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P.W. Sammarco

Louisiana Universities Marine Consortium

A.D. Atchison

Louisiana Universities Marine Consortium

G.S. Boland

Bureau of Ocean Energy Management

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Coral Settlement on Oil/Gas Platforms in the Northern Gulf of Mexico: Preliminary Evidence of Rarity

P. W. SAMMARCO, A. D. ATCHISON, AND G. S. BOLAND

In recent decades, there have been two areas of shallow hard substrate available for zooxanthellate coral colonization in the North Gulf of Mexico: the Flower Garden Banks (FGB) and oil and gas platforms. We assessed coral recruitment on platforms possessing adult corals around the FGB. In this preliminary experiment, we used terra cotta plates mounted on racks, deployed on six platforms at depths of 15–27 m for a duration of ≤ 1 yr in two consecutive years. Data on coral spat taxonomic identification, distribution, and densities were collected. Platform spat densities on plates averaged $< 1/450$ cm², a low value when compared with the East-FGB (E-FGB; data from earlier similar experiment), other Caribbean sites, or the Great Barrier Reef. Spat density was not significantly different between platforms, suggesting that distance between the platforms and the E-FGB, a potential larval source, was large enough (> 0.6 – 1.2 km) to permit extensive larval diffusion. Total spat density also did not vary significantly between settlement racks, indicating that settlement at the spatial scale of meters was relatively homogeneous. Only three species of spat were found—*Tubastraea coccinea*, *Madracis decactis*, and *Montastraea* sp.; the taxonomic composition of coral spat varied from those observed earlier on the E-FGB—*Agaricia* and *Porites*. The dominant recruits matched the dominant adults on the platforms—an unusual situation. *Tubastraea* and *Madracis* spat densities, respectively, did not vary significantly between platforms or between racks. Because of low recruitment levels, these artificial reef communities may be considered fragile in comparison to many natural ones because of the time required for recovery in the event of a mass coral mortality. These low recruitment levels, however, when integrated over ~ 30 yr, can result in the successful establishment of adult coral communities on the platforms.

INTRODUCTION

Coral reefs of the Flower Garden Banks (FGB) in the northern Gulf of Mexico (GOM) 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), being separated by hundreds to thousands of kilometers from neighboring coral reefs (Rezak et al., 1985; Sammarco et al., 2004). Corals are sessile, epibenthic organisms, and colonization of habitats such as the FGB is achieved via larval dispersal. Coral larvae can potentially travel such distances to successfully settle on remote reefs (Richmond, 1981, 1987; Graham et al., 2008; van Oppen et al., 2008). The FGB represent a healthy coral community, based on observations of a well-developed adult coral community (Gittings, 1992), mass coral spawning (Bright et al., 1992; Gittings et al., 1992), and the high recruitment levels observed there (Brazeau et al., 2011). Gittings (1992) suggested that the reefs were self-sustaining, primarily as a result of self-seeding of coral larvae within the Bank system.

The FGB are not the only hard bottom available in shallow water in the northern GOM. This area is also home to $\sim 3,000$ oil and gas production platforms (Pulsipher et al., 2001), located primarily in the coastal shelf waters of Louisiana and Texas (see Franco, 1993, for overview). The bottom there is characterized almost entirely by soft sediment (Rezak et al., 1985). Prior to the deployment of production platforms, hard substratum was limited to scattered banks and shoals, often in deep water (Rezak et al., 1985), as were the organisms requiring this type of habitat. These platforms provided thousands of artificial islands that have introduced suitable substratum in shallow water for zooxanthellate coral settlement over a large geographic area, where little had existed until the 1940s.

The FGB and the surrounding platforms represent sites for coral populations, which are dependent on gene flow between them for population growth. It is known that gene flow is one of the most important processes determining the genetic structure and diversity of populations in general (Mayr, 1970). Our understanding of the factors affecting the genetic

diversity of scleractinian coral populations in particular, however, is limited. Since coral adults are sessile, dispersal of coral planulae is largely responsible for gene flow among populations. Thus, defining the sources and sinks of their larvae is critical to understanding factors influencing coral genetic diversity, stability, and the role that individual reefs or structures play in maintaining that diversity.

Coral larvae are produced via 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 (broadcasters) have larvae that spend more time in the plankton and have the potential for wider dispersal and a lower self-seeding capacity (Sammarco and Andrews, 1989; Sammarco, 1994). Some evidence exists that corals that brood their larvae may have a greater tendency to self-seed their own (natal) reefs or structures of origin (Szmant-Froelich, 1984; Szmant, 1986; Sammarco and Andrews, 1988, 1989; Grosberg, 1991).

A high degree of self-seeding is not necessarily a sign of long-term ecosystem stability. Self-seeding in an isolated system carries with it risk (Sammarco, 1996; Gold et al., 2001; Palumbi, 2003; Faunce, 2005; Froukh and Kochzius, 2007). For example, in the late 1970s and early 1980s, reefs of the Pacific coast of Panama suffered mass coral mortality due to coral bleaching caused by El Niño and associated high seawater temperatures (Glynn, 1983). Two hydrocoral species were driven locally extinct (Glynn and de Weerd, 1991). Isolation by distance and associated low recruitment levels can place a site at 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 remote, may require long periods of time (MacArthur and Wilson, 1967). Generally, the more remote a site is, the longer the time required for recovery. 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). The length of time required for population regeneration is 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).

The question of self-seeding vs external seeding for coral populations is a question that has received a considerable amount of attention. In

the case of the FGB, it appears that they are seeding platforms up to hundreds of kilometers away (Atchison, 2005; Atchison et al., 2008; Sammarco et al., 2012b). If recruitment is occurring on 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, 1998; Lugo-Fernandez et al., 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; G. Boland, pers. obs., pers. comm.; K. Deslarzes, pers. comm.). Before any of these questions can be addressed, basic data need to be collected regarding coral recruitment on oil/gas platforms surrounding the FGB.

Initial evidence suggests that there is little coral recruitment on platforms near the FGB. Baggett and Bright (1985) examined coral recruitment on the East-FGB (E-FGB) and the nearby platform HI-A-389 and 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. More recent data demonstrate, however, that there is substantial adult coral community development on platforms in that region (Sammarco et al., 2004). When recruitment does occur on the platforms, it is not known what species settle there and how they compare to the adult coral community already present. In fact, little is known about coral recruitment in the GOM. The questions raised in this study are 1) What are the densities of coral recruitment on oil/gas platforms surrounding the FGB, within a maximum radius of 45 km?; 2) What is the species distribution and density of those recruits?; 3) Does recruitment vary significantly between platforms?; 4) Does recruitment vary significantly at a spatial scale of meters to tens of meters between replicate settlement racks within platforms?; 5) Do coral recruit densities vary significantly at a spatial scale of centimeters to tens of centimeters between plates?; and 6) Are recruitment rates similar to other known rates on the E-FGB or in the Caribbean?

MATERIALS AND METHODS

Original experimental design.—The original experimental design to assess coral settlement on the platforms followed a two-way, mixed-model, nested analysis of variance (ANOVA) design. The first factor (random) was the study platforms, of which

there were originally 13. The second factor (fixed) was year—annual deployments and retrievals for two consecutive years. One year would allow sufficient time for growth of spat into a size suitable for visual recognition and identification via a dissecting microscope in the laboratory. Settlement racks were deployed in 2001 and 2002 and retrieved in 2002 and 2003 by teams of SCUBA divers. The third factor (random) was settlement racks, to be deployed on each platform at 15–27-m depth depending upon availability of horizontal support struts. The purpose of this level was to obtain information for distributional effects at the spatial scale of meters to tens of meters. The fourth factor was replicate settlement plates, nested within each rack. Five plates were used on each rack. These replicates were designed to provide an estimate of within-site, intrarack variability in coral settlement at the spatial scale of centimeters to tens of centimeters. The plates may be considered independent settlement sites because coral planulae are classified as “coarse-grained” organisms, according to the criteria laid out by Levins (1968). That is, they perceive their environment only within a radius of several millimeters from their perimeter and are not aware of the presence or absence of nearby settlement plates when making settlement choices.

Settlement plates were ceramic terra cotta tiles (Versatile®, Canton, OH; unglazed, vitreous, partially glass, ceramic quarry tiles). 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, polyvinyl chloride, concrete, and coral/limestone blocks. Each tile measured 15.2×15.2 cm. The total area of a tile, including top, bottom, and sides, was 494.4 cm^2 . Coral spat densities on these plates have been standardized to “No./ 450 cm^2 .”

Tiles were center-drilled; mounted on stainless-steel, all-thread rods; and secured with plastic and steel lock-washers and nuts (see Sammarco and Andrews, 1988, 1989; Sammarco, 1991). The all-thread was mounted on a galvanized steel rack. The rugose sides of the tiles were oriented downward to provide planulae with their preferred surface irregularity and positioned at an angle of $37\text{--}45^\circ$ from the horizontal (Carleton and Sammarco, 1987; also see Bak and Engel, 1979; Oakley, 1988; Mundy, 2000). Racks were preassembled in the laboratory. Upon retrieval, plates were placed in Ziploc® freezer bags filled partially with high salt buffer

to preserve the coral tissue. The bags were then stored in small ice chests, frozen at -20°C on shipboard, and stored in the laboratory at this temperature for subsequent processing.

Plates 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; 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 local and FGB adult coral populations. Because of the limited number of racks involved in the experiment, no attempt was made to differentiate temporal or depth effects. In cases in which we were only able to retrieve one rack, it was not possible to calculate within-platform, between-rack variability.

In some cases, inclement weather conditions made it difficult to retrieve racks, or the oil companies could not allow access to the platform for rack retrieval. This caused some of the exposure durations of plates and times of deployment and retrieval to vary. It is understood that recruitment of sessile epibenthic organisms can be patchy in space and time and that the issues encountered here could represent confounding effects; however, the low levels of coral recruitment encountered over the 2-yr block of time for this study suggest that these effects were likely negligible in this case.

More plates per rack would have been preferred, of course, as has been used in other coral recruitment studies, in which this number ranged from 15 (Green and Edmunds, 2011) to 64 (Carlon, 2001) plates per site (also see Fisk and Harriot, 1990; Banks and Harriott, 1996; Gleason, 1996; Harriott and Simpson, 1997; Dunstan and Johnson, 1998; Hughes et al., 1999; Adjeroud et al., 2007). The logistic and safety constraints of moving these heavy settlement units under water against currents, in unfavorable sea conditions; of handling and mounting them onto the oil platform in a difficult working environment; and of the time required for processing once retrieved, however, prevented the use of more plates per rack. We believe that our replication was sufficient, as similar levels of replication have been used successfully in previous studies (Sammarco, 1980, 1991; Brazeau et al., 2011).

TABLE 1. Oil and gas platforms and coral settlement rack deployment information.^a

| Depth (m) | Platform reference no. | Platform code | Deployment | Retrieval | Months of exposure | No. of racks | Distance to FGB (km) | Platform age (yr) | Total no. of racks | Latitude | Longitude |
|----------------|------------------------|---------------|------------|-----------|--------------------|--------------|----------------------|-------------------|--------------------|-----------|-----------|
| 15–21 (year 1) | 6 | HI-A-571-A | | | | | 15.0 | 23 | 1 | 27.570000 | 94.010002 |
| | 5 | HI-A-382 | May 2001 | May 2002 | 12 | 2 | 16.4 | 15 | 3 | 27.540001 | 93.550003 |
| | 1 | HI-A-330A | May 2001 | May 2002 | 12 | 2 | 14.1 | 26 | 2 | 28.070000 | 93.300003 |
| | 3 | HI-A-368-B | May 2001 | May 2002 | 12 | 2 | 2.0 | 5, 2 | 3 | 27.583020 | 93.310690 |
| | 2 | HI-A-349-B | May 2001 | May 2002 | 12 | 2 | 12.9 | 24 | 2 | 28.040001 | 93.285004 |
| | 4 | HI-A-376-A | Oct. 2001 | May 2002 | 7 | 2 | 2.0 | 20 | 2 | 27.559999 | 93.400002 |
| 21–27 (year 2) | 6 | HI-A-571-A | May 2002 | May 2003 | 12 | 1 | | | | | |
| | 5 | HI-A-382 | May 2002 | May 2003 | 12 | 1 | | | | | |
| | 3 | HI-A-368-B | May 2002 | May 2003 | 12 | 1 | | | | | |

^a List of oil and gas platforms in the northern Gulf of Mexico upon which coral settlement racks were deployed, spanning 2001–2003. Dates of deployment and retrieval are shown, along with the number of months during which plates were exposed, distance between the study platform and the FGB, age of platform, and number of racks per platform. In all cases, the number of plates per rack was five. Definition of platform name: e.g., HI-A-571-A, HI-A = High Island (A) petroleum extraction sector, a large area south of Lake Sabine, TX. 571 = Specific block within that sector leased to an oil or gas company. A = first platform deployed in that lease block. FGB, Flower Garden Banks.

We used the M/V *Fling* (Freeport, TX) to access the study sites and as a base for offshore dive operations. Racks and tools were transported to the platform using a buoyancy device and were hung beneath the horizontal support struts of the platform. 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.

Technical considerations and amended design.—Several factors caused the loss of some replicate settlement racks. Poor weather conditions frequently caused the cancellation or premature abortion of cruises. We also encountered technical problems with the deployment and retrieval of racks. These factors resulted in the alteration of dates of deployment and retrieval and a reduction in the number of racks retrieved per platform, particularly at deeper stations. In addition, during processing, we noticed a paucity of spat on the settlement plates, requiring large amounts of time for processing. For these reasons, the number of racks and plates processed was decreased. As a result of the limited number of racks and plates, data from the 2 yr of the study were pooled, making the experimental design a one-way, unbalanced, nested ANOVA. No attempt was made to assess annual recruitment effects; we considered the 2-yr experimental period as a single block of time. Thus, this study should be considered preliminary. 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 (see Table 1 for details regarding all study platforms).

Statistical analyses.—Univariate parametric statistical analyses were performed on the data (Sokal and Rohlf, 1981) using BIOMStat V3.2 and V3.3 (Rohlf and Slice, 1996), particularly a one-way nested ANOVA. Data were compared between platforms, racks, and plates. Data were transformed by square root ($Y + 0.5$) where necessary for normalization purposes and to correct for zero data.

RESULTS

Overall coral settlement on the plates was rare. Average spat densities on the platforms varied between 0 and <1 per 450 cm² (Fig. 1). Total coral spat density was not significantly different between platforms or between racks (Fig. 2; $P > 0.05$, one-way nested ANOVA).

The two most abundant adult scleractinian species on platforms were *Tubastraea coccinea* and *Madracis decactis*. These species were also

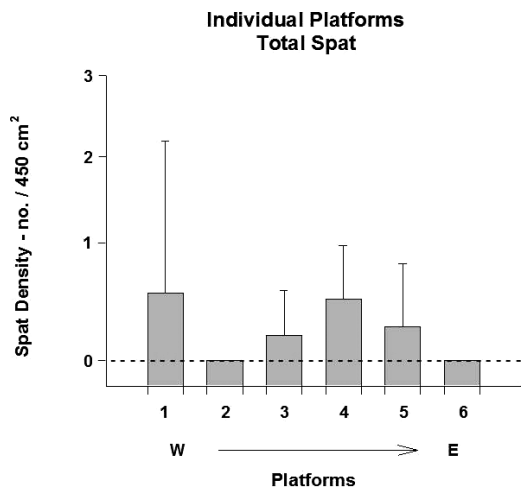


Fig. 1. Average density of coral spat in “No. per 450 cm²” on six oil/gas platforms in the northern Gulf of Mexico in the vicinity of the NOAA Flower Garden Banks National Marine Sanctuary, by platform. The platforms, listed west to east, are HI-A-330, HI-A-349B, HI-A-368B, HI-A-376A, HI-A-571A, and 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 15–27 m for 1 yr during 2001–02 or 2002–03. Data combined for depths and times (see text for discussion). Mean and 95% confidence limits shown. Y 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).

common coral spat found on settling plates on the platforms, although their densities were quite low. *Tubastraea coccinea* was the most abundant spat, and *Madracis* was second in number (Fig. 3). Only one newly settled spat of *Montastraea* sp. was found on the plates. With respect to reproductive modes (see Fadlallah, 1983; Harrison and Wallace, 1990; Richmond and Hunter, 1990; Moulding, 2009 for reviews), *Tubastraea* and *Madracis* are brooders, and *Montastraea* is a broadcast spawner.

With respect to *T. coccinea*, there was no significant difference in density of coral settlement between platforms ($P > 0.05$, nested ANOVA; Fig. 4). There was also no significant difference between racks with respect to *T. coccinea* spat densities ($P > 0.05$; Fig. 5). There was no difference in density of *Montastraea* sp. between platforms and racks.

Other taxonomic groups colonizing the plates were typical of early successional stages for artificial substratum—hydroids, filamentous algae, bryozoans, telestacean corals, etc. The only organism that was in some cases a formidable competitor for space was *Didemnum perlucidum*,

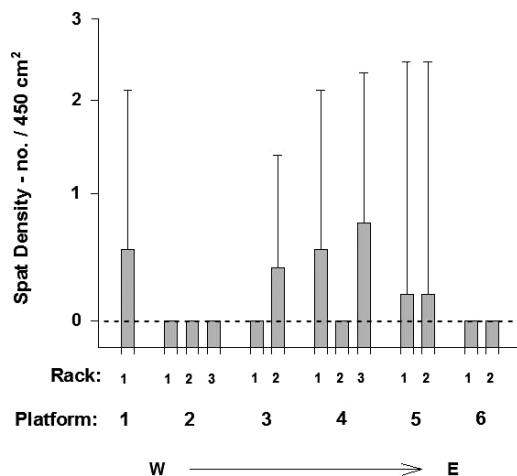


Fig. 2. Average density of coral spat in “No. per 450 cm²” on six oil/gas platforms in the northern Gulf of Mexico in the vicinity of the Flower Garden Banks. Data shown for individual settlement racks within platforms. The platforms, listed east to west, are HI-A-330, HI-A-349B, HI-A-368B, HI-A-376A, HI-A-571A, and HI-A-382, labeled 1–6, respectively. Data derived from coral settlement on terra cotta plates mounted on steel racks and deployed at depths of 15–27 m for 1 yr during 2001–02 or 2002–03. Data combined for depths and years (see text for discussion). Mean and 95% confidence limits shown. Y 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).

an invasive colonial ascidean from the Indo-Pacific that had the capability to overgrow settlement plates and their supporting racks entirely within 1 yr. This species is known to have colonized offshore platforms in the northern GOM, in some cases covering large areas of the structure (Lambert, 2001, 2002; Culbertson and Harper, 2002; Locke and Hanson, 2011). During plate processing, when this species occurred on the plates, the colonies were peeled back and removed to determine whether any coral spat had been overgrown by it.

DISCUSSION

The density of coral settlement observed on plates deployed on these study platforms, when compared to that observed in the E-FGB and elsewhere in the Caribbean, was unusually low (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, 2011; Vermeij and Sandin, 2008; but

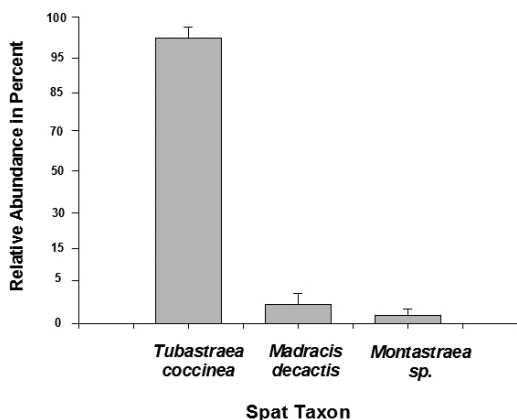


Fig. 3. Relative abundances for all spat of different coral genera found on six oil/gas platforms in the northern Gulf of Mexico in the vicinity of the Flower Garden Banks. Data derived from coral settlement on terra cotta plates mounted on steel racks and deployed at depths of 15–27 m for 1 yr during 2001–02 or 2002–03. Data combined for platforms, racks, depths, and plates. Proportion and 95% confidence limits shown. Y data transformed by arcsine for normalization purposes.

see Quinn and Kojis, 2005). Average densities on the platforms were $<1.0/450 \text{ cm}^2$. By comparison, on the E-FGB average total spat density was ~ 6 per 450 cm^2 , which is similar to reports from elsewhere in the Caribbean. Interannual differences may, of course, be expected, but an order of magnitude difference in settlement rates was not expected.

The structure of the platforms may have affected settlement. They are not solid in form, but rather reticulate, allowing a flow-through of seawater. They do not present a single, solid obstruction to far-field flow. Eddies formed by such currents would be at the microscale, rather than the mesoscale, 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, 1991; Black and Moran, 1991; Gay and Andrews, 1994; Sammarco, 1994). The platforms are known to possess large areas of substratum (e.g., a single platform in 33-m depth of water possesses $\sim 8,100 \text{ m}^2$ of area; Shinn, 1974). By comparison, each of the FGB covers approximately $45,000,000 \text{ m}^2$ (radius of cap = $\sim 4.5 \text{ km}$). It is possible that other factors could have deterred coral settlement on the platforms, such as reduced light conditions beneath the platform or the presence of metal ions or other materials in antifoulants. This is unlikely, however, since the platforms used in this study were all over 15 yr old and were characterized by a substantial

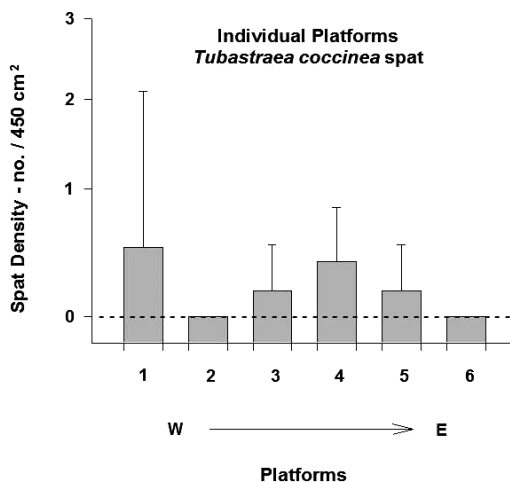


Fig. 4. Average density of *Tubastraea coccinea* spat in “No. per 450 cm^2 ” on six oil/gas platforms in the northern Gulf of Mexico in the vicinity of the NOAA Flower Garden Banks National Marine Sanctuary, by platform. The platforms, listed east to west, are HI-A-330, HI-A-349B, HI-A-368B, HI-A-376A, HI-A-571A, and HI-A-382, labeled 1–6, respectively. Data derived from coral settlement on terra cotta plates mounted on steel racks and deployed at depths of 15–27 m for 1 yr during 2001–02 or 2002–03. Data combined for depths (see text for discussion). Mean and 95% confidence limits shown. Y data transformed by square root ($Y + 0.5$) for normalization purposes. No significant difference in spat densities of *T. coccinea* between platforms ($P > 0.05$; one-way nested ANOVA).

sessile epibenthic community on the pilings, measuring up to 0.5 m thick. We believe that the cause is more likely a matter of larval supply affecting population levels.

Baggett and Bright (1985) reported an absence of coral recruitment on the oil-producing platform in close proximity to the E-FGB. This platform is outside of the 600-m radius of the reef—a distance demonstrated to be potentially the highest area of coral settlement on a reef in an earlier study performed on the Great Barrier Reef (The Helix Experiment; Sammarco and Andrews, 1988, 1989; see Fig. 6). This presumes that far-field current velocity and direction and bathymetric contours are conducive to forming mesoscale eddies that will retain coral larvae.

The probability of coral larvae encountering the platform substrate is probably reduced as a result of the absence of these mesoscale eddies near these structures. This rarity in settlement indicates that the platforms represent unique and fragile artificial reef environments in the GOM—unique because of their unusual spat settlement patterns and fragile because of the low level of potential for population regeneration

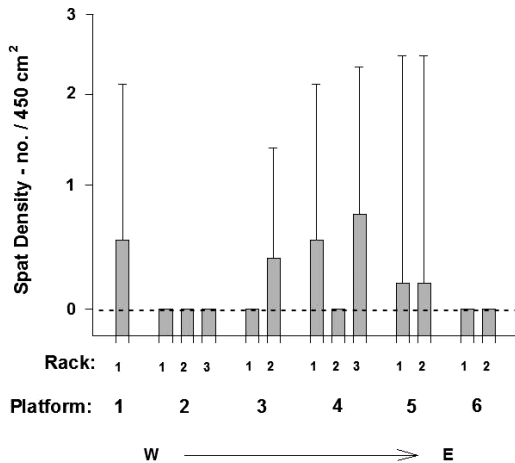


Fig. 5. Average density of *Tubastraea coccinea* spat in "No. per 450 cm²" on six oil/gas platforms in the northern Gulf of Mexico in the vicinity of the NOAA Flower Garden Banks National Marine Sanctuary. The platforms, listed east to west, are HI-A-330, HI-A-349B, HI-A-368B, HI-A-376A, HI-A-571A, and HI-A-382, labeled 1–6, respectively. Data shown for individual settlement racks within platforms. Data derived from coral settlement on terra cotta plates mounted on steel racks and deployed at depths of 15–27 m for 1 yr during 2001–02 or 2002–03. Data combined for depths. Mean and 95% confidence limits shown. Y 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).

in the event of a mass mortality of corals on the platforms. The populations that are there have taken decades to establish themselves.

The low levels of settlement were homogeneous between platforms. Thus, settlement was equitable over the period of the study. This was evident when considering data for all spat and at the species level for *T. coccinea*. It also suggests that the distance between the source of larvae, most likely the FGB (Sammarco et al., 2004, 2012a,b) and the points of settlement (the platforms) was sufficiently large to permit substantial diffusion of larvae (Okubo, 1980, 1994; Okubo and Levin, 1989).

Rarity of coral settlement was not the only characteristic that was unusual on the platforms. The species composition of coral spat settling there was unusual, varying substantially from the settlement pattern observed earlier on the FGB (see Baggett and Bright, 1985; Sammarco and Brazeau, 2001; Sammarco, 2002, 2003, 2005; Brazeau et al., 2005, 2011). On the platforms, *T. coccinea* and *M. decactis* were the most abundant spat. This varied substantially from coral settlement patterns observed on plates implanted on the E-FGB (Brazeau et al., 2011). There, *Agaricia*

and *Porites* spat were by far the most common spat. Indeed, throughout the Caribbean, *Porites* and *Agaricia* have been the most common spat observed settling (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). Peculiarly, the recruit species occurring on the platforms also matched the dominant species in the local adult coral community. In general, the community composition of juveniles does not resemble that of the adults (Sammarco, 1980, 1982). *Agaricia* and *Porites* spp. are often dominant recruits at a number of different series of coral community development (stages of community succession; Odum, 1971). These genera are generally not the dominant adults in the mature community. This implies that the platforms may be seeding themselves, as has also been implied in related genetic studies (Atchison, 2005; Atchison et al., 2008; Sammarco et al., 2012b).

The two most abundant coral recruits on the platforms were the azooxanthellate coral *T. coccinea* and the zooxanthellate *M. decactis*, both of which are brooders. *Montastraea* sp., a broadcast spawner, was also present. *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 Flower Garden Banks National Marine Sanctuaries, 2008; Sammarco et al., 2010). In addition, *T. coccinea* was not observed to recruit at all to plates on the E-FGB. On the other hand, it is common on platforms in this region. Recent experiments examining the population genetics of *T. coccinea* have demonstrated that it has greater dispersal capabilities than *M. decactis* (Sammarco et al., 2012b). Its cross recognition between platforms near the mouth of the Mississippi River is much higher than that of *Madracis*, suggesting that it is much more effective at larval dispersal. This is consistent with the recruitment patterns observed here. These patterns of low volume recruitment underscore the unusual aspects of the platform environment as an artificial reef.

The question arises as to why coral settlement was so low and relatively homogeneous on the platforms when we compare our results to those of other settlement studies in the Caribbean (Bak and Engel, 1979; Sammarco, 1980, 1982, 1985, 1987, 1994, 2002, 2003, 2005; Rylaarsdam,

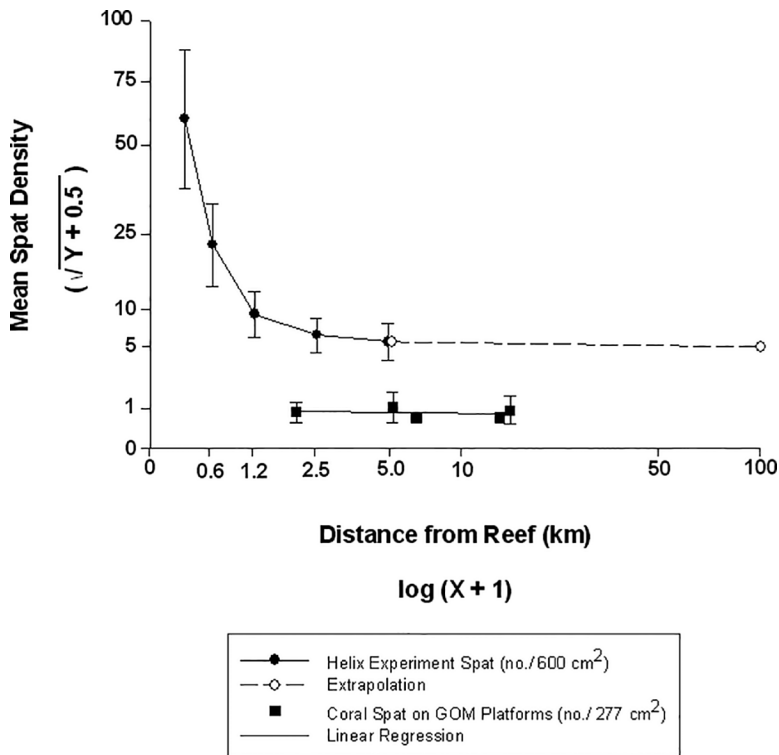


Fig. 6. Relationship between coral spat density on oil and gas platforms studied here and distance in kilometers from the nearest perimeter (30-m isobath) of the nearest Flower Garden Bank (squares). Average density of *Montastraea* sp. spat in "No. per 450 cm²" on six oil/gas platforms in the northern Gulf of Mexico in the vicinity of the Flower Garden Banks, 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 terra cotta plates mounted on steel racks and deployed at depths of 15–27 m for 1 yr during 2001–02 or 2002–03. Data combined for depths and times (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; open circles represent values extrapolated from that empirical data using a hyperbolic/asymptotic relationship. Means and 95% confidence limits shown. Y data transformed by square root ($Y + 0.5$) for normalization purposes.

1983; van Moorsel, 1983; and others cited above) or those on the FGB themselves (Brazeau et al., 2011). One possible explanation may be found by comparing these results with those of an earlier experiment. In the Helix Experiment (Great Barrier Reef), coral settlement around an isolated reef was enhanced locally by associated eddies that helped to retain larvae in the lee of currents around the reef (Sammarco and Andrews, 1988, 1989; Andrews et al., 1989; Gay and Andrews, 1994; Sammarco, 1994). It also demonstrated that recruitment within 600 m of the reef was five to 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 driven by advection processes derived from currents that carry the larvae away from the reef and diffusion

processes that 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 to 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 (Fig. 6). This potentially places them in a region where they may be approaching an asymptote of low recruitment due to diffusional 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.

Eddies are mesoscale currents that may affect recruitment on the scale of hundreds of meters to kilometers. Larger scale currents may help to explain larger scale recruitment patterns. Currents potentially driving patterns of coral recruitment in the study region are well known. Lugo-Fernandez (1998) and Lugo-Fernandez et al. (2001) have described anti-clockwise, mesoscale circulation patterns (on the order of hundreds of kilometers) near the FGB that could support self-seeding of the FGB (see Sammarco and Heron, 1994, for general discussion). Another major current from the west, particularly the Tampico region, Bahia de Campeche, Mexico (e.g., Salas-de-Leon et al., 1998), or the Alacran region of southern GOM, impinging on the study region is the macroscale clockwise Western Boundary Current (Vidal Lorandi et al., 1999). The Caribbean Current could also feed the northern GOM from the Cozumel and Cancun regions. Northerly jet currents and the Loop Current (Sturges and Blaha, 1976; Hamilton et al., 1999; Lugo-Fernandez and Gravois, 2010) could feed the region from the Alacran region. It is also possible for the region to receive larvae from the Florida Keys, including the Tortugas Bank and Pulley Ridge (Jarrett et al., 2000; Meyers et al., 2001). Hurricanes in the region can promote larval dispersal by producing high-speed currents from the Caribbean (Lugo-Fernandez and Gravois, 2010). With respect to this study, however, it is not possible to tell which of these was responsible for driving coral recruitment on the platforms, mainly because recruitment was integrated over the course of 2 yr. These currents change seasonally, annually, and in an ad hoc fashion, depending upon the individual current being considered.

Despite the fact that the platforms exhibit low recruitment levels, when coral recruitment and growth is integrated over ~30 yr, they can clearly still result in the development of adult coral communities. There has also been substantial development of associated benthic and demersal reef fauna and flora. If there were to be a mass mortality of zooxanthellate corals on the platforms, community regeneration would most likely require decades. Nonetheless, even at these low levels of recruitment, it is possible that the coral populations on the platforms could be serving to seed themselves, other platforms in the vicinity, and the FGB themselves, as has been documented through defining the genetic affinities between coral populations derived from

these three habitats (Atchison et al., 2008; Sammarco et al., 2012b).

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- (PWS, ADA) LOUISIANA UNIVERSITIES MARINE CONSORTIUM (LUMCON), 8124 HIGHWAY 56, CHAUVIN, LOUISIANA 70344-2110; (PWS, ADA) DEPARTMENT OF OCEANOGRAPHY AND COASTAL SCIENCES, LOUISIANA STATE UNIVERSITY A&M COLLEGE, BATON ROUGE, LOUISIANA; AND (GSB) BUREAU OF OCEAN ENERGY MANAGEMENT (BOEM), U.S. DEPARTMENT OF THE INTERIOR, 381 ELDEN STREET, HERNDON, VIRGINIA 20170-4817. Send reprint requests to PWS. Date accepted: July 22, 2014.