Gulf of Mexico Science

Volume 16
Number 2 *Number 2*

Article 7

1998

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DOI: 10.18785/goms.1602.07

Gulf of Mexico Science, 1998(2), pp. 180–187

Fertilization in Broadcast-Spawning Corals of the Flower Garden Banks National Marine Sanctuary

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Broadcast spawning is considered to be the dominant reproductive strategy for reef corals, but little is known about two critical postspawning processes, fertilization and early larval development. Instead, most efforts have focused on dispersal and recruitment. Since 1993, we have examined coral fertilization and development at the Flower Garden Banks, which contain two isolated reefs with predictable and dramatic annual mass spawning events in the northwestern Gulf of Mexico. Observations of in vitro fertilization indicate that the hermaphroditic scleractinian species *Colpophyllia natans, Diploria strigosa, Montastraea faveolata,* and *M. franksi* all have high fertilization potentials when outcrossing. However, although *D. strigosa* can self-fertilize readily, self-fertilization levels within *C. natans* and the *Montastraea* species are low. In addition, interspecific crossing attempts among the hermaphroditic species of *Montastraea* (*M. franksi, M. faveolata,* and *M. annularis*) yielded low levels of fertilization. The differences observed in the timing of spawning and the low hybridization success between the *Montastraea* siblings lend additional support to their recent reclassification as separate species. Spawned egg samples collected immediately upon release from female colonies of the gonochoric species *M. cavernosa* and *Stephanocoenia intersepta* produced an unexpected observation—very high levels of fertilization. This suggests internal fertilization prior to egg release, a process that has not heretofore been observed in a broadcast-spawning scleractinian.

Broadcast spawning has been known for some time to be the dominant reproductive strategy utilized by scleractinian corals (see review by Harrison and Wallace, 1990). Associated with this process, several significant obstacles must be overcome to ensure reproductive success and species longevity. Most relate to maximizing fertilization while minimizing hybridization and involve factors that affect sperm/egg encounters, species recognition, synchronicity of gamete release, and prevailing environmental conditions.

With regard to sperm/egg encounters, studies of several invertebrate species, including corals, have emphasized the mechanisms by which individuals achieve acceptable levels of success (Hendler and Meyer, 1982; Harrison et al., 1984; Heyward and Babcock, 1986; Levitan, 1991; Levitan et al., 1991; Lasker and Stewart, 1992; Oliver and Babcock, 1992; Babcock et al., 1994). One obstacle is ensuring appropriate and adequate gamete contact. As gamete densities increase, so to does the likelihood of chance encounters between conspecific gametes. Aquatic environments and multispecific spawning events pose a particular challenge to successful fertilization simply due to high levels of dilution (Harrison et al., 1984; Pennington, 1985; Heyward and Babcock, 1986; Levitan, 1991; Levitan et al., 1991; Lasker and Stewart, 1992; Oliver and Babcock, 1992; Babcock et al., 1994). Mass spawning events, as described by Willis et al. (1985), may involve more than 100 species across wide taxonomic ranges. This poses a significant challenge in that each individual must ensure fertilization with conspecifics to avoid wastage through hybridization.

Spawning corals have overcome the effects of dilution, in part, by using any or all of the following: mass production of gametes (Szmant-Froelich et al., 1980; Szmant, 1986, 1991; Babcock et al., 1994), simultaneous hermaphroditism (Heyward and Babcock, 1986; Harrison and Wallace, 1990), and the use of species-specific sperm attractants (Coll et al., 1994). Investigations of other invertebrates have identified species-specific binding proteins and receptors present in sperm and eggs (e.g., Gilbert, 1994; see also Palumbi, 1994) that are necessary for appropriate egg–sperm fusion. With regard to avoiding self-fertilization, no clear mechanism has yet been described in corals, although observational evidence suggests such mechanisms exist (e.g., Heyward and Babcock, 1986). Furthermore, the sheer magnitude of sperm production in hermaphroditic species suggests that these species emphasize out-crossing over self-fertilization (Szmant, 1986). Marine invertebrates that spawn synchronously also increase fertilization

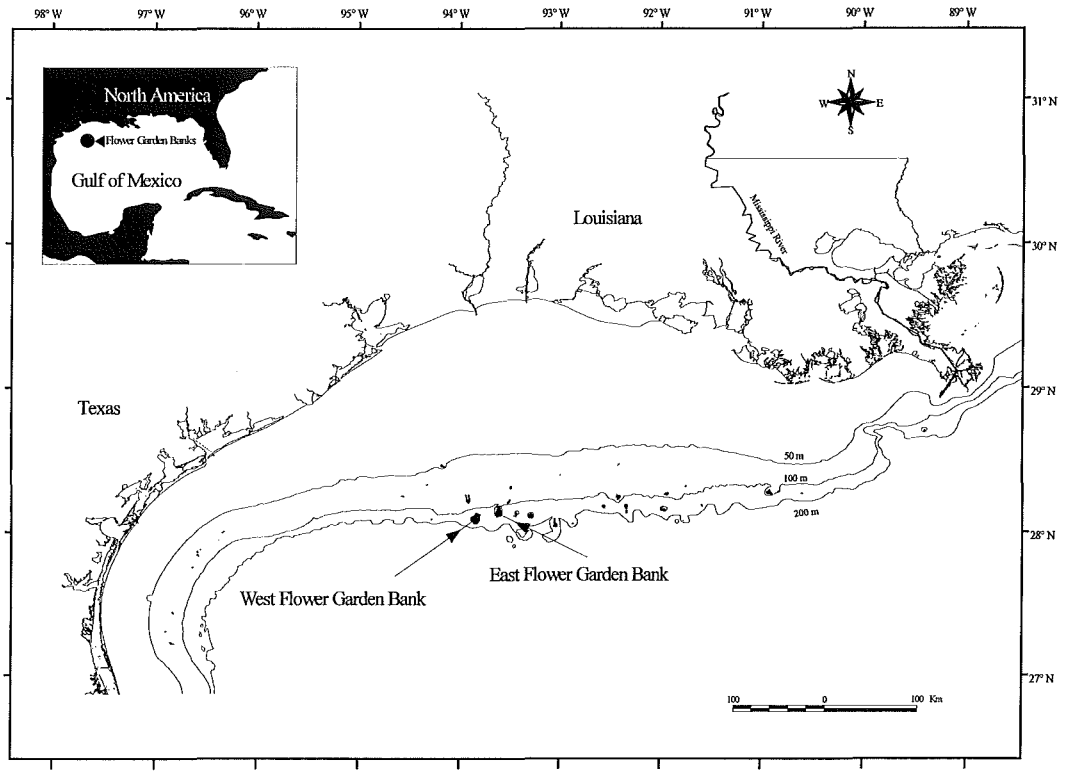

Fig. 1. Location of the East and West Flower Garden Banks on the outer Texas–Louisiana continental shelf, northwest Gulf of Mexico.

success by spawning during times of year likely to enhance the probability of fertilization (Ballard, 1942; Hendler and Meyer, 1982; Harrison et al., 1984; Pennington, 1985; Babcock et al., 1986; Harrison and Wallace, 1990; Oliver and Babcock, 1992; Babcock et al., 1994).

We report here on observations of fertilization mechanisms and the success of six western Atlantic reef-building corals, their apparent abilities to distinguish between conspecifics, and the tendency to avoid self-fertilization. In a separate paper (Hagman et al., 1998), issues related to population synchronicity and environmental factors are also addressed.

Methods

Study site.—The Flower Gardens are two small coral reefs situated atop banks formed by salt diapirism on the outer Texas–Louisiana shelf, roughly 190 km south-southeast of Galveston, TX (Fig. 1). These banks rise to within 18 m of the sea surface from surrounding depths of 100 to 150 m. Above the 35-m isobath, reef corals cover nearly 50% of an area totaling 1.3 km^2 (Bright et al., 1984; Gittings et al., 1992b,c). Twenty hard coral species have been identified on these banks, but nearly 90% of the total coral cover is comprised of the broadcast-spawning corals *Colpophyllia natans, Diploria strigosa, Montastraea annularis, M. faveolata, M. franksi,* and *M. cavernosa* (Bright et al., 1984; Gittings et al., 1992b,c). Spawning on these banks was first documented in 1990 (Bright, 1991). Observations made since that time suggest that the reefs exhibit some of the most prolific and predictable spawning in the Caribbean Province (Gittings et al., 1992a).

Field sampling.—Noninvasive sampling techniques were used in this study due to the lack of access to laboratory facilities on site and the status of these reefs as protected areas. Collections were conducted in situ on nitrox gas mixtures that allow divers 90–100 min of bottom time. Still and video cameras were used to document the timing and behavior of spawning corals and other organisms.

Gamete collections were made using 0.5-m diameter, hand-held, 333-μm mesh nets that were held or swept over the surface of individual colonies as the animals spawned. Each sam-

DOI: 10.18785/goms.1602.07

ple was then transferred to a prelabeled, sealable 4-liter plastic bag and sent to the surface via a lift-bag retrieval system.

Self- and cross-fertilization rates and levels were determined for all species, except as noted, by isolating gamete bundles from each sample in a separate container (self), or by combining gamete material from two colonies of the same species (cross). As a result, the crossing trials conducted were likely to include some fertilization resulting from selfing. All gamete manipulations were conducted in 500-ml plastic containers. In addition, hybridization or interspecific crossings were conducted using the three *Montastraea* sibling species (*M. franksi, M. faveolata,* and *M. annularis*).

Between 1993 and 1995, all fertilization estimates and observations of embryonic and larval development were made under dissecting scopes using live material at a field laboratory established on a natural gas production platform, Mobil HI-A389 "A," located 2 km from the reef. Subsequently, observations were conducted aboard the research vessel or at shore-based facilities using preserved material. Samples were preserved by transferring 1 aliquot of material into 5-ml vials, followed by the removal of most of the seawater and the addition of MEMFA [0.1 M 3-(*N*-morpholino)propanesulfonic acid (MOPS), pH 7.4; 2 mM EGTA; 1 mM $MgSO_4$; 3.7% formaldehyde]. Fertilization percentages for all samples were determined by counting the number of unfertilized eggs and cleaving embryos under dissecting scopes. The ratio of cleaving embryos to the total number of cleaving embryos and unfertilized eggs from a subsample (roughly 100 eggs) of each self or crossing trial yielded a fertilization percentage. For each sample, this was done three times, the average providing an estimate of the level of fertilization. To evaluate fertilization rates (percent fertilization through time), 1993–1995 samples were evaluated hourly for 7 hr following initiation of the experiments.

Results

Intraspecies crosses for *D. strigosa* yielded fertilization levels exceeding 90%, whereas selfed samples ranged from 45 to 90% fertilization (Table 1). Maximum levels of fertilization were measured within 2 hr of gamete crossing (outcrossing results presented in Fig. 2). Crossing within species for *C. natans* and *M. faveolata* also produced high levels of fertilization (> 75%; Table 1). Self-fertilization in these species however, was low (~ 10%). Although self-fertilization levels for *M. franksi* were comparable to those of *C. natans* and *M. faveolata,* rarely exceeding 10%, crossing experiments did not perform as well. Indeed, this species demonstrated highly variable levels of fertilization (45–85%; Table 1).

A significant observation was the difference in fertilization rates between *M. faveolata* and *M. franksi.* For *M. faveolata,* maximum fertilization was typically attained within 4.5 hr after the gametes were combined, whereas its sibling species *M. franksi* took up to 7 hr (outcrossing results presented in Fig. 2). We were able to successfully obtain only a single sample of *M. annularis* during the course of this study (very few individuals were observed spawning), limiting our data for this species. Hybridization trials between the *Montastraea* siblings yielded low fertilization levels, which were similar to the individual selfing rates for these species (Table 1).

For the gonochoric species, *S. intersepta* and *M. cavernosa,* most of the sampling effort focused on collecting spawned eggs. Sperm samples were only obtained for *S. intersepta,* limiting crossing trials. Upon examination of the "eggs only" samples for both species, more than 95% were undergoing cleavage within 3 hr of collection. Similar levels of fertilization were obtained for the combined egg/sperm crossing trials for *S. intersepta* (Table 1).

Discussion

Due to crowding in sample containers, in vitro studies may yield unrealistically high measures of fertilization (Heyward and Babcock, 1986; Levitan et al., 1991; Lasker and Stewart, 1992). Accordingly, fertilization data herein should be considered a measure of maximum potential and not in situ levels or rates of fertilization.

The simultaneous hermaphrodites observed in this study, *M. annularis, M. franksi, M. faveolata, D. strigosa,* and *C. natans,* all released eggs/sperm bundles, each bound by a thin mucus sheath. These buoyant bundles, upon reaching the surface, generally ruptured within minutes. It is during this time period, bundle formation to rupture at the surface, that self-fertilization was most likely. However, there was no evidence of fertilization prior to gamete bundle breakdown for any of these species, suggesting delayed receptivity of eggs. Furthermore, for all species examined, self-fertilization was limited even after gamete bundle rupture, with crossing trials yielding significantly higher

TABLE 1. Levels of cross- and self-fertilization in (a) hermaphroditic species and (b) gonochoric species at the Flower Garden Banks. Values presented are combined means with standard deviations for all years in which data for a given species were collected. NA, not attempted (due to lack of material).[a]

	Cross (%)	n	Self (%)	n	Notes
(a) Hermaphroditic species					
Diploria strigosa	93.5 ± 6.46	46	62.2 ± 25.43	29	Peak within 2 hr of spawning
Colpophyllia natans	75.9 ± 14.23	6	12.8 ± 7.19	4	
Montastraea annularis	NA	0	9.4	1	
Montastraea faveolata	90.4 ± 6.89	8	9.5 ± 13.91	13	Peak 4.5 hr after spawning
Montastraea franksi	66.6 ± 21.98	27	10.77 ± 11.79	22	Peak 7 hr after spawning
M. faveolata × *M. franksi*	20.3 ± 13.45	30	—	—	Supports separate species hypothesis with limited hybridization
M. faveolata × *M. annularis*	5.8	1	—	—	Supports separate species hypothesis with limited hybridization
M. franksi × *M. annularis*	23.0 ± 14.52	3	—	—	Supports separate species hypothesis with limited hybridization
	Cross (%)	n	Single female colonies (%)	n	Notes
(b) Gonochoric species					
Montastraea cavernosa	NA	0	97.8 ± 1.71	4	> 95% of spawned eggs developing without apparent crossing; possibly fertilized prior to release
Stephanocoenia intersepta	96.5 ± 1.06	2	97.4 ± 3.75	2	> 95% of spawned eggs developing without apparent crossing; possibly fertilized prior to release

[a] Taxonomic identification of the genera *Montastraea* and *Stephanocoenia* are based on the recent reclassification by Weil and Knowlton (1994) and the descriptive paper by Foster (1987).

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DOI: 10.18785/goms.1602.07

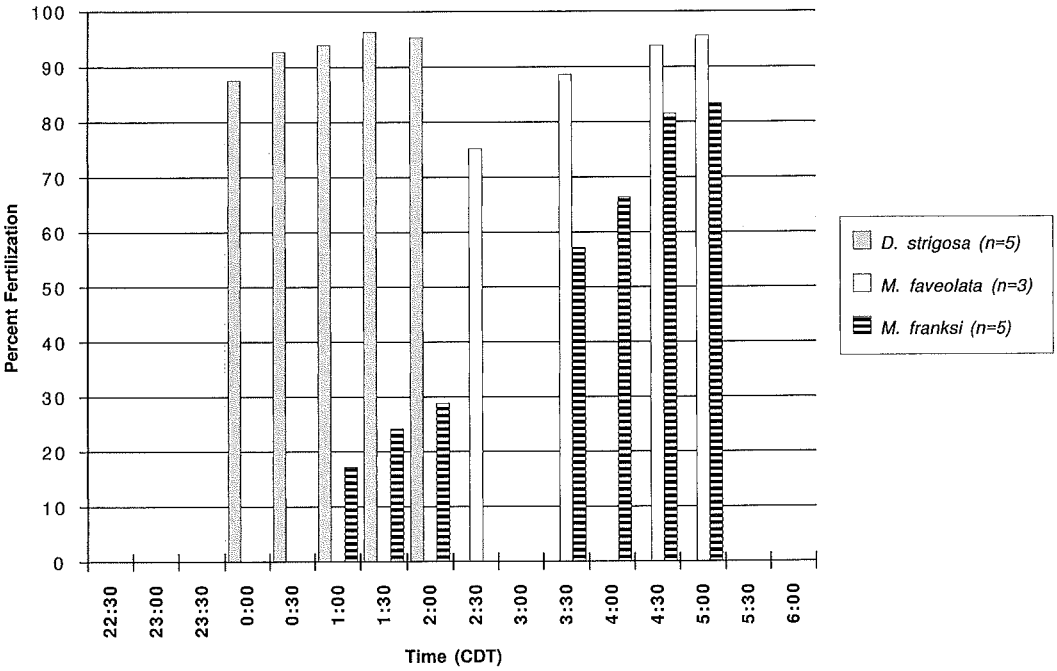

Fig. 2. Fertilization rates for intraspecies crosses from the three dominant spawners at the Flower Gardens. Crosses for *D. strigosa* and *M. franksi* were initiated between 21:45 and 22:15 CDT and those for *M. faveolata* were initiated between 23:30 and 00:00 CDT. n, the number of specimens for each species repeatedly sampled during the time period presented.

levels of fertilization (similar to Heyward and Babcock, 1986).

Diploria strigosa exhibited both rapid development and high levels of fertilization in selfing and crossing trials. For the other three simultaneous hermaphroditic species, crossing within species yielded much higher levels of fertilization than selfing (Table 1). Although not experimented on directly, observational evidence of larvae produced from both self and crossing trials using *D. strigosa* and *M. franksi* yielded marked differences in terms of viability and settlement. In general, fewer larvae reached the planulae stage, and settlement was almost absent in larvae produced from selfing trials. Although further efforts are necessary, this does suggest the existence in some form of a postreproductive barrier to self-fertilization. Furthermore, as there were observed delays of between 4 and 7 hr (Fig. 2) in reaching maximum levels of fertilization for *M. faveolata* and *M. franksi,* it seems likely that the mechanism preventing self-fertilization may be related to sperm recognition and the prevention of binding by "self" sperm, as initially suggested by Heyward and Babcock (1986). This same barrier may also help to explain observations of delayed fertilization in crossing trials.

Although sperm concentrations were high within the fertilization trials, half of the sperm present was "self" sperm and as a result may have reduced the combined sperm concentration to a level where additional time would be necessary to ensure appropriate egg–sperm encounters (Levitan et al., 1991). Furthermore, delayed receptivity itself may have reduced the likelihood of self-fertilization simply because dilution probably reduced the potential for encounters between gametes from the same parent.

Our limited observations of hybridization between *M. annularis* and *M. franksi* differ from both Knowlton et al. (1997) and Szmant et al. (1997), who found no evidence of barriers between these species, although differences in spawning times were observed. The remaining hybridization attempts between *M. annularis* and *M. faveolata* and *M. faveolata* and *M. franksi* (Table 1) lend additional support to the reclassification effort by Weil and Knowlton (1994). Their initial description was based on morphological, genetic, and behavioral variation, with more recent observations on the timing of spawning (e.g., Palumbi, 1994; Hagman et al., 1998) and hybridization potentials endorsing this hypothesis (Palumbi, 1994; see

also Knowlton et al., 1997; Szmant et al., 1997). At the Flower Gardens, *M. franksi* begins spawning up to 2.5 hr before *M. faveolata,* and closer to 3 hr before *M. annularis* (Hagman et al., 1998).

The most remarkable observations made during this study were the high fertilization levels of eggs collected from the gonochoric broadcasters, *M. cavernosa* (Soong, 1991; Szmant, 1991; Acosta and Zea, 1997) and *S. intersepta* (e.g., Harrison and Wallace, 1990). It has generally been assumed that fertilization and development take place externally for broadcast-spawning species (e.g., Harrison and Wallace, 1990). Yet, here there were no significant differences in the levels of fertilization between trials containing separately spawned sperm and egg samples and those containing only spawned eggs. Similar observations were made by Brazeau and Lasker (1989) in their investigation of the gorgonian coral *Plexura* A, which led them to suggest that fertilization was occurring internally or at the surface of the female colonies.

The only scleractinian species presently known to utilize internal fertilization are brooders (Szmant, 1986). Like broadcast spawners, brooders also exhibit both simultaneous hermaphroditism and gonochorism (Szmant, 1986). Because male gonochoric brooders "spawn" sperm, females must be able to selectively remove sperm from the surrounding water column. Our observations suggest that *M. cavernosa* and *S. intersepta* may have similar mechanisms to achieve internal fertilization.

Alternatively, external fertilization should be considered, albeit immediately upon release (Brazeau and Lasker, 1989). Yet this option seems unlikely. To achieve the levels of fertilization observed for *M. cavernosa* and *S. intersepta,* the sperm concentration surrounding individual female colonies would have to be exceptionally high (Pennington, 1985; Levitan et al., 1991). Sperm densities and fertilization rates have been shown to decline drastically within several meters of male colonies of *Plexaura* A [Lasker and Stewart, 1992; see also Pennington (1985) and Levitan et al. (1991) for sea urchins and Babcock et al. (1994) for *Acanthaster planci*]. Although numerous male colonies of both *M. cavernosa* and *S. intersepta* were seen releasing sperm (in some cases reducing visibility within 20–25 cm of the colony), the volume of sperm released probably did not attain concentrations elevated enough to remain in the area for an extended period of time. Furthermore, in vitro fertilization trials using hermaphroditic spawners rarely reached equivalent levels of fertilization seen in gonochoric species.

Proximity between male and female colonies would be likely to enhance the level of fertilization of eggs upon release [e.g., Brazeau and Lasker (1992) for *Briareum asbestinum*]. Soong (1991), Szmant (1991), and Acosta and Zea (1997) all demonstrated that *M. cavernosa* populations exhibit a 1:1 sex ratio. Our observations of spawning do not suggest otherwise at the Flower Gardens. At reasonably high population levels, this would provide proximate sources of sperm for female colonies. Although populations of *M. cavernosa* and *S. intersepta* are fairly high at the Flower Gardens, our observations of spawning activity reveal that male colonies of both species begin spawning up to 1 hr before the females (Hagman et al., 1998). Although this provides ample time for sperm plumes to reach female colonies (e.g., Babcock et al., 1994), it also results in substantial dilution of sperm concentration (e.g., Levitan et al., 1991; Lasker and Stewart, 1992). Male first spawning has also been suggested to act as a stimulus, inducing female colonies to spawn (e.g., Fadlallah, 1983), a circumstance noted in other marine invertebrates (e.g., Giese and Pearse, 1974; Pennington, 1985). When considered together, it is highly unlikely that this earlier spawning by males serves only to induce spawning or that the high levels of fertilization observed could be accomplished externally for either coral species. Instead, the observed timing differences in spawning by male and female colonies of these species may in fact provide the time necessary for females to collect significant quantities of sperm to ensure high levels of fertilization internally, prior to release.

Finally, parthenogenesis could produce similar observations. However, it has only been suggested for two scleractinian species with highly skewed populations (toward females; Fadlallah, 1983) and has actually been documented in only one octocoral species (Brazeau and Lasker, 1989). Based upon the available evidence, we suspect that there is a much higher likelihood that the broadcast spawners *M. cavernosa* and *S. intersepta* utilize internal fertilization.

Acknowledgments

We extend our gratitude to the divers and data collectors who participated on this project, with a special thanks to T. Bright, G. Boland, C. Beaver, S. Cox, Q. Dokken, H. Guiter-

rez, J. Reeves, and most importantly, Clyde Jones; we all miss you. We also thank K. Deslarzes, N. Knowlton, and J. Lang for their comments on the initial drafts of this manuscript and those of the anonymous reviewers. Financial, technical, and logistical support for this research was provided by Mobil Exploration and Producing U.S. Inc.; Oryx Inc.; Texaco Inc.; the Flower Gardens Fund of the Gulf of Mexico Foundation; the National Oceanic and Atmospheric Administration/Sanctuaries and Reserves Division; the National Fish and Wildlife Foundation; the Center for Coastal Studies at TAMU-CC; Ocean Management Systems; Florida State University's Academic Diving Program; the U.S. Department of the Interior/Minerals Management Service; Rinn Boats Inc.; SeaSpace Inc.; the Texas Gulf Coast Council of Dive Clubs; Oceanographic Expeditions; Texas A&M Sea Grant College Program; and the University of Texas at Austin Vice President's Office. All research activities were conducted in accordance with NOAA/SRD regulations outlined in the FGBNMS permits 08-93, 03-94, 04-95, 04-96, 05-97, and 5-98. This paper is dedicated to the memory of Clyde Jones. It was his insight and willingness to help scientific programs that lead to the realization of the Flower Gardens Ocean Research Program, a cooperative between the offshore petroleum industry and academic institutions. Today, this program provides countless new opportunities for graduate studies related to marine systems and, more importantly, was the catalyst necessary to initiate work described in this paper. Thanks again, Clyde.

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(DKH, PDV) DEPARTMENT OF ZOOLOGY, UNIVERSITY OF TEXAS, AUSTIN, TEXAS 78712; AND NOAA/SANCTUARIES AND RESERVES DIVISION, SSMC-4, N/ORM2, SILVER SPRING, MARYLAND 20910. Date accepted: August 16, 1998.

DOI: 10.18785/goms.1602.07