population on Platform #7 was found to be genetically homogeneous with the W-FGB ($\Phi_{ST} = 0.010$), but not with the E-FGB ($\Phi_{ST} = 0.115$).

Although the Φ_{ST} values were generally low in *M. cavernosa*, as inter-site distance increased, there was an increase in genetic differentiation between coral populations (Table 8a; $p < 0.05$, Kendall's rank correlation analysis, $T = 0.674$; $p < 0.05$, Sum of Squared Difference in Ranks). The variance was high, but the increase was nonetheless significant. The pattern is similar to that of *M. decactis*. (The sample sizes encountered here for *M. cavernosa* prohibit meaningful direct comparisons with results derived from *D. strigosa*.) The AFLPOP analyses allocated $\geq$ 68% of the *M. cavernosa* colonies on both FGBs and the sample platform back to their reference populations (Table 8b). Unlike *M. decactis* and *D. strigosa*, however, *M. cavernosa* populations on both banks exhibited high levels of self-allocation. The number of platform populations was not sufficient to test for platform-age effects.

As in *M. decactis* and *D. strigosa*, the *M. cavernosa* populations appear to be highly variable with respect to self-allocation, although it did reach high levels in some cases (Table 8b). Cross-allocations decrease rapidly, becoming significantly different, however, as distances between populations increase (Figure 24c; $p < 0.01$, 2-parameter hyperbolic decay regression analysis, $Y = (47.383 * 2.740)/(2.740 + X)$. The exponential decay is less dramatic than in the other two species, but this is most likely an artifact of sample size.

Table 8.

Assessment of Genetic Differentiation among Populations of the Coral *Montastraea cavernosa*

Reference Population			
	W-FGB	**E-FGB**	**Platform 7**
N_i	27	25	8
	(a)AMOVA		
Compared to ↓			
W-FGB		**P<0.001**	0.995
E-FGB	0.0881		**P<0.001**
Platform 7	0.0101	0.1154	
Overall Φ_{ST} =	0.08		
	(b) AFLPOP		
Allocated to ↓			
W-FGB	**68.20%**	0.20%	0.90%
E-FGB	1.50%	**85.20%**	0.20%
Platform 7	1.20%	0.10%	**74.20%**
CANM	29.10%	14.50%	24.70%
Totals	100.00%	100.00%	100.00%

4.0 DISCUSSION

4.1 ADULT CORAL COMMUNITIES ON PLATFORMS SURROUNDING THE FLOWER GARDEN BANKS

Nine of the 11 species found on the platforms surrounding the FGB are commonly found on reefs of the Caribbean, GOM, and Florida Keys (Wells, 1973, Humann and DeLoach, 2002; Table 4). Most occur on the FGB (Gittings, 1992; Bright et al., 1991). Two are normally found in the early stages of succession on Caribbean reefs-represented as recruits (Sammarco, 1980, 1982): *Millepora alcicornis* and *Porites astreoides.* They are also characteristic of disturbed communities (Edmunds, 1999; Lirman and Fong, 1996 Aronson and Precht, 2001). *P. astreoides* was, however, rare on the study platforms. Adults of *Agaricia* spp., a common pioneer species (characteristic of early successional stages; McNaughton and Wolf, 1979; Miller and Ricklefs, 1999; Smith and Smith, 1999) were completely absent, as were their recruits, which is highly unusual (Sammarco, 1987). The low abundances of these pioneer species indicated that the adult coral community observed on the platforms exhibits a stronger affinity to later, more mature stages of succession, not that of a young or disturbed habitat (McNaughton and Wolf 1979; Miller and Ricklefs, 1999).

The lack of *Porites* and *Agaricia* could be caused by several factors, such as 1) successional events associated with this unique platform environment (e.g., availability of hard substratum without sedimentation stress; 2) a higher probability of success in corals characteristic of later successional stages when involved in competition for space against associated epibiota on the platforms (Sammarco, 1980 1982; Coll et al., 1988; Alino et al., 1992) ; and/or 3) a lack of abundant larval recruitment of early successional species because of their being primarily brooders confounded by distance from the nearest source of such larvae, which is the FGB (Sammarco and Andrews, 1988, 1989; Harrison and Wallace, 1990; Sammarco, 1991, 1994). The answer is not yet known. Data from related experiments regarding coral recruitment and genetic affinities between the platforms, the FGB, and the wider GOM and western Atlantic region have indicated that these regions are genetically distinct (Sammarco and Brazeau, 2001; Atchison, 2003; Brazeau et al., in press). Additional data are currently being processed and will be presented elsewhere (Sammarco et al., work in progress). Preliminary data suggest that the FGB themselves experience abundant coral recruitment, most likely from self-seeding.

Tubastraea coccinea was present in abundance, as has been observed in earlier studies (e.g., Castello et al., 2001). This species was introduced from the Pacific into the Caribbean in 1943 and spread throughout the Caribbean in the 1950s (Cairns, 2000; Fenner 2001), and was reported to be present in high numbers in the GOM in the 1990s (Fenner, 2001). Because of this, and its high capacity to colonize natural and artificial substrata, its presence on the platforms was not surprising. It was previously reported to be absent on the FGB (Bright et al., 1984) but has recently been sighted there in very low abundance (NOAA, 2008; E. Hickerson, pers. comm.). Although the presence of the platforms may have facilitated the spread of this invasive species, it is unlikely that the platforms are solely responsible for the spread or that the absence of platforms would have prevented such because of the species' innate high capacity for effective dispersal. Note its spread, as stated above, throughout the Caribbean. Because *Tubastraea* is not present in any substantial numbers on the FGB, it is most likely colonizing the northern GOM

from elsewhere. *Acropora palmata* was also recently observed to colonize both the E-FGB and W-FGB (Precht and Aronson, 2006; Hickerson, pers. comm.), and its presence there is believed to be part of a natural range extension.

Of the 11 corals found, five were spawners and four were brooders (see Table 4). Mode of reproduction is not known for one (*Phyllangia americana*); *M. alcicornis* is a colonial hydroid species rather than a true scleractinian coral and is presumed to release medusae, like its congenerics (Soong and Cho, 1998). The most abundant coral, *Madracis decactis*, is a brooder. The second most abundant, *Diploria strigosa*, is a broadcaster. The *Montastraea* species complex, mass spawners and abundant on the FGB, were absent from the platforms. The platforms were not dominated by either brooders or broadcast spawners. There was also no relationship between coral abundance and distance from the FGB, a key potential source of larvae. From the data generated here, there does not appear to be any advantage for a species to use one mode of reproduction or the other to colonize platforms. Both brooders and spawners are dispersed equally well in this region of the GOM.

Initially, it was surprising to find no significant relationship between coral abundance and distance from the FGB. One would expect that there would be, because the FGB are the only two well-developed reefs in the northern GOM, a point-source distance effect might be evident, and platforms more remote from the FGB would possess more limited coral populations. We were not able to confirm this, however; the variance in coral abundance was high, and no trends were present in the data for distance from the FGB.

There are four possible explanations for this lack of a significant relationship between coral abundance and distance from the FGB. 1) Our sample size at this point in the study (13 platforms) may not be sufficient to demonstrate a significant effect. Increasing the number of platforms sampled may raise the "power of the test" (Sokal and Rohlf, 1981), allowing detection of such. This would include not only sampling more platforms within the current study area, but also expanding the study area by $\geq$ 3 times the radius ($\geq$ 150-200 km) of the current one. 2) The distances from the FGB may be sufficiently far away to allow coral larvae being released from there to be evenly diffused and mixed, so that recruitment on the platforms is relatively even between them. Preliminary data derived from the coral settlement portion of this study (to be presented elsewhere) will examine this hypothesis in greater detail (Sammarco et al., work in progress). 3) The FGB may not be the point source of larvae for these platforms. For example, Stetson Bank possesses a coral community less developed than the FGB and is only 60 km away. In addition, scleractinian corals (e.g., *Montastraea cavernosa)* occur on numerous mesophotic (low light) banks throughout the northern GOM (Schmahl, 2003). Larvae derived from this and other banks could be confounding any distance effect examined here. Data currently being processed regarding the genetic affinity between coral populations of *M. decactis, D. strigosa,* and *M. cavernosa* on the platforms *versus* those on the FGB (Atchison, 2005; Atchison et al., 2008; Sammarco et al., 2012) should help shed light on this question. 4) Platform age is significantly confounding any distance effect which may be present (discussed below) within the distance range examined here. Nonetheless, data collected thus far indicate that distance from the FGB is not associated with adult coral community structure on oil and gas platforms–at least at the spatial scale considered here-within a radius of $\leq$50 km.

Expanding surveys to a radius of ≥ 200-300 km may reveal a distance effect, based on probable larval survival time and diffusion effects (Bassim and Sammarco, 2003). Such a survey would also help to identify the geographic limits of coral settlement and survival, as potentially influenced by temperature, salinity, turbidity, oxygen, etc.. It is possible that coral populations on sister submerged banks could influence populations on the platforms, but populations on the FGB are so abundant that that effect would likely be swamped by the latter.

The fact that many coral community variables were positively associated with platform age indicates that, as the platform grows older, so does development and complexity of the coral community; coral abundance and species diversity are increasing through natural successional processes. Colony size, as indicated by *M. decactis*, was also, on the average, larger on platforms ≥ 14 years in age (Table 5). The fact that coral species diversity also increased with platform age supported the concept that community development was increasing with time, as supported by both the univariate and multivariate/pattern-seeking analyses. This is important, because platforms are removed from service shortly after all production within a lease block has ceased. These data indicate that environmental value of the platforms in service will increase with time. This "age-value" relationship may have implications for decision-making regarding decommissioning of the platforms.

The positive association between platform-age and coral community development appears to be linear in nature. A close examination of the data indicates that there is little development, however, visible to the naked eye, during the first 12-15 years of the platform's life. This was also confirmed by the pattern-seeking analysis. After this time, community development is steady. There are three possible reasons why this may be occurring. First, *M. decactis*, a dominant coral on the platforms, and some other late successional species may not be adapted to compete well with early successional species of the associated epibiota (e.g., certain sponges, bryozoans, hydrozoans, tunicates, and algae) but may be better adapted to compete with later successional species. That is, they may reach the platform in a continuous flow over the first 15 years or so, but those spat that settle on the platforms do not necessarily survive under early successional conditions. This would be a post-settlement control. Second, the early successional species of epibiota may simply provide the wrong cues for larval settlement, and the planulae respond to them with a negative preference for settlement, which would be a pre-settlement control. Third, it may be possible that the larvae for these species simply did not encounter the platforms until a later age in the life of the platform. I believe that this is unlikely, however, because so many species exhibit the same distributional pattern. This may also have been influenced by the level of resolution of surveys for adult populations of corals on the platforms, i.e., corals ≤ 1 cm were generally not detected and counted by divers. The coral settlement part of the study did, however, take into account coral spat > 500 μm in diameter.

It is also possible that physical characteristics of the platforms may have affected coral recruitment during the first 12-15 years after deployment. Anti-corrosion paints are sometimes used on the platforms, along with large sacrificial zinc anodes, and induced cathodic currents on some of the newer platforms. High densities of *T. coccinea*, however, were observed directly on the anodes. When production wells are being drilled or producing, the upper levels of the platforms (≤ 6 m) may have been exposed to drilling muds and cuttings.

The fact that *D. strigosa* abundance showed no relationship with platform age indicated that it survives equally well as a pioneer or a late successional species. Abundance of *T. coccinea* in shallow water significantly decreased with age. This implies that, of all of the corals observed in this study, *T. coccinea* resembles a pioneer species more than any other species. It is possible that, in the long term, its dominance in the community might decrease. Abundance of *M. decactis* did not show any relationship to platform age in shallow water, but, on the other hand, was clearly positively associated with platform age at deeper depths and in both sets of depths combined. It is possible that *D. strigosa*, *T. coccinea,* and *M. decactis* are capable of colonizing a platform, particularly in shallow-water, at any platform age and easily outcompeting the associated sessile epibiota for space. Further, coral diversity clearly increased with age, and this is known to occur in many communities, particularly during the early and intermediate stages of succession (Odum, 1969; Mellinger and McNaughton, 1975), including coral reefs (Yu and Zou, 1996; Miller and Barimo, 1999).

There was clearly differential settlement and/or survival of corals with respect to depth, as is known to occur in the Indo-Pacific (Sammarco, 1994). Depth distributions observed here were significantly different from uniform; different species exhibited depth-specific patterns of settlement and/or survival between 0 and 33 m. This type of study design is particularly good for distinguishing depth effects because it allows vertical transects across the depth gradient over a uniform substrate. In normal studies of coral depth-distribution, transects must be performed over wide areas of reef with varying bottom types in order to cover the entire depth range of a gently sloping forereef. Here, rather than the substrate having an average slope of 1:10, it has a slope that is almost vertical (e.g., 1:0.1). Thus, the depth distributions become readily discernible through vertical surveys. Platforms also have additional hard substratum created by diagonal and horizontal support structures. The depths of these structures are fairly consistent among platforms at ~11-14 m, 26-27 m, and below. Rezak et al., (1985) reported broad biotic zonation with depth on the FGB. Here, we have demonstrated species-specificity in coral depth-distribution on the platforms at a higher degree of resolution. Any bias in the depth-distribution data associated with these structures was eliminated by standardizing coral abundance by area.

When platforms become part of the Rigs-to-Reefs Program, they are sometimes cut at a depth of $\geq$ 26 m to leave sufficient depth for navigation by larger vessels. The top portion may be deposited on the bottom or removed and brought to shore. Another option is to cut the structure below the mudline and topple it in place, leaving at least 26 m clearance to the surface. Because *M. decactis* had a relatively larger proportion of its colonies occurring below 27 m depth, it is well adapted for deeper reefs and would probably be retained in the case of a cut platform. *D. strigosa*, another common Caribbean coral, had the highest proportion of its populations at ~10 m and no colonies occurring below 27 m. Thus, most if not all colonies of *D. strigosa* would be lost in a Rigs-to-Reefs placement. *T. coccinea*, with its near-normal depth distribution, exhibited its mode at ~16.5 m, differing from the other two species. It had significantly higher representation in waters < 27 m depth, indicating that abundance of this species would be reduced with Rigs-to-Reefs placements, particularly in the short-term. Deeper surveys are required to determine the maximum depth of these corals and the character of their deeper distributions.

The general homogeneity of *M. decactis* colony size on older platforms reinforces the finding that the population may reach a mature stage of development after ~15 yrs. Nonetheless, the sample sizes were probably too small to confirm this. Once again, a wider geographic survey may make it possible to detect relationships that may exist between colony size and platform age or distance from the FGB.

It would appear that those oil and gas platforms in the GOM that possess coral populations clearly have positive environmental value. The fact that platforms occurring in offshore environments capable of supporting coral growth are supporting coral populations where there were none before the mid-twentieth century implies that they may play some role in the broader ecology of coral community dynamics within the GOM region as a whole.

4.2 CORAL RECRUITMENT ON NORTHERN GULF OF MEXICO OIL AND GAS PLATFORMS

The low density of coral settlement observed on these study platforms compared to the E-FGB and elsewhere in the Caribbean is unusual (Bak and Engel, 1979; Sammarco, 1980, 1982, 1985, 1987, 1994, 2002, 2003, 2005; Rylaarsdam, 1983; van Moorsel, 1983; Rogers et al., 1984; Johnson, 1992; Edmunds, 2000; Miller et al., 2000; Sammarco and Brazeau, 2001; Brazeau et al., 2005, 2008; Vermeij and Sandin, 2008; Brazeau and Sammarco, in prep.; but see Quinn and Kojis, 2005). This rarity in settlement indicates that the platforms are unique and fragile artificial reef environments in the GOM. Spat density data were standardized to no./450 cm^2 ; thus, comparative amounts of total surface area available for settlement was most likely not important. What may have affected settlement, however, is the fact that these structures are not solid obstructions to far-field flow. They are reticulated, allowing flow-through of water. Eddies formed by such currents would be at the micro-scale, rather than the meso-scale, known to retain larvae (Hamner and Hauri, 1981; Hamner and Wolanski, 1988; Sammarco and Andrews, 1988, 1989; Wolanski and Hamner, 1988; Andrews et al., 1989; Wolanski et al., 1989; Black et al., 1990; Black and Moran, 1991; Black et al., 1991; Andrews and Gay, 1994; Sammarco, 1994). The probability of encounter with the substrate due to the absence of meso-scale eddies capable of retaining larvae near these structures was probably reduced.

The homogeneity of settlement density between platforms indicates that, in general, settlement was equitable over the period of the study. This was evident in the overall settlement data and in *T. coccinea*. It also suggests that the distance between the source of larvae, most likely the FGB, and the points of settlement–the platforms-was sufficiently large to permit substantial diffusion of larvae (Okubo, 1980, 1994; Okubo and Levin, 1989). The few significant differences observed between racks was most likely due to minor, small-scale patchiness in settlement (see Lewis, 1996; Dunstan and Johnson, 1998; Adjeroud et al., 2007).

The species composition of coral spat settling on the platforms surrounding the FGB was unusual. It was inconsistent with the settlement pattern observed on the FGB (Sammarco and Brazeau, 2001; Sammarco, 2002, 2003, 2005; Brazeau et al., 2005, 2008; Brazeau and Sammarco, in prep.). On the platforms, *T. coccinea* and *Montastraea* sp. dominated the spat community, which was different from general recruitment patterns observed on many Caribbean reefs, including the FGB where *Porites* and *Agaricia* dominate the spat community (Bak and Engel, 1979; Sammarco, 1980, 1982, 1985, 1987, 1994; Rylaarsdam, 1983; van Moorsel, 1983;

Rogers et al., 1984; Johnson, 1992; Edmunds, 2000; Miller et al., 2000; Quinn and Kojis, 2005; Vermeij and Sandin, 2008). These latter two genera are considered to be pioneer species, settling in high numbers compared to other scleractinian corals (Sammarco, 1980, 1982, 1985, 1987).

Another peculiar aspect of the results is that the species of the primary recruits matched the dominant species in the adult coral community. In general, the community composition of juveniles on natural coral reefs does not resemble that of the adults (Sammarco, 1980, 1982). *Agaricia* and *Porites* spp. are often the dominant recruits in natural, mature, later sere reef communities. These genera are generally not the dominant adults in the same community as measured by percent-cover or number of colonies. In addition, the species composition of coral spat settling on the platforms considered here did not resemble that of spat settling on the E-FGB– as documented either in the sister study on the E-FGB or that of Baggett and Bright (1985). These latter investigators also reported an absence of coral recruitment on the oil producing platform in close proximity to the E-FGB–HI-A-389-located only 2.1 km from the E-FGB. This platform is well outside of a 600 m radius from the reef, a distance demonstrated to be potentially the highest area of coral settlement on a reef. This 600 m distance is based on far-field current velocity and direction, and bathymetric contours being conducive to forming meso-scale eddies that will retain coral larvae (Sammarco, 1988, 1989).

The two most abundant species of coral spat that recruited to the platforms were the ahermatypic coral *T. coccinea,* a brooder, and the hermatypic *Montastraea* sp*.,* a broadcaster. The hermatypic coral *M.* sp. is a brooder. *Madracis* and *Montastraea* are dominant as adults on the FGB (Monaco et al., 2008; Precht et al., 2008), while *T. coccinea*, an invasive species from the Indo-Pacific, is rare as an adult on the FGB (Fenner and Banks, 2004; NOAA National Marine Sanctuaries, 2008; Sammarco et al., work in progress) but common on platforms in this region. These unusual recruitment patterns underscore the unique aspects of the platform environment as an artificial reef. The reason that *Montastraea* sp. was significantly higher on two platforms and on the E-FGB than on the other platforms was most likely an artifact of differential sample sizes and variances between samples.

The question arises as to why coral settlement was so low and relatively homogeneous on the platforms when compared to the results of other settlement studies in the Caribbean (Bak and Engel, 1979; Sammarco, 1980, 1982, 1985, 1987, 1994, 2002, 2003, 2005; Rylaarsdam, 1983; van Moorsel, 1983), or on the FGB themselves (Brazeau and Sammarco, 2009; Sammarco et al., work in progress). One possible explanation may be found by comparing these results with those of an earlier experiment. This experiment performed on the Great Barrier Reef, showed that coral settlement around an isolated reef could be enhanced locally by associated eddies that helped to retain larvae in the lee of currents around the reef (The Helix Experiment; Sammarco, 1988, 1989; Andrews et al., 1989; Sammarco, 1994; Andrews and Gay, 1994). It also demonstrated that recruitment within 600 m of the reef was 5-20 times higher than that further away. Beyond this distance, density of coral recruitment fell dramatically, approaching a low asymptote starting at distances of 1.2 km from the reef. This phenomenon was being driven by advection processes derived from currents which carry the larvae away from the reef, and diffusion processes which spread the larvae through space as they are being advected (Okubo, 1980, 1994; Okubo and Levin, 1989). When one compares the coral settlement density observed

here with that observed in the Helix Experiment, plotting it against distance from the FGB and distance from Helix Reef, respectively, it becomes apparent that the platforms considered here all fall beyond 1.2 km from the FGB (Figure 26). This potentially places them in a region where they may be approaching an asymptote of low recruitment due to diffusion effects, associated with distance from the potential larval source. This is consistent with the generally homogeneous low level of overall recruitment observed on the platforms. It would appear that the diffusion and possibly mixing processes in this region for larvae are particularly strong. The comparison also demonstrates that recruitment levels on platforms in the GOM are much lower than those on the FGB or in the central region of the Great Barrier Reef.

The oil and gas platforms in the northern GOM represent unique ecological environments and generally exhibit very low levels of coral recruitment when compared to other locations in the tropical western Atlantic. Nonetheless, this recruitment, when permitted to continue for up to ~30 years, has clearly resulted in the development of adult coral communities, albeit at a slow rate. There has also been substantial development of associated benthic, demersal, and pelagic reef biota. These coral communities are to be considered fragile because of low recruitment rates and slow community development. If there were to be a mass mortality of corals on the platforms, community regeneration would most likely require decades.

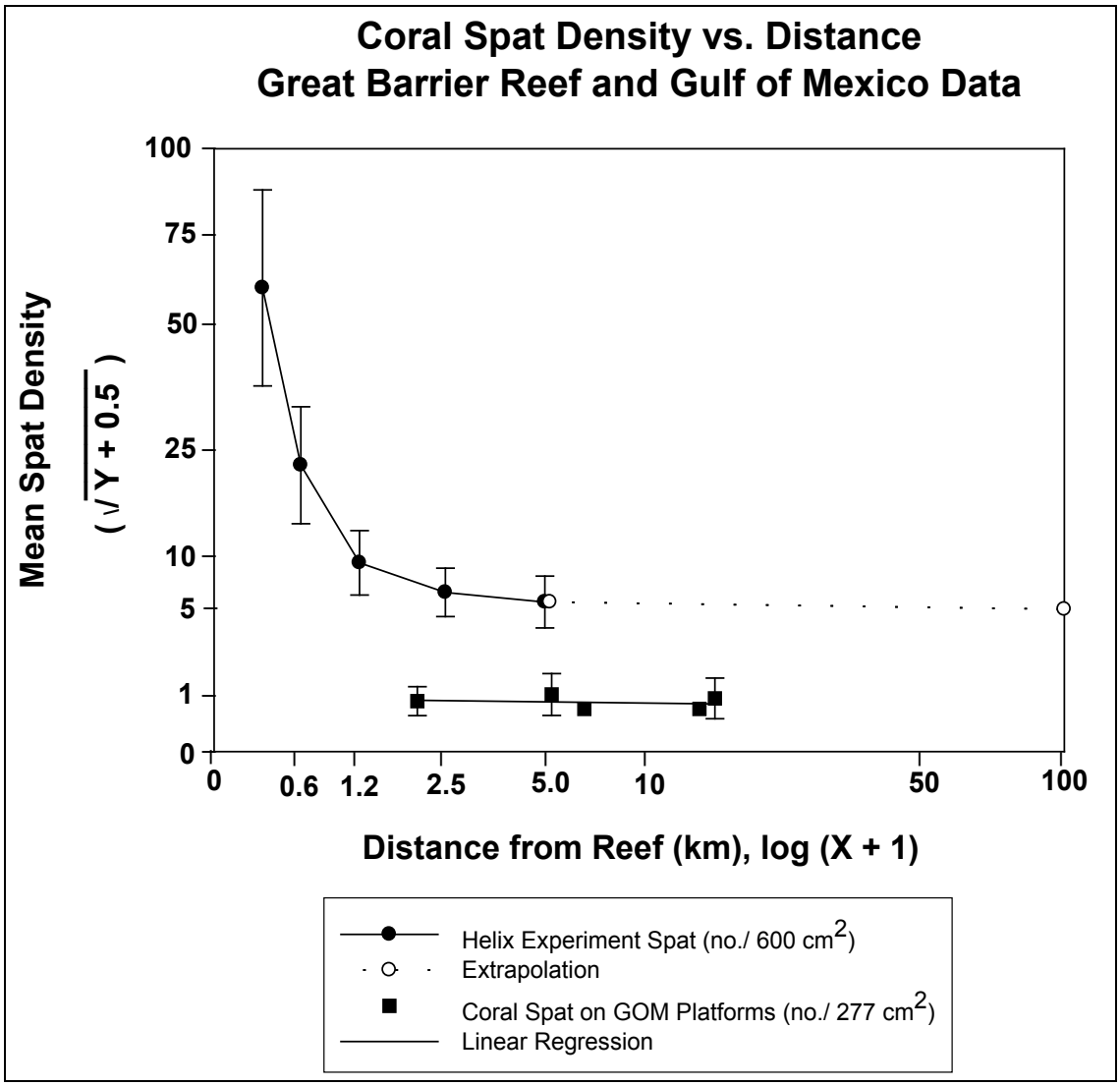

Figure 26. Relationship between coral spat density on oil and gas platforms studied here and distance in km from the nearest perimeter (30 m isobath) of the nearest FGB (squares). Average density of *Montastraea* sp. spat in no. per 450 cm^2 on six oil and gas platforms in the northern GOM in the vicinity of the FGB, by platform. The platforms are HI-A-330, HI-A-349B, HI-A-368B*, HI-A-376A, HI-A-571A*, and HI-A-382. Data derived from coral settlement on terracotta plates mounted on steel racks and deployed at depths of 15 and 27 m for one year during 2001-2002 or 2002-2003*. Data combined for depths (see text for explanation). Comparative data also shown for coral settlement on plates derived from the Helix Experiment, performed on the Great Barrier Reef, from distances of > 300 m from the reef perimeter (Sammarco and Andrews, 1988, 1989). Solid black circles represent empirical data; hollow circles represent values extrapolated from that empirical data, using a hyperbolic/asymptotic relationship. Means and 95% confidence limits shown. Data transformed by square-root (Y + 0.5) for normalization purposes.

4.3 GENETIC CONNECTIVITY IN CORALS ON THE FLOWER GARDEN BANKS AND SURROUNDING OIL AND GAS PLATFORMS, GULF OF MEXICO

Homogeneity in *M. decactis* populations between the two FGBs is not surprising, because these reefs have co-existed in close proximity (<12 km) for 16,000-18,000 years (Rezak et al., 1985). This genetic connectivity also extended to the *Madracis* populations within 10 km to the west (Platform #2) and 25 km to the east (Platform #4). There was less self-assignment in populations of the more central sites, near and including the FGB's, than at the outermost sites. Assignment to the "CANM" (Criteria for Allocation Not Met) category does not, of course, necessarily imply lack of any assignment for a colony; rather, because we used a threshold of log 1.0, it implies less than a 10-fold margin of probability of a colony "belonging to" one population and only one population compared with the next most probable population. Generally this meant that the population had a nearly equal probability (less than a 10 fold difference) of being assigned to more than one population.

If one considers the genetic divergence between *M. decactis* populations *versus* distance to the FGB, the patterns in Φ_{ST} suggest that populations on the FGBs are indeed seeding the surrounding platforms–or at least are more frequently seeding those in the immediate vicinity. Also, the increasing dissimilarity with distance could be a sign of founder effect; that is, fewer and fewer larvae are successfully recruiting on the platforms with distance from the FGB, carrying with them a smaller and smaller sample of the gene pool of origin and presenting an increasingly skewed representation of the source population. Thus, the genetic signature appears to be more different with distance. As distance increases, genetic affinity to the FGB is reduced and populations become more distinct.

The fact that genetic differentiation increased in *M. decactis* between all sites as geographic distance between them increased, also suggests that gene flow is restricted by inter-site distance. The same pattern appeared in *M. cavernosa,* where genetic differences increased with geographic distance. In *M. decactis*, the distance after which all population comparisons were significantly different was 55 km, indicating that gene flow is probably severely restricted beyond this distance. The pattern of increasing genetic differentiation with geographic distance in *M. cavernosa* was also significant, but it is difficult to make in-depth interpretations of the data with the limited sample sizes encountered here.

This concept is reinforced in *M. decactis* by the AFLPOP self-allocation data. Increasing levels of self-allocation with distance from the FGB indicates that the populations become more distinct with distance from these reefs. It also implies that the FGB may well be a source of larvae for colonization of these structures over the past 30 years, but again with strong founder effects occurring due to very low levels of successful recruitment on an annual basis. Data that we have collected in a sister study demonstrate that annual coral settlement rates on the platforms are extremely low–and that *M. decactis* is one of the only two species that settled there (Sammarco and Atchison, 2002; Sammarco, Atchison, and Boland, work in progress).

Patterns in inter-site allocations in *M. decactis* along with self-allocations yielded by AFLPOP analyses reinforce this conclusion. Clearly, differences in the genetic structure of the platform populations emerge immediately with any distance between sites. The observed pattern

in *M. decactis* was mimicked directly by *D. strigosa* and, to a lesser degree, by *M. cavernosa*. The higher variance in this last case is surely due to small sample size.

The linear decreasing pattern in inter-site recognition levels with distance (excluding self-allocation) in *M. decactis* reinforces the conclusion that populations are becoming increasingly distinct as distance between them increases. This is evident even when overall cross-recognition levels are very low.

Both *M. decactis* and *D. strigosa* populations on the two FGBs were genetically homogeneous. Even though platform population sizes were small, the data suggest gene flow between the FGBs and Platform #3, located between the two banks. As in *Madracis*, the two eastern-most *Diploria* populations, Platform #5 and Platform #7, showed no affinity to the banks or Platform #3. Platforms #3, #5, and #7 all had higher self-allocation proportions, ranging from 83-100%, perhaps due to founder effects. Platform age appears to have had no effect on the patterns observed; all platforms were exposed to possible colonization over a period of 15-26 yrs.

Patterns of cross-site recognition through AFLPOP in *M. decactis versus D. strigosa* contrasted strikingly. First, this response could have been produced by simple genetic drift (founder effects). Sample sizes are indeed different between our two key species, and recruitment to these sites may be rare and sporadic. It is surprising, however, that, given the possible age of these sites ($\leq$ 27 years) population structure didn't exhibit some integration of multiple recruitment events. Second, small sample sizes could have produced the observed patterns, which were statistically significant (i.e., non-random). Once again, our samples represent the entire populations within a given depth-range at these sites and thus should be a good estimate of population differentiation, despite the low probability of observing the phenomenon.

A third explanatory hypothesis is that the more dissimilar patterns with seemingly greater rates of differentiation at intermediate distances between sites may have resulted from *Diploria*'s broadcasting mode of reproduction. Larvae settling at the longer distances may actually have been more closely related to the source population than those at intermediate distances. Upon spawning, buoyant coral eggs are fertilized externally and require 48-96 hours before they are competent to settle (Harrison and Wallace, 1990). During this time, they have little or no swimming capabilities (primarily used for depth control; Sammarco, 1994; Stake and Sammarco, 2003) and are subject to currents for advective dispersal. Assuming a patch of larvae experiences an average current velocity in the region is ~15 cm/s (Lugo-Fernandez, 1998, 2006; Lugo-Fernandez et al., 2001) during the spawning period, it would require a minimum of 2.3 days to travel 30 km barely entering its period of viability to settle. The observed pattern implies that, under these conditions, these larvae may remain in the water column for 4.7 days before settling in larger numbers, thus generally bypassing locations of an intermediate distance from the source in preference to locations encountered after about twice the travel time. Current velocities vary widely in the GOM, of course, and are highly dependent upon numerous large-scale oceanographic structures.

These results plus self-allocation patterns with respect to distance to the FGB suggest that *D. strigosa* is much more easily isolated than its brooding counterpart, *M. decactis*. In this case, differentiation of populations appear to be rapid and complete within distances of $\leq$25 km compared with 60 km in *M. decactis.* We believe this is a function of extreme founder effect due to negligible levels of recruitment over ecological time (15-27 years).

Unlike *Madracis* and *Diploria, Montastraea* populations on the E- and W-FGB were genetically distinct. The small population on Platform #7 (easternmost) was homogeneous with the W-FGB but genetically distinct from the E-FGB. This suggests that the colonies making up this population may be derived from the W-FGB (or a genetically similar population).

In an earlier study of *Agaricia agaricities* (a brooder), we found that populations on Crocker and Conch Reefs, Florida Keys, which occur within 20 km of each other, exhibit relatively strong genetic affinities (Brazeau et al., 2005). Similar patterns have been observed in *Seriatopora hystrix* in the Red Sea (Maier et al., 2005), *Lophelia pertusa* in the deep sea of the NE Atlantic (Le Goff-Vitry et al., 2004), and *Balanophyllia europaea* in the Mediterranean (Goffredo et al., 2004). Regarding the E-FGB, genetic connectivity did not extend to the far western (Platform #1; 15 km) or far eastern (Platforms #6 and #7; 50-65 km) platforms. With respect to the W-FGB, some connectivity was observed to the east, but not to the west. There appears to be some evidence of cross-colonization between platforms or "island hopping" (Atchison, 2005; Atchison et al., 2008; Sammarco et al., 2012). Such events are very effective in spreading the introduction of a species, whether under natural or anthropogenic conditions (Elton, 1977; e.g., Garb and Gillespie, 2006). The level of this seeding, however, is low. Potential mechanisms of cross-seeding in the region have been identified. That is, it is known that larvae may be carried from the FGB inshore to the north, then to a nearshore westerly current, and then to a southerly coastal jet, carrying them back to the W-FGB region again (Lugo-Fernandez 1998, Lugo-Fernandez et al., 2001; see Figure 2).

Small coral population sizes on the platforms are probably due to the relative sizes of the platforms, their structure (comprised of cylinders), their distances from the nearest potential larval source, and community age. Small sample sizes decrease the power of the test (Sokal and Rohlf, 1994) and make it more difficult to demonstrate significant differences between populations. Here, any significant differences found between small populations would imply that these differences are relatively robust. Small sample sizes should thus be less of a problem for interpreting the data in this study because we are dealing with total population size on the platforms. However, they may still pose a problem for extrapolating results to other studies.

The generally low levels of genetic connectivity observed in all species here could be the result of colonization by larvae from more distant sources (Ahlroth et al., 2003). The nearest source would be the Lobos-Tuxpan Reef System (13 km off Cabo Rojo or 640 kmSW of the FGB) or the Campeche Bank Reefs (181 km off the Yucatan Peninsula), although Lugo-Fernandez et al., (2006) have found that Alacran may also be considered a potential source. There are similarities in coral community structure between the FGB and Campeche reefs, and the FGB are believed to be an extension of communities that occur in the southern GOM (Bright et al., 1984). This recruitment would most likely be a rare event. Unfortunately, we have no genetic data from these southerly regions with which to compare our results. *M. decactis* and

other spp. occur on other platforms throughout the northern GOM (Sammarco et al., 2006), and related molecular genetic analyses are being performed to determine potential connectivity there (Sammarco et al., work in progress). Another explanation for the generally low levels of genetic affinity is that a source coral could actually have been present on the FGB but that recruits onto the platforms represent sampling error or bias, resulting in founder effect. Such bias might be expected to decrease over time with successive recruitment events, if self-seeding did not occur.

Much debate has surrounded the dispersal capabilities of brooding compared with broadcasting corals (Sammarco and Andrews, 1989; Sammarco, 1994; Ayre and Hughes, 2000; Miller and Mundy, 2003). It is now known that dispersal among brooding species may be more variable than broadcasters (Harii and Kayanne 2003; Magalon et al., 2005; Sammarco et al., 2004). The dispersal potential of larvae is influenced by, among other things, larval competency period and currents carrying the larvae (Harii and Kayanne, 2003; Olson, 1985). The larval competency period of *M. decactis* may be greater than that of the other two study species, since its planulae are relatively large (Vermeij et al., 2003) and have a high lipid content, making them well-suited for long-distance dispersal (Richmond, 1981).

In this study, the brooder *M. decactis* was the most abundant and widely dispersed species. It has been more successful at recruiting to nearby sites than either of the broadcasting species (*Diploria* or *Montastraea*), which release several orders of magnitude more reproductive propagules than *Madracis*. The major advantage that *Madracis* has over the two broadcasters is its repeated release of planulae for a period of 8-10 days per month encompassing major changes in tidal amplitude. It does this over 8-10 months of the year (McGuire, 1998), subjecting the larvae to an array of circulation patterns, traveling in a multitude of directions throughout the year. These conditions would allow *Madracis* to take advantage of the platforms to successfully extend its geographic range. The newly established populations on the platforms can produce larvae that can in turn settle on neighboring platforms (Barber et al., 2002), acting as a stabilizing force in the ecosystem in the event of a disturbance. This suggests that the species with the greatest potential for widest dispersal will not necessarily exhibit the highest population densities and widest geographic distribution. Some species with crawling larvae and apparently highly limited dispersal capabilities exhibit a very broad geographic range (Sammarco, 1994), such as some gastropods (Hoskin, 1997), teredinid bivalves (Calloway and Turner, 1983), and corals (e.g., *Balanophyllia elegans*; Gerrodette, 1981). *Pocillopora damicornis*, a brooding coral, has among the widest geographic range of any known coral, extending from the Red Sea to the eastern Pacific.

Another possible reason why *M. decactis* has been more successful at colonization and exhibited the highest level of genetic affinity between sites is the nearly-immediate readiness of its larvae to settle (e.g., four hours after release). This is suggested by the distribution pattern of the broadcasters on the two eastern-most sites and the pattern of Φ_{ST} in *D. strigosa*. The probability of a larva encountering a target site is dependent upon advection and diffusion, and decreases as a function of the square of the distance between the source and the target (Okubo, 1994). It is also possible that these two species of spat have different abilities with respect to competing for space with other sessile epifauna after settlement.

Diploria and *Montastraea* are annual mass spawners and have only a single opportunity each year to disperse their larvae. Dispersal is entirely dependent on current patterns at that time (see Willis and Oliver, 1990; Baums et al., 2006). The genetic heterogeneity of these small islands indicates that these broadcasting species are less effective colonizers of new habitats patchily-distributed at the meso-scale. One reason that may explain why these two species have different population distributions on the platforms and different patterns of genetic differentiation on the two FGBs is that the population sizes (using percent-cover) for *D. strigosa* on the FGB are 1.2-4.5 times greater than those of *M. cavernosa* (Dokken et al., 1999, 2003; Precht et al., 2007; Zimmer et al., 2010).

In summary, the genetic data suggest that the coral populations on the oil and gas platforms in the northern GOM exhibit genetic affinity to the FGB, which decreases with distance from them–and from each other. The brooder, *M. decactis,* with its extended larval release periods and its lack of extended delay for competence to settle, shows greater affinity to the FGB with distance than *D. strigosa*, a broadcaster. *M. decactis* appears to be more effective at colonizing small, nearby target sites and expanding their geographic range at the meso-scale. By contrast, the broadcaster *D. strigosa* is less effective in expanding its range, colonizing these relatively short-distance targets in a more haphazard fashion. It may be more effective at colonizing habitats $\geq$ 60 km from their source. All species examined here exhibited substantial founder effect on the platforms, generally increasing with inter-site distance. These young coral populations appear to be much more highly differentiated at the meso-scale during these early stages of community succession (ecological time) than their older, more established counterparts (Ayre and Hughes, 2004). This implies that a great deal of time may be required, encompassing repeated larval colonization of patchy habitats around larger established potential sources, before genetic equilibrium or homogeneity is reached between them in regards to evolutionary time (Hellberg, 2007).

5.0 CONCLUSIONS

The major conclusions of this study are listed in the bulleted lists below.

5.1 ADULT CORAL COMMUNITY STUDY

- Corals occurred on most of the oil and gas platforms surveyed around the NOAA FGB National Marine Sanctuary.
- Eleven species of scleractinian corals were found: eight hermatypic, two ahermatypic, and one hydrozoan.
- The most abundant corals were *Madracis decactis*, *Diploria strigosa,* and *Tubastraea coccinea*.
- Distance from the FGB was not related to the coral community variables measured, including total coral abundances of the dominant three species in shallow water ($\leq$ 14 m), deep water (14-33 m), or both depths combined.
- Total coral abundance increased significantly with platform age. The coral community was best developed on platforms $\geq$ 12-15 years in age.
- Abundance of *M. decactis* increased significantly with platform age in deeper water and both depths combined, as did coral species diversity.
- Abundance of *D. strigosa* showed no relationship with platform age, indicating that it may not be associated with any given successional sere.
- Abundance of *T. coccinea* was associated with platform age only in shallow water, where it decreased in abundance with age, indicating that it may be an opportunistic pioneer species.
- All corals exhibited a significantly non-uniform depth distribution, with total coral abundance peaking at 20 m and 28 m depths, even after standardizing for depth-related structural anomalies of the platforms.
- *M. decactis* exhibited a similar bimodal depth distribution, with disproportionately high abundances at $\geq$ 27 m depths.
- *D. strigosa* exhibited abundance peaks at depths of 10- and 23-m depth and was not found at $\geq$ 27 m depths.
- *T. coccinea* exhibited a near-normal distribution, with a mode at 17 m depth.
- Oil and gas platforms have facilitated the expansion of coral populations in the GOM. Such platforms have intrinsic environmental value through the presence of coral populations.
- Oil and gas platforms have also facilitated expansion of exotic coral populations in the GOM.
- The low levels of recruitment observed on the platforms here, cumulative over a period of up to 27 years, has permitted the development of adult coral communities and their associated benthic, demersal, and pelagic biota. These communities should be considered fragile because of their slow development rate. Mass coral mortality on these platforms would require decades for recovery.

5.2 CORAL SETTLEMENT STUDY

- Density of coral spat settlement on plates exposed, for ~one year, on the oil and gas platforms was extraordinarily low when compared with the E-FGB, other Caribbean sites, or the Great Barrier Reef, averaging < 1/450 cm^2.
- Such low recruitment rates emphasize the uniqueness and fragility of these artificial reef sites in comparison to natural sites, perhaps due to associated flow structure that might influence coral recruitment.
- There was no significant difference in coral spat density between platforms.
- The pattern of settlement suggests that the distance between the platforms and the E-FGB (2.1 km) and their potential larval source may have been large enough (> 0.6-1.2 km) to allow a high diffusion of larvae, suppressing planktonic larval densities.
- Spat density varied significantly between racks, indicating highly localized patchiness in settlement patterns.
- There was a significant difference between coral settlement densities on platforms *versus* the E-FGB (data derived from a related experiment), where settlement was much higher.
- Only three species of coral spat were found on the platforms: *T. coccinea*, *Montastraea* sp. (most likely *M. cavernosa*), and *Madracis* sp. (most likely *M. decactis*), in order of abundance.
- Species composition of coral spat varied substantially from that observed on the E-FGB, which was characterized by *Agaricia* and *Porites*.
- Dominant recruits on the platforms matched those in the adult community on the platforms; this is an unusual situation.
- *Tubastraea* and *Montastrea* spat densities did not vary significantly between platforms or between racks.

5.3 CORAL MOLECULAR GENETICS STUDY

- Analysis of Molecular Variance (AMOVA) indicates that the E- and W-FGB are genetically homogeneous for the coral species *M. decactis* and *D. strigosa* populations.
- Populations of *Montastraea cavernosa* were significantly different between the two Banks.
- In all species, genetic distance (Φ_{ST}) increased significantly with geographic distance between populations, indicating that coral populations become more isolated with distance and acquire a stronger genetic self-identity or signature.
- This pattern was strong in *M. decactis,* when considering distance between the platforms and distance from the perimeters of the FGB, particularly the nearest FGB. This suggests that the FGB may be a primary source of larvae for many coral populations on the platforms.
- Amplified Fragment Length Polymorphism Population (AFLPOP) analyses showed that the degree of self-allocation to home sites also increased with inter-site distance. Cross allocations between sites dropped significantly and exponentially in all species within only one to several kilometers of the FGB.
- *M. decactis,* a brooder with extended larval release periods and near-immediate settlement competence, showed greater affinity to the FGB with distance than *D.*

strigosa, a broadcaster. This brooder appears to be more effective at colonizing small, nearby target sites and expanding its geographic range at the meso-scale.

- The low degree of genetic affinity exhibited by all species on the platforms may be attributed to genetic drift/founder effect or relatively small samples sizes, although it should be noted that total populations were sampled within the study sites.
- In general, genetic affinity between coral populations decreased with inter-site distance. Young coral populations were highly differentiated in this meso-scale analysis during early stages of community succession. This implies that much time and repeated colonization of these habitats that are patchily distributed around larger potential larval sources will be required before genetic equilibrium or homogeneity is reached.

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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.