Expansion of coral communities within the Northern Gulf of Mexico via offshore oil and gas platforms

3 authors, including:

Paul W. Sammarco
Louisiana Universities Marine Consortium
161 PUBLICATIONS **7,675** CITATIONS

Gregory S Boland
Bureau of Ocean Energy Management Retired 2018
102 PUBLICATIONS **1,661** CITATIONS

Expansion of coral communities within the Northern Gulf of Mexico via offshore oil and gas platforms

Paul W. Sammarco[1,2,*], Amy D. Atchison[1,2], Gregory S. Boland[3]

[1]Louisiana Universities Marine Consortium (LUMCON), 8124 Highway 56, Chauvin, Louisiana 70344, USA

[2]Department of Oceanography and Coastal Sciences, Louisiana State University A & M College, Baton Rouge, Louisiana 70803, USA

[3]US Department of the Interior, Minerals Management Service, 1201 Elmwood Park Boulevard, New Orleans, Louisiana 70123-2394, USA

ABSTRACT: Approximately 4000 oil and gas platforms exist in the northern Gulf of Mexico. 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 coral reefs of the Flower Garden Banks (FGB), ~200 km S–SE of Galveston, Texas, USA. We determined whether extensive scleractinian coral populations had colonized these platforms, quantified them, and determined 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 36 m depth, encompassing an ellipse around the FGB. Corals occurred in abundance on most of the platforms. We found 11 species, comprising 8 hermatypic scleractinians, 2 ahermatypic scleractinians and 1 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 3 species in shallow water (<14 m), deep water (14 to 36 m), or both depths combined. Total coral abundance increased significantly with increasing platform age, and the community was best developed on platforms >12 to 15 yr old. Abundance of *M. decactis* increased significantly with increasing platform age in deeper water 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 increasing age, indicating that this species may be an opportunistic pioneer species. All corals combined exhibited a significantly non-uniform depth distribution, with total coral abundance peaking at ~20 and 28 m depths. *M. decactis* exhibited a similar bimodal depth distribution, with a disproportionately high peak at depths >27 m. *D. strigosa* exhibited peaks at ~10 and 23 m depth and was not found at depths >27 m. *T. coccinea* exhibited a near-normal distribution, with a mode at ~17 m depth. Platforms have facilitated the expansion of coral populations in the GOM. Such platforms possess an intrinsic environmental value through the presence of coral populations, and this may influence future decisions regarding their removal.

KEY WORDS: Coral · Platform · Oil · Diversity · Reef · Flower Garden Banks · Artifical

———————————— Resale or republication not permitted without written consent of the publisher ————————————

INTRODUCTION

Approximately 40 000 oil and gas wells have been drilled in the northern Gulf of Mexico (GOM) since the 1940s (Francois 1993). At present, ~4000 structures are in operation there (Francois 1993, Knott 1995, Dauterive 2000, our Fig. 1). These platforms extend throughout the euphotic zone as rigidly attached struc-
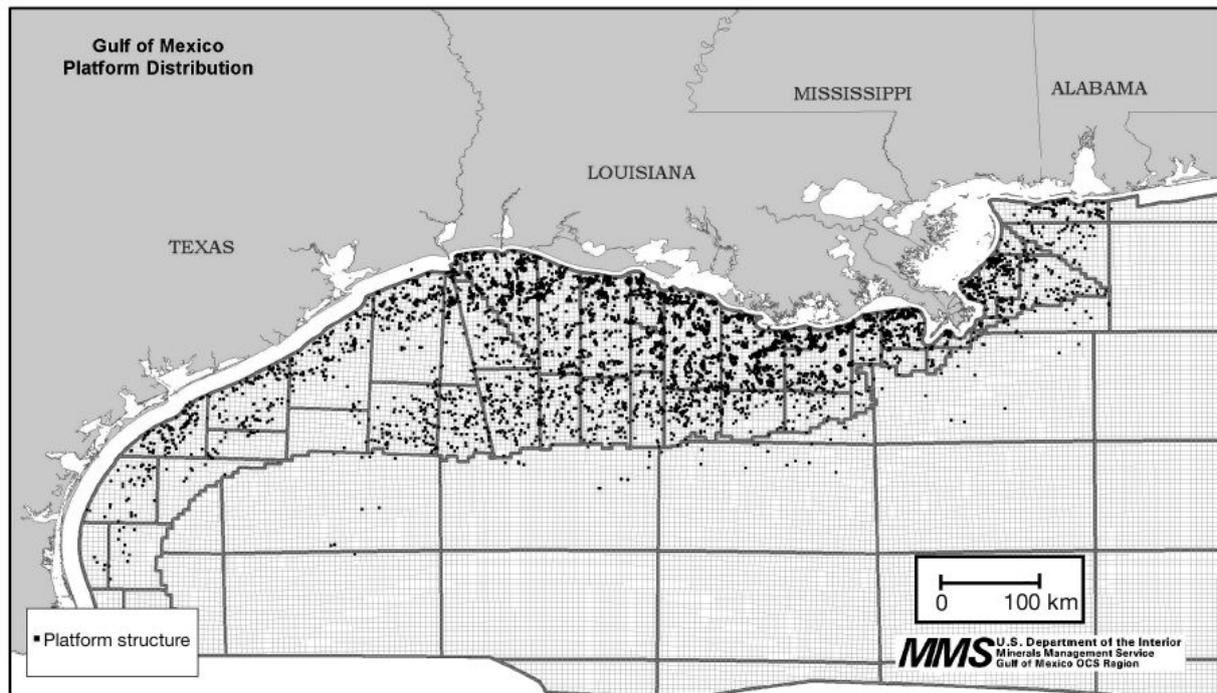
Fig. 1. Northern Gulf of Mexico, showing location of oil and gas platforms present in 2003. Total number of platforms: ~4000, total number of wells drilled since the 1940s: ~40 000

tures (as opposed to floating structures) and act as hard substratum upon which many reef organisms can settle and grow (Gallaway & Lewbel 1981, Driessen 1989, Bright et al. 1991, Adams 1996, Boland 2002, K. Deslarzes pers. comm.). The northern GOM is a region in which very little hard substratum now exists, nor has existed in recent geological time (Curray 1965a,b, Blum et al. 2001, see also Frost 1977, Schroeder et al. 1995 and Blum et al. 1998). The Flower Garden Banks (FGB), which rise to within 18 m of the surface, are the most remarkable exceptions in the Gulf and support thriving coral populations (Rezak et al. 1985, Gittings 1992, 1998, Bright et al. 1993).

There are 35 named banks on the northern shelf of the northwestern GOM, including the FGB, which developed on top of 2 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, G. Boland pers. obs.), which might be able to support substantial coral reefs, are either too deep or lack other appropriate environmental conditions to do so. A number of banks do possess limited populations of reef-building corals, but these are not sufficiently developed to be considered true coral reefs, i.e. 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 et al. 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 & Atchison 2003), and these are considered to be among the most isolated coral reefs in the western Atlantic (Rezak et al. 1985, Snell et al. 1998).

The GOM has experienced several sea-level changes in recent geological history (Curray 1965a,b, Frost 1977, Schroeder et al. 1995, Blum et al. 1998, 2001). During periods with sea levels 30 m below the 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 Gulf of Mexico 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 probably allowed exchange of coral larvae relatively easily via the 'island model' of gene flow (Futuyma 1998). However, as sea level rose over the next 6000 to 10 000 yr, the reefs were drowned, and the FGB now represent the only true coral reefs in the northern Gulf of Mexico. The nearest shallow reefs are those off the northern coast of Yucatan peninsula

(Alacran and associated reefs: 650 km), Tampico, Mexico (700 km), and the Florida Keys (1089 km). External sources seeding the FGB are at present unknown. From what is known about current regimes in the region, sources of larvae may include the above north Mexican areas, including Bahia de Campeche (e.g. Salas-de-Leon et al. 1998), with larvae being transported via the Western Boundary Current (Vidal et al. 1999); and the Cozumel and Cancun regions, with larvae being transported north by the Caribbean Current into the Gulf and then west via the Loop Current (see Sturges & 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, see also 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 spat there are 100 % differentiable from adults from the Bahamas and Florida Keys (D. Brazeau et al. unpubl., P. Sammarco et al. unpubl.), and the data suggest that the FGB are self-seeded, at least with respect to brooders. Recent physical oceanographic research using drifters deployed during nights of broadcast spawning supports these findings. Lugo-Fernandez (1998) and Lugo-Fernandez et al. (2001) have demonstrated mesoscale patterns of circulation in the vicinity of the FGB, which could drive self-seeding there (see Sammarco & Heron 1994 for general discussion). Affinities between adults and spat in this region are presently being investigated by Brazean et al. (unpubl.) and Sammarco et al. (unpubl.).

When oil and gas platforms were introduced into the Gulf of Mexico in the 1940s (Francois 1993), they represented the only substratum other than the FGB and a few other banks in shallow water that were capable of supporting coral communities. In the absence of these structures, survival of coral larvae 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 transportation into nearshore habitats unsuitable for settlement (low salinity, low temperatures, high turbidity, etc.). A previous study showed that a single platform in 33 m of water exposes ~8100 m hard surface to the surrounding waters (e.g. Shinn 1974).

Until the present study, 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., authors pers. obs.), but no quantitative studies had been performed. Expansion of organisms, both terrestrial and marine, via 'leap-frogging' or 'stepping stone' mechanisms have been well-documented (Elton 1958,

Futuyma 1998). In the case of reef fish, such distribution expansions have been enabled by anthropogenic activity by introducing new suitable habitats, such as oil and gas platforms (Shinn 1973, Winfield 1973, Sonnier et al. 1976, Boland et al. 1983, Shinn & 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 are experiencing a severe global decline in health and mass coral mortalities due to bleaching, poor fishing techniques, nutrient enrichment, etc. (Sammarco 1996, Souter & Linden 2000, Hughes et al. 2003, McClanahan et al. in press), it is important to determine whether systems exist in which coral populations are still expanding their distributions.

According to federal legislation, all oil and gas platforms introduced into US waters must be removed within 1 yr of termination of a lease within a lease block (usually ~3 × 3 nautical miles; Minerals Management Service [MMS] Regulation 30CFR250.1718; see www.mms.gov). Some platforms are used by the states bordering the GOM in their 'Rigs to Reefs' programs (e.g. Louisiana, Texas, Alabama, Florida; see Dauterive 2000, www.tpwd.state.tx.us/fish/reef/artreef.htm, www.gomr.mms.gov/homepg/regulate/environ/rigs-to-reefs/information.html). These programs are administered in cooperation with the US Department of the Interior, Minerals Management Service. Within these programs, the platforms are permitted to remain either on site or are brought to another site and used as artificial reefs. In addition, scleractinian corals are protected from 'harvest and take' by federal legislation (Magnuson-Stevens Fisheries Conservation Management Act 1975, amended October 11, 1996; Public Law 94-265) and from trade via international treaty. These laws were devised prior to any knowledge of coral populations being present on the platforms. If corals are present, this implies that the structures may have additional environmental value and, if not removed, may contribute to the benefit of the environment as artificial reefs. One of our aims was to determine (for the first time) the extent to which corals colonize such platforms prior to their removal or designation as artificial reefs.

Herein we investigate several questions regarding these platforms: (1) Being situated in subtropical 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 (i.e. is there any indication that the FGB may be a possible source of larvae for the platform)? (5) How does density and species distribution relate to depth? (6) What is the average size of colonies on the platforms? (7) How does colony size relate to platform age and distance from the FGB?

Table 1. Details of oil and gas platforms studied. Platform number is coded by lease area; MMS (Minerals Management Service) reference number; distance from FGB: distance from perimeter of Flower Garden Banks; bearing: bearing from FGB

Platform no.	MMS ref. no.	Corporate owner	Location Lat.	Long.	Deployment date (yr)	Age at time sampling (yr)	Distance from FGB (km)	Bearing from FGB (°)
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

MATERIALS AND METHODS

To address these questions, we initiated a set of field surveys and experiments, followed by laboratory analyses and sample processing. To determine whether platforms support substantial coral communities, we chartered a dive vessel (MV, 'Fling', Freeport, Texas) and surveyed 13 oil and gas platforms (Table 1) over a period of 2 yr. 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 (Fig. 2). Divers examined the platform jacket from the surface down to a depth of 36 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 by approximate area surveyed. Architectural structural drawings of the plat-
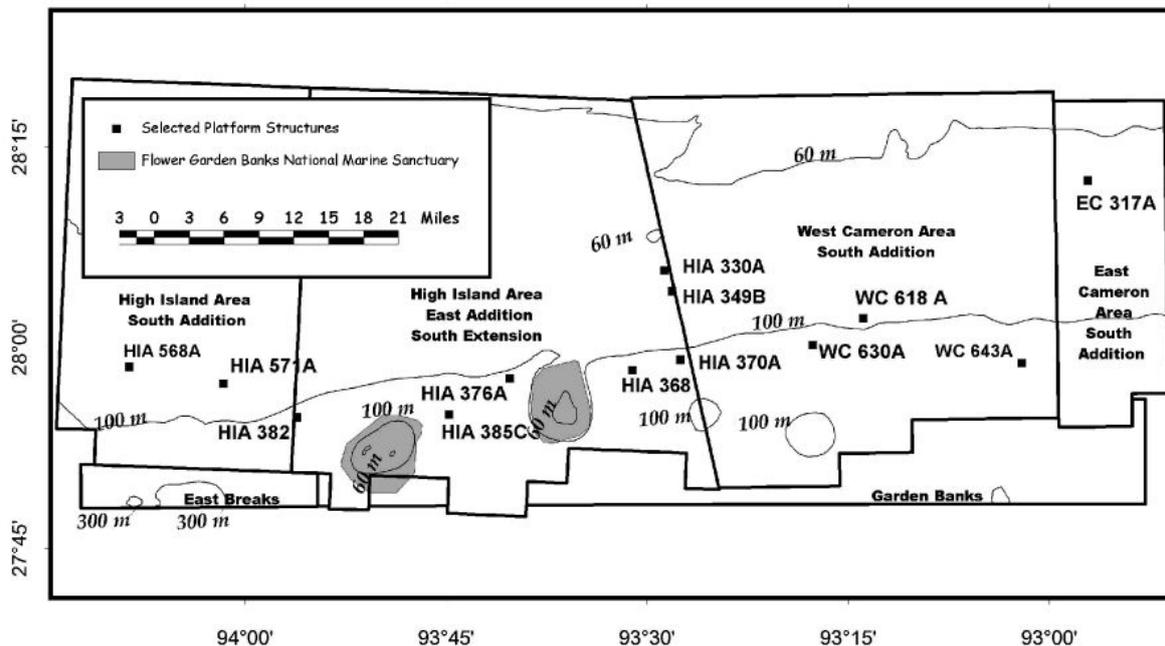

Fig. 2. Northwestern Gulf of Mexico showing location of Flower Garden Banks, ~200 km S–SE of Galveston, Texas and 13 platforms used in this study. Sampling regime skewed to east because of known prevailing currents in the region; scale bar is in nautical miles

form jackets were obtained from the oil and gas companies concerned. Total surface area was estimated for each platform along with the surface area for each 3 m interval of depth, in order to compensate for increased area added by horizontal support structures which occurred at 10 to 15 m and 24 to 27 m.

Data on coral colony size was also collected. Due to 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 length of the longest axis of the colony and widest width (see Sammarco 1980, 1982). Area was estimated by calculating elliptical area.

Data were also gathered about the platforms themselves. Date of installation was determined from MMS records (Table 1). Distance of the platforms from the nearest reef perimeter, along with their bearing from the FGB, was determined via nautical charts, also provided by MMS.

Standard parametric univariate statistical analyses were performed on the data. Data were transformed via square-root $(y + 0.5)$ where necessary for purposes of normalization (Sokal & Rohlf 1981). Kolmogorov-Smirnov frequency tests of independence were performed on the coral depth distribution data to test for variation from a uniform distribution. 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 & 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 are presented in the figure and table legends. Only significant results are discussed.

RESULTS

The diver surveys revealed a total of 11 species of corals on the platform jackets, occurring between 0 and 36 m depth. Of these, 8 were hermatypic scleractinians, 2 were ahermatypic scleractinian corals, and 1 was a hydrozoan (Table 2). The dominant hermatypic scleractinian corals were *Madracis decactis* and *Diploria strigosa.*

Effect of distance from Flower Garden Banks (FGB) on corals

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) *Madracis decactis* abundance per platform; (3) *Diploria 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

Table 2. Coral species observed on oil and gas platforms in Northern Gulf of Mexico. Authority: original description; reproduction times: data are for whole Caribbean, and show months (e.g. 1, 3 = January, March). Sources were 1: Hagman et al. (1998); 2: Vermeij et al. (2003); 3: Steiner (1995); 4: Bassim & Sammarco (2003); 5: Bassim et al. (2002); 6: Acosta & Zea (1997); 7: Gittings et al. (1994); 8: Soong (1993); 9: Gittings et al. (1992); 10: Szmant (1991); 11: Wyers et al. (1989); 12: Gleason et al. (1999); 13: McGuire (1998); 14: McGuire (1995); 15: Chornesky & Peters (1987); 16: Ayre & Resing (1986); 17: Hebbinghaus (2001); 18: Soong & Cho (1998)

Species	Authority	Reproduction Mode	Reproduction Times	Source
Scleractinia (hermatypic)				
Colophyllia 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	3–12	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)

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 increasing 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.

Abundance of hermatypic corals

Abundance of shallow hermatypic corals (≤14 m depth) increased significantly with increasing age of the platforms, as indicated by linear regression analy-
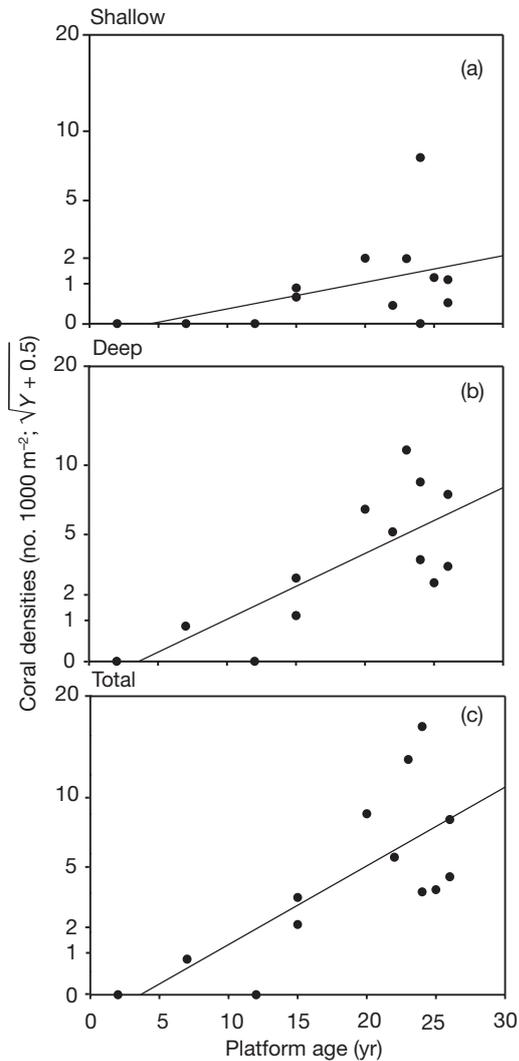
Fig. 3. Hermatypic corals. Relationship between abundance in (a) shallow water (0 to 14 m) (b) deeper water (mean <14 to 27 m; max. 36 m) and (c) both combined, on platforms versus platform age. Data represent total number of corals standardized by area (no. 1000 m^{-2}) on each platform. For comparison purposes, data were scaled down to area of smallest platform considered (2450 m^2); thus, total coral abundance is probably conservative. (a) Significant positive regression (least-squares linear regression analysis. $y = 0.035x + 0.553$, p < 0.05. Pearson's product-moment correlation coefficient: r = 0.478, p > 0.05, not significant; Kendall's rank correlation coefficient: t = 0.340, p = 0.05). (b) Significant positive relationship (regression, $Y = 0.085x + 0.403$, p < 0.01; correlation, r = 0.756, p < 0.01). (c) Significant positive relationship (regression, $Y = 0.100x + 0.344$, p < 0.01; correlation, r = 0.740, p < 0.01)
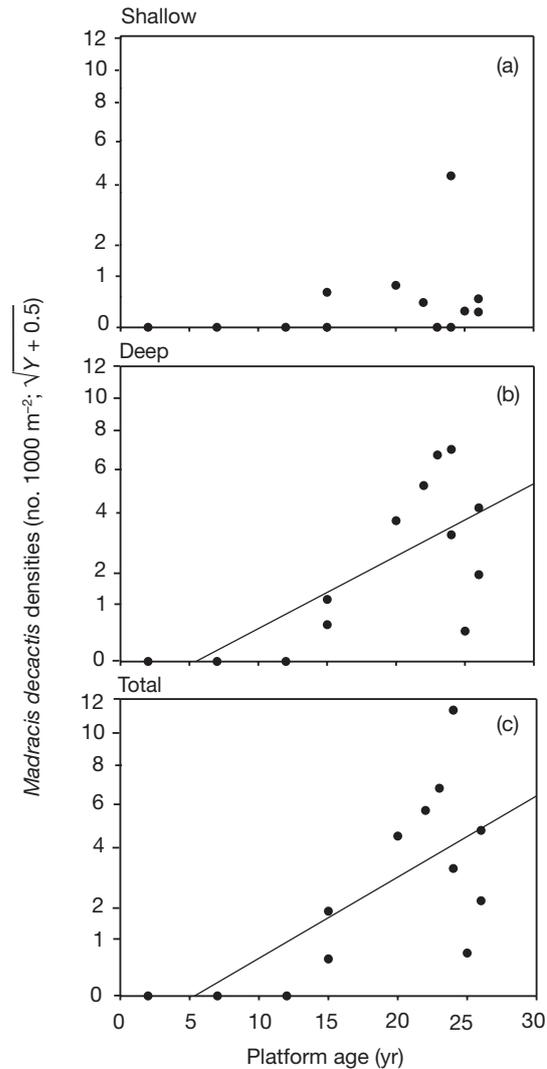

Fig. 4. *Madracis decactis*. Relationship between total abundance on platforms in (a) shallow water (0 to 14 m) (b) deeper water and (c) both combined versus platform age; further details as for Fig. 3. (a) No significant relationship found (p > 0.05, least-squares linear regression analysis; Pearson's product-moment correlation coefficient: r = 0.335, p > 0.05; Kendall's Rank correlation coefficient, t = 0.2910, p > 0.05). (b) Significant positive relationship (regression: $y = 0.069x + 0.332$, p = 0.01; correlation: r = 0.711, p < 0.01). (c) Significant positive relationship (regression: $y = 0.076x + 0.29$, p = 0.01; correlation: r = 0.693, p < 0.01)
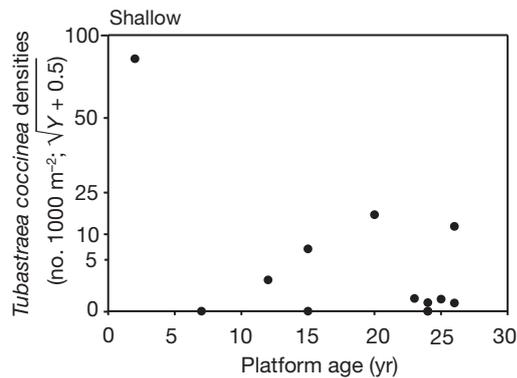
Fig. 5. *Tubastraea coccinea.* Relationship between total abundance in shallow water (0 to 14 m) on platforms versus platform age; further details as for Fig. 3. Significant relationship found (Pearson's product-moment correlation coefficient: r = −0.544, p = 0.05). No significant relationship was found in deep water or in both depths combined (p > 0.05, regression, correlation, and Kendall's rank correlation)

sis and non-parametric correlation analysis (Fig. 3a). This pattern of increasing abundance as a function of increasing platform age was also significant for corals in deeper water (>14 to 36 m), as indicated by both linear regression and correlation analyses (Fig. 3b). The pattern was as strong or stronger when data from both depths were combined (Fig. 3c). A clear relationship was a marked increase in coral abundance after ~12 to 15 yr; prior to this, coral growth visible to the naked eye was nominal or absent.

Madracis decactis, the most abundant coral found on the platforms, showed no significant relationship between abundance and platform age in shallow water (Fig. 4a). However, a clear positive relationship was found between these variables in deeper water (Fig. 4b), and for both sets of depths combined (Fig. 4c).

Diploria strigosa was also one of the most abundant species of corals found on the platforms. In this species, however, no significant relationship was found between abundance and platform age for shallow water, deeper depths, or for 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 *Tubastraea coccinea* in shallow water but, unlike *Madracis decactis*, this correlation was negative (correlation, r = −0.544, p = 0.05; Fig. 5). No similar significant relationship was found at deeper depths or for all depths combined (p > 0.05, linear regression analyses, correlation analysis, Kendall's rank correlation analysis).

Coral species diversity

A highly significant relationship was found between coral species diversity, measured simply by number of species (S), and platform age. This was pronounced in shallow water (Fig. 6a), even more so in deep water (Fig. 6b), and was highly significant when data from both sets of depths were combined (Fig. 6c).

A similar significant pattern was found for all corals when H' (species diversity; $H' = -\sum_{1}^{n} p_i \log p_i$, Shannon-Wiener index, Shannon & Weaver 1949, Pielou, 1969
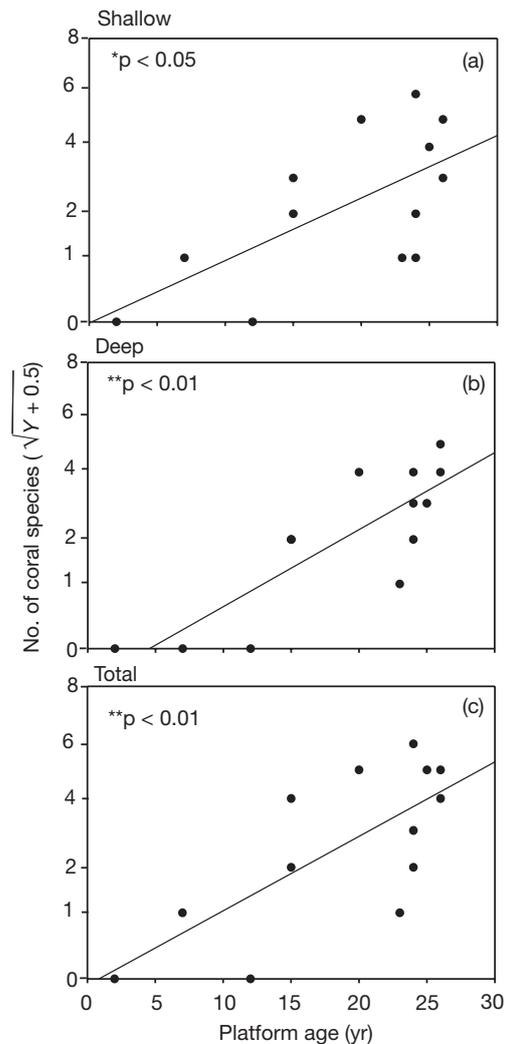

Fig. 6. Hermatypic corals. Relationship between coral species diversity, as number of species (S) in (a) shallow water and (b) deeper water on platforms studied versus platform age; further details as in Fig. 3. (a) Significant positive relationship (p < 0.01, least-squares linear regression analysis, $y = 047x - 0.519$; correlation: r = 0.590, p < 0.05). (b) Significant positive relationship (regression: p < 0.01, $y = 0.062x - 0.508$, p < 0.01; correlation: r = 0.822, p < 0.001). (c) Significant positive relationship (regression: $y = 0.064x - 0.569$, p < 0.01; correlation: r = 0.795, p < 0.01)
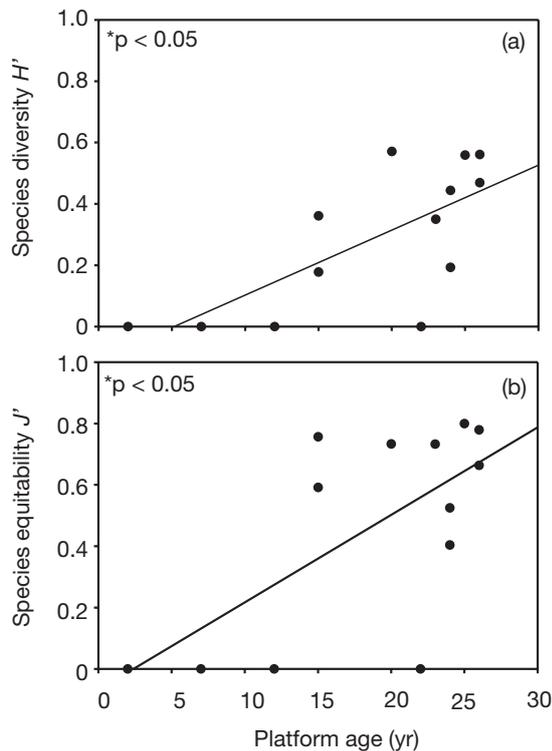
Fig. 7. Hermatypic corals. Relationship between (a) coral species H' and (b) equitability J' on platforms versus platform age. (a) Significant positive relationship found (least-squares linear regression analysis: $y = 0.021x - 0.109$, $p < 0.05$; correlation: $r = 0.707$, $p < 0.01$). (b) Significant positive relationship (regression: $y = 0.028x - 0.068$, $p < 0.05$; correlation: $r = 0.655$, $p < 0.05$)

1975; our Fig. 7a) and J' (species equitability; $J' = H'/\log S$; Fig. 7b) were used as species diversity measures.

Depth distribution

None of the corals considered here were distributed uniformly as a function of depth, regardless of substrate availability, even after standardization for available area (which varied greatly with depth through the differential presence of horizontal support structures). Total coral abundance exhibited a bimodal distribution, with peaks at depths of ~20 and 28 m, and with few corals at 0 to 6 m (Fig. 8a). The abundance of *Madracis decactis* peaked at the same depths (Fig. 8b). Unlike *M. decactis*, *Diploria strigosa* exhibited peaks in abundance at ~10 and 23 m (Fig. 9). *Tubastraea coccinea*, unlike either of the other 2 species, exhibited a single peak in abundance at 12 to 21 m depth (Fig. 10).

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 vs. 2). Total coral abundance showed no significant difference above vs. below 27 m depth. The same was true for *Madracis decactis*. No *Diploria strigosa* were found below 27 m depth on any of the platforms surveyed. *Tubastraea coccinea* occurred in much greater numbers at depths shallower than <27 m; the difference was highly significant.
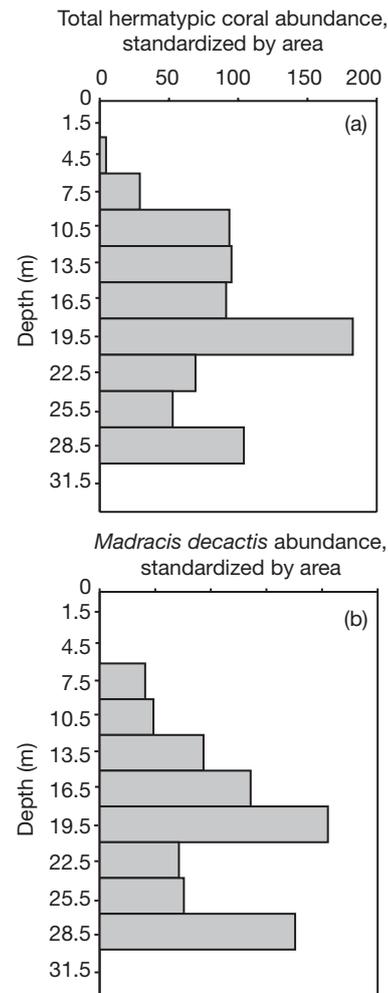

Fig. 8. Hermatypic corals. (a) Depth distribution of (a) all corals on platforms (0 to 36 m) and (b) *Madracis decactis.* (a) Significantly different from uniform distribution ($p < 0.01$, Kolmogorov-Smirnov frequency test); no significant difference in average total coral abundance above versus below 27 m depth ($p > 0.05$, Komolgorov-Smirnov frequency analysis). (b) Significantly different from uniform distribution ($p < 0.01$, Kolmogorov-Smirnov frequency test); no significant difference in average *M. decactis* abundance above versus below 27 m depth ($p > 0.05$, Komolgorov-Smirnov frequency analysis)
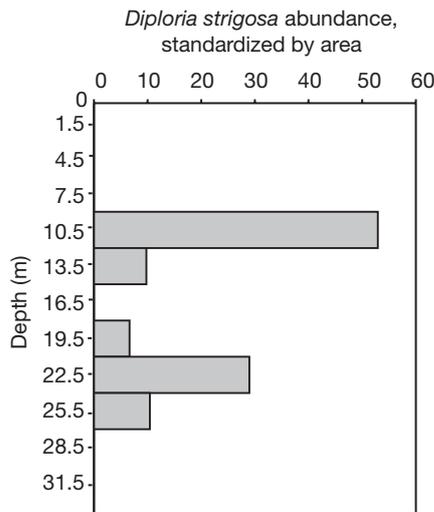
Fig. 9. *Diploria strigosa.* Depth distribution (0 to 36 m) on platforms. Significantly different from uniform distribution (p < 0.01, Kolmogorov-Smirnov frequency test)

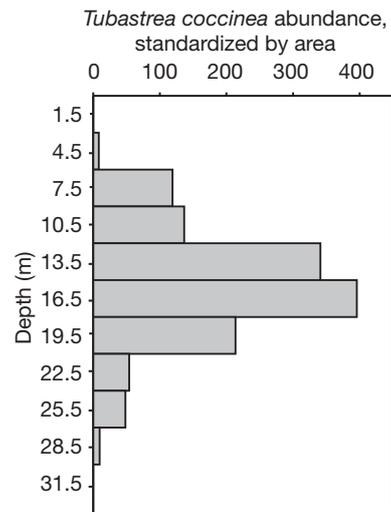

Fig. 10. *Tubastraea coccinea.* Depth distribution (0 to 36 m) on platforms. Significantly different from uniform distribution (p < 0.01, Kolmogorov-Smirnov frequency test). Significant difference in average abundance above versus below 27 m depth, with much higher numbers in shallower water (p < 0.001, Komolgorov-Smirnov frequency analysis)

Pattern-seeking analysis of adult coral communities

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 yr in age. The pattern-seeking analysis identified a major split in the similarity index between the communities at fusion values below 1.79 (Fig. 11). It placed the platforms into 2 age groups: (1) A large group of platforms with coral communities between 14 and 26 yr old (HI-A-382, HI-A-370, HI-A-330, HI-A-571, WC-630, HI-A-568, WC-618, HI-A-376, WC-643, HI-A-349), and (2) a second group that was smaller in number and consisted of platforms in the lower age range of 0 to 13 yr (HI-A-385, HI-A-368, and EC-317).

Coral colony size

A sufficient number of samples for colony size was available only for *Madracis decactis* (see 'Materials and methods'); for other species, data from older platforms (14 to 26 yr of age) were used. There were significant differences between mean colony size on the different platforms, although no particular pattern emerged (Table 3). In addition, a variety of *a posteriori* tests revealed no significant differences between plat-

forms. In addition, colony size did not vary significantly with platform age or distance from the FGB.

DISCUSSION

Of the 11 species found, 9 are commonly found on reefs of the Caribbean, Gulf of Mexico and Florida Keys (Wells 1973, Humann & DeLoach 2002). Most occur on the FGB (Bright et al. 1991, Gittings 1992).
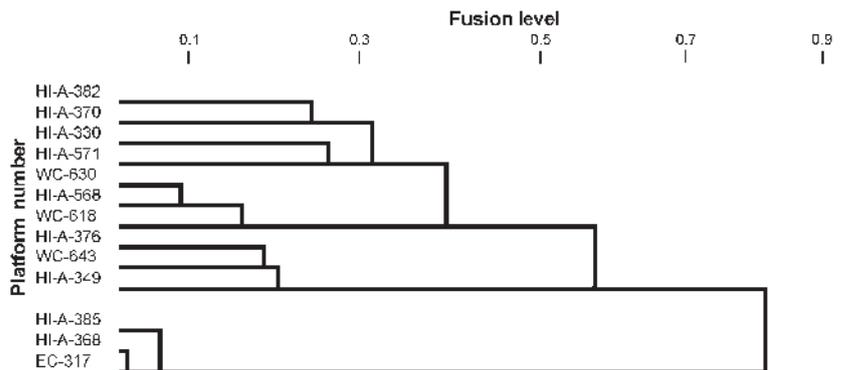

Fig. 11. Hermatypic corals. Results of pattern-seeking analysis (PATN), examining relatedness of coral community structure on individual platforms; data used were species abundance. We identified 2 major groups, one characteristic for older platforms, one for platforms generally ≤12 yr of age. See 'Results' for further details

Table 3. *Madracis decactis*. Colony size on oil and gas platforms in northern Gulf of Mexico near Flower Garden Banks. Colony size estimated as elliptical area (see 'Materials and methods'). Data are raw mean, mean of log *y*-transformed data, upper and lower confidence limits for transformed mean, standard deviation for transformed mean (s_t) and sample size (n). Platform age and distance of platform from FGB are also shown. There was a general significant difference between means (p < 0.01, 1-way ANOVA), which was not revealed as significant by *a posteriori* tests (p > 0.05; SS-STP, T', T-K, GT2, and Games & Howell tests). There was no significant relationship between colony size and platform age (p > 0.05, least-squares linear regression analysis), nor, between colony size and distance from FGB (p > 0.05, linear regression analysis)

Parameter	Platform no.					
	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	1813.8	2396.1	3146.8	3369.2	3770.1
$\bar{Y}_t$	2.72	3.19	3.13	3.40	3.16	3.45
95% CL						
Lower	2.18	2.07	2.61	3.21	2.52	3.16
Upper	3.25	4.31	3.66	3.59	3.80	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 (yr)	26	20	26	23	24	22
Distance from FGB (km)	48.7	2.0	14.1	15.0	8.0	24.5

The other 2 species (*Millepora alcicornis* and *P. astreoides*) are normally found in early stages of succession on Caribbean reefs (represented by recruits; Sammarco 1980, 1982). These 2 species are also characteristic of disturbed communities (Lirman & Fong 1996, Edmunds 1999, Aronson & Precht 2001). *Porites astreoides* was rare on the platforms. *Agaricia* spp., another common pioneer species (characteristic of early successional stages, Sammarco 1997, Smith & Smith 1999) was absent from the platforms. The low abundances or absence of these pioneer species indicated that the adult coral community on the platforms was more representative of later, more mature stages of succession, i.e. not that of a disturbed habitat (see McNaughton & Wolf 1979, Miller & Ricklefs 1999).

This phenomenon 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) the higher probability of success of later successional stages of corals during competition for space with associated epibiota on the platforms (Sammarco 1980, 1982, Coll et al. 1988, Alino et al. 1992); and/or (3) lack of abundant larval recruitment of early successional species (being primarily brooders, settlement of such species would be confounded by distance from the nearest source of such larvae, i.e. the FGB Sammarco & Andrews 1988, 1989, Harrison & Wallace 1990, Sammarco 1991, 1994). The reason is not yet known. Data from related experiments regarding coral recruitment and genetic affinities between the platforms, the FGB and the wider Gulf of Mexico and western Atlantic region have indicated that these regions are genetically distinct (Sammarco & Brazeau 2001, Atchison 2003, Brazeau et al. in press). Additional data are currently being processed and will be presented elsewhere (P. Sammarco et al. unpubl.). Preliminary data suggest that the FGB themselves experience abundant coral recruitment, most probably through self-seeding.

Tubastraea coccinea was present in abundance, as observed in earlier studies (e.g. J. Castello, S. Gittings et al. in: Fenner 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), reaching the Gulf of Mexico by the 1960s. Because of this and its high capacity to colonize natural and artificial substrata, its presence on the platforms was not surprising. This invasive species was not detected through surveys to be present on the FGB in 1984 (Bright et al. 1984), but has recently been sighted there in very low abundance (E. Hickerson pers. comm.). Although the presence of the platforms may have facilitated the spread of this invasive species, because of this species' innate high capacity for effective dispersal, it is unlikely that they are solely responsible for it, or that their absence would have prevented it. Since *T. coccinea* is not present on the FGB, it is clearly colonizing this region from elsewhere. *Acropora palmata* was also recently observed to colonize the FGB (E. Hickerson, pers. comm.) and its presence there is believed to be part of a natural range extension.

Of the 11 corals found, 5 were spawners, 4 were brooders (see Table 2), the mode of reproduction is not known for *Phyllangia americana*, and *Millepora alcicornis* is presumed to release medusae, like its congenerics (Soong & Cho 1998). The most abundant coral, *Madracis decactis*, was a brooder. The second

most abundant, *Diploria strigosa*, was a spawner. The *Montastraea*, also a mass spawner and abundant on the FGB), was also present on 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 these data, there does not appear to be any advantage for a species to use one mode of reproduction in preference to another. Both brooders and spawners are dispersed equally well in this region of the Gulf.

It was initially surprising to find that no significant relationship was found between coral abundance and distance from the FGB. One would expect that, because the FGB are the only 2 well-developed reefs in the northern Gulf of Mexico, a point-source distance effect might be evident, and platforms more remote from the FGB would possess more limited coral populations. This was not confirmed; however, variance in coral abundance was high, and no trends were present in the data distance from the FGB.

There are 4 possible explanations for this: (1) Our sample size (13 platforms) may not have been sufficient to reveal a significant effect. Increasing the number of platforms sampled might raise the 'power of the test' (Sokal & Rohlf 1981). This would involve not only sampling more platforms within the current study area, but also expanding the study area by ≥3 times the radius of the current area (≥150 to 200 km). (2) The distances from the FGB may be sufficient to allow coral larvae released there to become evenly diffused and mixed, so that recruitment to the various platforms is relatively even. Using preliminary data derived from the coral settlement portion of this study this hypothesis will be examined in greater detail elsewhere (P. Sammarco et al. unpubl.). (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, recent observations by Schmahl et al. (2003) confirmed coral development on some nearby deeper banks, including MacNeil Bank, which rise from 130 m to a minimum depth of 43 m. Larvae derived from this and other banks could be confounding any distance effect. Data currently being processed regarding the genetic affinity between coral populations of *Madracis decactis*, *Diploria strigosa*, and *Montastrea cavernosa* on the platforms versus those on the FGB (A. Atchison unpubl., Atchison et al. unpubl.) should help shed light on this question. (4) Platform age is significantly confounding any distance effect which may be present. Nonetheless, data collected thus far indicate that distance from the FGB is not associated with adult coral community structure on oil and gas platforms within a radius of ≤50 km.

Expanding surveys to a radius of ≥200 to 300 km might reveal a distance effect, based on probable larval survival time and diffusion effects (Bassim & Sammarco 2003). Such surveys would also define the geographic limits of waters suitable (temperature, salinity, turbidity, etc.) to support coral settlement and survival.

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 *Madracis decactis*, is also substantial on older platforms. The trends in coral community development with increasing age were supported by both the univariate and multivariate PATN. This is important, because platforms are removed from service shortly after production has ceased, whereas our data indicate that the environmental value of the platforms in service will increase with time. This age-value relationship may have implications for decisions regarding the decommissioning of such platforms.

The positive platform-age/coral-development association appears to be linear in nature, but a close examination of the data indicates that there is little development visible to the naked eye during the first 12 to 15 yr of a platform's life — also confirmed by PATN. After this time, community development is steady. There are 3 possible reasons for this. (1) *Madracis 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 yr or so, but those spat that settle on the platforms may not necessarily survive under early successional conditions. This would constitute a post-settlement control. (2) The early successional species of epibiota may simply provide the wrong cues for larval settlement, and the planulae thus respond to them with a negative preference for settlement. This would constitute a pre-settlement control. (3) The larvae of these species may simply not have encounterd the platforms until a later age in the life of the platform; we believe that this is unlikely, however, since so many species exhibit the same distributional pattern.

It is also possible that physical characteristics of the platforms may have affected coral recruitment during the first 12 to 15 yr 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 *Tubastraea coccinea*, however, were observed directly on the anodes.) When production wells are being drilled, the upper levels of the platforms (≤6 m) may have been exposed to drilling muds and produced waters/brines.

The fact that *Diploria strigosa* abundance showed no relationship with platform age indicated that it survives equally well as a pioneer or late successional species. Abundance of *Tubastraea coccinea* in shallow water significantly decreased with increasing platform age. This implies that, of all of the corals observed in this study, *T. coccinea* resembles a pioneer species more than any other. It is possible that, in the long term, its dominance in the community might decrease. Abundance of *Madracis decactis* did not show any relationship to platform age in shallow water, but was clearly positively associated with platform age at deeper depths and for 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 of easily outcompeting the associated sessile epibiota for space.

Coral diversity clearly increased with increasing platform age; this is known to occur in many communities, including coral reefs (Yu & Zou 1996, Miller & Barimo 1999), particularly during the early and intermediate stages of succession (Odum 1969, Mellinger & McNaughton 1975).

There was clearly differential settlement and/or survival of corals as a function of depth, as is known to occur in the Indo-Pacific (Sammarco 1994). Depth distributions observed in our study differed significantly; different species exhibited different depth-specific patterns of settlement and/or survival between 0 and 33 m. Our type of study facilitates the separation of depth effects. In normal studies of coral depth-distribution, transects are performed over wide areas of reef with varying bottom types in order to cover the entire depth range over a gently sloping forereef. In our study, 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, depth distributions are 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 to 14 m, 26 to 27 m, and below). Rezak et al. (1985) reported broad biotic zonation as a function of 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 and toppled' at a depth of ≥26 m to leave sufficient depth for navigation by larger vessels. The top portion may be deposited on the bottom or removed and brought ashore. Since a relatively larger proportion of *Madracis decactis* colonies occur below 27 m depth, it is well adapted for deeper reefs and would probably be retained on a 'toppled' platform. However, *Diploria strigosa*, another common Caribbean coral, had the highest proportion of its populations at ~10 m and no colonies below 27 m. Thus, most if not all colonies would be removed after 'toppling' of a platform. *Tubastraea coccinea*, with its near-normal depth distribution, exhibited a mode at ~16.5 m, differing from the other 2 species. It had significantly higher representation in waters <27 m depth, indicating that, again, abundance of this species would be reduced on 'toppled' platforms, particularly in the short-term. Deeper surveys are required to determine the maximum depth of these corals and the detailed character of their distributions.

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

The oil and gas platforms in the Gulf of Mexico that possess coral populations clearly appear to have a positive environmental value. The corals themselves, protected by federal and international law on natural reefs, have an intrinsic value, suggesting that the extent of coral colonization on a structure should be considered prior to decommissioning. In addition, the fact that platforms in offshore environments capable of maintaining coral growth support coral populations in areas where there were none prior to the mid-1900s implies that they may play some role in the broader ecology of coral community dynamics within the Gulf of Mexico as a whole.

LITERATURE CITED

Acosta A, Zea S (1997) Sexual reproduction of the reef coral *Montastrea cavernosa* (Scleractinia: Faviidae) in the Santa Marta area, Caribbean coast of Colombia. Mar Biol 128: 141–148

Adams CL (1996) Species composition, abundance and depth zonation of sponges (Phylum Porifera) on an outer continental shelf gas production platform, northwestern Gulf of Mexico. Final report and MSc thesis, Texas A&M University, Center for Coastal Studies, Corpus Christi, TX

Alino PM, Sammarco PW, Coll JC (1992) Competitive strategies in soft corals (Coelenterata, Octocorallia). IV. Induced reversals in competitive advantage. Mar Ecol Prog Ser 81: 129–145

Aronson RB, Precht WF (2001) White-band disease and the changing face of Caribbean coral reefs. Hydrobiol. 460: 25–38

Atchison AD (2003) Drilling platforms as stepping stones for expansion of coral communities: a molecular genetics approach. Abstract Graduate Student Symposium, University South Alabama, Dauphin Island Sea Laboratory, Dauphin Island, AL. Department of Biological Sciences, University of South Alabama

Ayre DJ, Ressing JM (1986) Sexual and asexual production of planulae in reef corals. Mar Biol 90:187–190

Bassim KM, Sammarco PW (2003) Effects of temperature and ammonium on larval development and survivorship in a scleractinian coral. Mar Biol 142:241–252

Bassim KM, Sammarco PW, Snell T (2002) Effects of temperature on fertilization success and embryogenesis in *Diploria strigosa* (Coelenterata, Scleractinia). Mar Biol 140: 479–488

Belbin L (1995) PATN: pattern analysis package. CSIRO, Sustainable Ecosystems, Canberra

Blum MD, Misner TJ, Collins ES, Scott DB (1998) Rapid sea level rise and highstand (+2 m) during the middle Holocene, central Texas coast. Abstr Geol Soc Am 30:7

Blum MD, Misner TJ, Collins ES, Scott DB, Morton RA, Aslan A (2001) Middle Holocene sea-level rise and highstand at 12 m, central Texas coast. J Sediment Res 71:4

Boland GS (2002) Fish and epifaunal community observations at an artificial reef near a natural coral reef: nineteen years at High Island platform A-389-A, from bare steel to coral habitat. Proceedings at Gulf of Mexico Fish and Fisheries: bringing together new and recent research. US Dept Interior, Minerals Management Service, New Orleans, LA, MMS 2002–004

Boland GS, Gallaway BJ, Baler JS, Lewbel GS (1983) Ecological effects on energy development on reef fish of the Flower Garden Banks. NOAA National Marine Fisheries, Galveston, TX (Contract No. NA80-GA-C-00057)

Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. Ecol Monogr 27: 325–349

Brazeau, DA, Sammarco, PW, Gleason, DF (in press) Multi-locus genetic differentiation of four western Atlantic coral populations and affinity of newly settled spat: technique and preliminary results. Mar Biol

Bright TJ, Draemer GP, Minnery GA, Viada ST (1984) Hermatypes of the Flower Garden Banks, Northwestern Gulf of Mexico: a comparison to other western Atlantic reefs. Bull Mar Sci 23:461–476

Bright TJ, Gittings SR, Zingula R (1991) Occurrence of Atlantic reef corals on offshore platforms in the northwestern Gulf of Mexico. Northeast Gulf Sci 12:55–60

Bright TJ, Gittings SR, Boland GS, Deslarzes KJP, Combs CL, Holland BS (1993) Mass spawning of reef corals at the Flower Garden Banks, NW Gulf of Mexico. Proc 7th Int Coral Reef Symp 1:500

Burr EJ (1970) Cluster sorting with mixed character types. II. Fusion strategies. Austral Comput J 2:98–103

Cairns SD (2000) Revision of the shallow-water azooxanthellate Scleractinia of the western Atlantic. Stud Nat Hist Caribb Reg 75:1–240

Childs J (1998) Nocturnal mooring and parking behavior of three monacanthids (filefishes) at an offshore production platform in the northwestern Gulf of Mexico. Gulf Mex Sci 16:228

Chornesky EA, Peters EC (1987) Sexual reproduction and colony growth in the scleractinian coral *Porites astreoides*. Biol Bull (Woods Hole) 17:161–177

Coll JC, Alino PM, Sammarco PW (1988) The importance of competitive interactions in the dominance of octocorals at Pandora Reef, North Queensland. Abstracts, 1988 Australian Mar Sci Assoc Jubilee Conf. Dept Biological Sciences, University of Sydney, Sydney, p 35

Curray JR (1965a) Late Quaternary history, continental shelves of the United States. In: Wright HE Jr, Frey DG (eds) The quaternary of the United States. Princeton University Press, Princeton, NJ, p 723–735

Curray JR (1965b) Sediments and history of Holocene transgression, continental shelf, northwest Gulf of Mexico: API Project 51. In: Proc AAPG, Tulsa, OK, p 221–266

Dauterive L (2000) Rigs to reefs policy, progress, and perspective. US Departement of the Interior, Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, LA, OCS Study MMS 2000–073

Driessen PK (1989) Offshore oil platforms: mini-ecosystems. In: Reggio VC Jr (ed) Petroleum structures as artificial reefs: a compendium. In: 4th International Conference on Artificial Habitats for Fisheries, Rigs-to-Reefs special session, Nov 1987, Miami, FL. OCS Study/MMS 89–0021, US Dept. Interior, Minerals Management Service, New Orleans, LA, p 3–6

Edmunds PJ (1999) The role of colony morphology and substratum inclination in the success of *Millepora alcicornis* on shallow reefs. Coral Reefs 18:133–146

Elton CS (1958) The ecology of invasions by animals and plants. Methuen & Co, London

Fenner D (2001) Biogeography of three Caribbean corals (Scleractinia) and the invasion of *Tubastraea coccinea* into the Gulf of Mexico. Bull Mar Sci 69:1175–1189

Francois DK (1993) Federal offshore statistics: 1992. Leasing, exploration, production, and revenues as of December 31, 1992. MMS 93-0066. US Department of the Interior, Minerals Management Service, Herndon, VA

Frost SH (1977) Oligocene reef coral biogeography Caribbean and western Tethys. In: Werger MJA (ed) Proc 2nd Int

Symp on Corals and Fossil Coral Reefs. Editions du B.R.G.M., B.R.G.M, Paris, p 342–352

Futuyma DJ (1998) Evolutionary biology, 3rd edn. Sinauer Associates, Sunderland, MA

Gallaway BJ, Lewbel GS (1981) The ecology of petroleum platforms in the northwestern Gulf of Mexico: a community profile, FWS 10BS-82/27, Open File Report 82–03. USFWS Office of Biology Services, Washington, DC

Gittings SR (1992) Long-term monitoring at the East and West Flower Garden Banks, Final Report. OCS Study MMS 92-0006. US Departement of the Interior, Minerals Management Service, Gulf of Mexico, OCS Regional Office, New Orleans, LA

Gittings SR (1998) Reef community stability on the Flower Garden Banks, Northwest Gulf of Mexico. Gulf Mex Sci 16:161–169

Gittings SR, Boland GS, Deslarzes KJP, Combs CL, Holland BS, Bright TJ (1992) Mass spawning and reproductive viability of reef corals at the East Flower Garden Bank, northwest Gulf of Mexico. Bull Mar Sci 51:420–428

Gittings SR, Inglehart WA, Rinn GS, Dokken QR (1994) Coral mass spawning on the Flower Garden Banks, NW Gulf of Mexico. Bull Mar Sci 54:1076

Gleason DF, Brazeau DA, Munfus D (2001) Can self-fertilizing coral species be used to enhance restoration of Caribbean reefs? Bull Mar Sci 69:933–943

Gross MG, Gross E (1995) Oceanography: a view of the earth, 7th edn. Prentice Hall, Englewood Cliffs, NJ

Hagman DK, Gittings SR, Vize PD (1998) Fertilization in broadcast-spawning corals of the Flower Garden Banks National Marine Sanctuary. Gulf Mex Sci 16:180–187

Hamilton P, Fargion GS, Biggs DC (1999) Loop current eddy paths in the western Gulf of Mexico. J Phys Oceanogr 29: 1180–1207

Harrison PL, Wallace CC (1990) Reproduction, dispersal, and recruitment of scleractinian corals. In: Dubinsky Z (ed) Ecosystems of the world, Vol 25. Coral Reefs. Elsevier Press, New York

Hebbinghaus R (2001) Larval development, hatching and care of the stony coral (*Tubastrea* cf. *coccinea*) in a closed system. Bull Inst Oceanogr Monaco 20:355–358

Hughes TP, Baird AH, Bellwood DR, Card M and 13 others (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301:929–933

Humann P, DeLoach N (2002) Reef coral identification: Florida, Caribbean, Bahamas. New World Publisher, Jacksonville, FL

Knott D (1995) US lessons for UK platform disposal. Oil Gas J 93:17–18

Jarrett BD, Hine AC, Neumann AC, Narr D, Locker S, Malinson D, Jaap W (2000) Deep biostromes at Pulley Ridge: Southwest Florida carbonate platform. In: Hallock P, French L (eds) Diving for science in the 21st century. American Academy of Underwater Science, Nahant, MA, p 14

Lirman D, Fong P (1996) Sequential storms cause zone-specific damage on a reef in the northern Florida Reef Tract: evidence from Hurricane Andrew and the 1993 storm of the century. Fla Sci 59:50–64

Love MS, Caselle JE, Snook L (2000) Fish assemblages around seven oil platforms in the Santa Barbara Channel area. Fish Bull Fish Wildl Serv US 98:96–117

Lugo-Fernandez A (1998) Ecological implications of hydrography and circulation to the Flower Garden Banks, Northwestern Gulf of Mexico. Gulf Mex Sci 2:144–160

Lugo-Fernandez A, Deslarzes DJP, Price JM, Boland GS, Morin MV (2001) Inferring probable dispersal of Flower Garden Banks coral larvae (Gulf of Mexico) using observed and simulated drifter trajectories. Contin Shelf Res 21:47–67

McClanahan T, Hoegh-Guldberg O, Buddemeier RW, Sammarco PW (in press) Trajectory and predictions for coral reefs. In: Polunin N (ed) Proc 5th Int Conference on the Environment Future (ICEF). EAWAG, Zurich. Cambridge University Press, Cambridge

McGuire M (1995) Aspects of reproduction, larval characteristics and juvenile growth in the coral *Porites astreoides*. Twenty-Third Benthic Ecology Meeting, New Brunswick, NJ. In: Grassle JP, Kelsey, Oates E, Snelgrove P (eds) Institute of Marine Coastal Sciences, Rutgers–the State University, New Brunswick, NJ

McGuire MP (1998) Timing of larval release by *Porites astreoides* in the northern Florida Keys. Coral Reefs 17: 369–375

McNaughton SJ, Wolf LL (1979) Community dynamics: succession, Chap 20. General ecology, 2nd edn. Holt, Rinehart & Winston, New York, p 410–449

Mellinger MV, McNaughton SJ (1975) Structure and function of successional vascular plant communities in central New York. Ecol Monogr 45:161–182

Meyers SD, Siegel EM, Weisberg RH (2001) Observations of currents on the West Florida shelf break. Geophys Res Lett 28:2037–2040

Miller GL, Ricklefs RE (1999) Ecology. WH Freeman & Co, San Francisco

Miller MW, Barimo J (1999) Assessment of juvenile coral populations at two reef restoration sites in the Florida Keys National Marine Sanctuary: indicators of success? Bull Mar Sci 69:395–405

Odum EP (1969) The strategy of ecosystem development. Science 164:262–270

Pattengill CV, Semmens BX, Gittings SR (1997) Reef fish trophic structure of the Flower Gardens and Stetson Bank, NW Gulf of Mexico. Proc 8th Int Coral Reef Symp 1: 1023–1028

Pielou EC (1969) An introduction to mathematical ecology, Wiley-Interscience, New York

Pielou EC (1975) Ecological diversity. Wiley-Interscience, New York

Rezak R, Bright TJ, McGrail DW (1985) Reefs and banks of the Northwestern Gulf of Mexico. John Wiley & Sons, New York

Rooker JR, Holt GJ, Pattengill CV, Dokken Q (1997) Fish assemblages on artificial and natural reefs in the Flower Garden Banks National Marine Sanctuary, USA. Coral Reefs 16:83–92

Salas-de-Leon DA, Monreal-Gomez MA, Sanvicente-Anorve L, Flores-Coto C (1998) Long-term influence of currents on zooplanktonic organisms distribution in the Bay of Campeche, Mexico. Oceanol Acta 21:87–93

Sammarco PW (1980) *Diadema* and its relationship to coral spat mortality: grazing, competition, and biological disturbance. J Exp Mar Biol Ecol 45:245–272

Sammarco PW (1982) Echinoid grazing as a structuring force in coral communities: whole reef manipulations. J Exp Mar Biol Ecol 61:31–55

Sammarco PW (1987) A comparison of ecological processes on coral reefs of the Caribbean and the Great Barrier Reef. UNESCO Rep Mar Sci 46:127–166

Sammarco PW (1991) Geographically specific recruitment and post-settlement mortality as influences on coral community structure: the cross-shelf transplant experiment. Limnol Oceanogr 36:496–514

Sammarco PW (1994) Larval dispersal and recruitment pro-

cesses in Great Barrier Reef corals: analysis and synthesis. In: Sammarco PW, Heron ML (eds) The bio-physics of marine larval dispersal. American Geophysical Union, Washington, DC, p 35–72

Sammarco P W (1996) Comments on coral reef regeneration, bioerosion, biogeography, and chemical ecology: future directions. J Exp Mar Biol Ecol 200:135–168

Sammarco PW, Andrews JC (1988) Localized dispersal and recruitment in Great Barrier Reef corals: the helix experiment. Science 239:1422–1424

Sammarco PW, Andrews JC (1989) The helix experiment: differential local recruitment patterns in Great Barrier Reef corals. Limnol Oceanogr 34:898–914

Sammarco PW, Atchison A (2003) Coral communities and recruitment on offshore drilling platforms in the northern Gulf of Mexico: summary. US Department of the Interior, Minerals Management Service Information Transfer Meeting, Kenner, LA. Minerals Management Service, New Orleans, LA, p 6–7

Sammarco, PW, Brazeau DA (2001) Genetic affinity between corals, including spat, at three tropical W Atlantic sites: Where do the larvae go? Proc 30th Sci Meet Assoc Mar Lab Caribb (AMLC), La Parguera, Puerto Rico. Dept Marine Science, University of Puerto Rico, Mayagüez, p 31

Sammarco PW, Heron ML (eds) (1994) The bio-physics of marine larval dispersal. American Geophysical Union, Washington, DC, p 352

Sammarco PW, Atchison A, Boland GL (2002) Drilling platforms as environmental assets: developing an assessment protocol using adult and juvenile corals. US Dept Interior, Minerals Management Service Information Transfer Meeting, Kenner, LA. Minerals Management Service, New Orleans, LA, p 183–200

Schmahl GP, Hickerson EL, Weaver DC (2003) Biodiversity associated with topographic features in the northwestern Gulf of Mexico. Proc US Dept Interior, Minerals Management Service Information Transfer Meeting, Gulf of Mexico OCS Region, Kenner, LA, Minerals Management Service, New Orleans, LA, p 84–88

Schroeder DM, Ammann AJ, Harding JA, MacDonald LA, Golden WT (2000) Relative habitat value of oil and gas production platforms and natural reefs to shallow water fish assemblages in the Santa Maria Basin and Santa Barbara Channel, California. In: Browne DR, Mitchell KL, Chaney HW (eds) Proc 5th California Islands Symp, US Departement of the Interior, Minerals Management Service, Pacific OCS Region, Camarillo, CA, p 493–498

Schroeder WW, Shultz AW, Pilkey OH (1995) Late Quaternary oyster shells and sea-level history, inner shelf, northeast Gulf of Mexico. J Coast Res 11:664–674

Shannon CE, Weaver W (1949) The mathematical theory of communication. University of Illinois Press, Urbana, IL

Shinn EA (1973) Pipes, plankton, and pompano. Shell News 17(1-463-6-73) 6–7

Shinn EA (1974) Oil structures as artificial reefs. In: Colunga L, Stone R (eds) Proceedings of Artifical Reef Conference(TAMU-56-74-103). Texas A & M University, Bryan, TX, p 91–96

Shinn EA, Wicklund RI (1989) Artificial reef observations from a manned submersible off Southeast Florida. Bull Mar Sci 44:1041–1050

Smith R L, Smith T M (1999) Ecology and field biology. Addison-Wesley, Reading, MA

Snell T, Foltz DW, Sammarco PW (1998) Variation in morphology vs conservation of a mitochondrial gene in *Montastrea cavernosa* (Cnidaria, Scleractinia). Gulf Mex Sci 16:188–195

Sokal RR, Rohlf FJ (1981) Biometry. The principles and practice of statics in biological research, 2nd edn. WH Freeman & Co, New York

Sonnier F, Teerling J, Hoese HD (1976) Observations on the offshore reef and platform fish fauna of Louisiana. Copeia 1:105–111

Soong K (1993) Colony size as a species character in massive reef corals. Coral Reefs 12:77–83

Soong K, Cho LC (1998) Synchronized release of medusae from three species of hydrozoan fire corals. Coral Reefs 17: 145–154

Souter DW, Linden O (2000) The health and future of coral reef ecosystems. Ocean Coast Manag 43:657–688

Steiner SCC (1995) Spawning in scleractinian corals from SW Puerto Rico (West Indies). Bull Mar Sci 56:899–902

Sturges W, Blama JP (1976) A western boundary current in the Gulf of Mexico. Science 92:367–369

Szmant AM (1991) Sexual reproduction by the Caribbean reef corals *Montastrea annularis* and *M. cavernosa.* Mar Ecol Prog Ser 74:13–25

Vermeij MJA, Sampayo E, Broeker K, Bak RPM (2003) Variation in planulae release of closely related coral species. Mar Ecol Prog Ser 247:75–84

Vidal Lorandi FV, Vidal Lorandi VMV, Rodriguez Espinoza PF, Sambrano Salgado L, Portilla Casilla J, Rendon Villalobos JR, de la Cruz BJ (1999) Gulf of Mexico circulation. Rev Soc Mex Hist Nat 49:1–15

Ward JH (1963) Hierarchical grouping to optimize an objective function. J Am Stat Assoc 58:236–244

Wells JW (1973) New and old scleractinian corals from Jamaica. Coral Reef Project — papers in memory of Dr. Thomas F. Goreau. Bull Mar Sci 23:16–58

Winfield T (1973) A fish story you can believe. In: Man-made oasis for fish, Shell News (Reprint) 17:1-463-6-73, 2–5

Wyers SC, Barnes HS, Smith SR (1991) Spawning of hermatypic corals in Bermuda: a pilot study. Hydrobiologia 216–217:109–116

Yu D, Zou R (1996) Current situation and dynamics of species diversity in hermatypic coral community on Luhuitou fringing reef. Acta Ecol Sin 6:559–564