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Timing, Species Participation, and Environmental Factors Influencing Annual Mass Spawning at the Flower Garden Banks (Northwest Gulf of Mexico)

DEREK K. HAGMAN, STEPHEN R. GITTINGS, AND KENNETH J. P. DESLARZES

Since 1990, highly predictable and intense annual mass spawning events have been witnessed at the Flower Garden Banks (northwestern Gulf of Mexico), and more recently at several other western Atlantic coral reefs as well. The annual reproductive period at the Flower Gardens coincided with the summer seawater temperature maximum and occurred between the seventh and 10th evenings following a full moon in August or September. Species-specific peaks of activity were centered on the eighth and 10th evenings. Coral spawning at the Flower Gardens began within 1 hr of sunset and continued for roughly 4 hr. On the eighth evening, coral species observed spawning during the first 2.5 hr were *Diploria strigosa*, *Montastraea cavernosa*, and *M. franksi*. Other reef-dwelling invertebrate species were also consistently seen spawning during this time. *Montastraea annularis*, *M. faveolata*, and *Stephanocoenia intersepta* spawned about 1 hr later, following a brief transition period during which little spawning activity was observed. The 10th evening was characterized by the successive spawning of *Colpophyllia natans* (early evening) and *S. intersepta* (late evening). Male colonies of the gonochoric species *M. cavernosa* and *S. intersepta* typically began spawning up to 30 min before females, although several individuals of *M. cavernosa* have been observed spawning more than 3 hr before females.

Sexual reproduction in scleractinian corals generally involves either brooding larvae or broadcasting gametes for external fertilization and development. Although brooding had long been thought to be the dominant reproductive strategy, field observations, primarily from Pacific reefs, over the last two decades confirm that broadcast spawning is more prevalent and occurs synchronously for many species, often during so-called "mass spawning" events (e.g., Willis et al., 1985; Harrison and Wallace, 1990). Prior to 1990, coral mass spawning within the Caribbean region had not been documented. This phenomenon was inferred, however, based on presumed coral spawn slicks (Butler, 1980), observations of spawning by individual coral colonies (Wyers, 1985; Szmant, 1986, 1991; Wyers et al., 1991), and in one instance, spawning by a population of a single gorgonian species (Brazeau and Lasker, 1989). Yet, mass spawning events similar to those seen along the Great Barrier Reef of Australia were thought to be nonexistent in the Caribbean (e.g., Richmond and Hunter, 1990; Babcock et al., 1994).

Since 1990, mass spawning events have been repeatedly documented throughout the Caribbean Province, with some of the most predictable and intense events occurring at the East and West Flower Garden Banks, two isolated coral reefs in the northwest Gulf of Mexico

(Gittings et al., 1992a, 1994; Hagman et al., 1998). Of the 20 reef-building coral species that densely populate these banks (> 45% coral cover; Gittings et al., 1992b,c; Dokken et al., 1998), seven participate in the annual mass spawning. These events have consistently occurred seven to 10 evenings following the August (occasionally September) full moon, between 1 and 4 hr after sunset. Moreover, there are now several other locations in the greater Caribbean, including Aruba, Bermuda, Curacao, the Florida Keys, Honduras, Panama, and Saba, that exhibit somewhat predictable mass spawning events (Wyers et al., 1991; Gittings et al., 1994; van Veghel, 1994; Knowlton et al., 1997; Szmant et al., 1997).

Little is known about the level of genetic isolation of the Flower Garden reefs, which are separated by more than 600 km of open ocean from any other coral reefs. Their population maintenance may therefore depend more on local reproduction than that on more distant reefs. Indeed, coral recruitment studies at the Flower Gardens and studies of coral species distribution on nearby oil and gas production platforms have consistently shown that the majority of recruits are species that already exist on these banks (Baggett and Bright, 1985; Bright et al., 1991). Tentatively, it appears that the Flower Gardens coral communities could be reproductively capable of replacing them-

selves even though they exist as marginal reefs at the northern latitudinal limits of coral reef development (Rezak et al., 1990).

Others have reported predictable and synchronous spawning on high-latitude reefs (Dai et al., 1992; Babcock et al., 1994; van Woosik, 1995; Fadlallah, 1996). It is not understood, however, how spawning intensity varies with latitude or what the regional influence on population maintenance might be.

The mass spawning at the Flower Gardens has facilitated studies on coral reproduction, emphasizing fertilization and hybridization, recruitment, dispersal, and gene flow, all of which affect the viability, resilience, and persistence of these reefs. The timing of reproduction is also likely to reflect the evolutionary history of coexisting species, particularly those that are closely related. From a resource manager's perspective, the phenomenon may influence decisions on issues as different as discharge regulations and environmental mitigation, education, public outreach, allowable activities, and research planning. To further evaluate the ecological, taxonomic, and resource management implications of these processes at the Flower Gardens, we examined differences in the timing of spawning between closely related and nonrelated species and the influence of moon phase, variation in temperature and light attenuation, and sea state on spawning episodes observed from 1990 to 1998.

METHODS

Study site.—The Flower Gardens are two small coral reefs situated atop banks formed by salt diapirism on the outer Texas–Louisiana continental shelf, roughly 180 km south-southeast of Galveston, TX (see Hagman et al., 1998). These banks rise to within 18 m of the sea surface from surrounding depths of 100–150 m. Above the 35-m isobath, reef corals cover more than 45% of an area totaling 1.3 km² (Bright et al., 1984; Gittings et al., 1992b,c). Twenty hard coral species have been identified on these reefs, but nearly 90% of the coral cover consists of broadcast-spawning corals *Montastraea annularis*, *M. faveolata*, *M. franksi*, *M. cavernosa*, *Diploria strigosa*, and *Colpophyllia natans* (Gittings et al., 1992b,c; Dokken et al., 1998).

Sampling and field observations.—Observations of in situ spawning activity have been made annually following August (and September when appropriate) full moons since 1990. Scientific and trained volunteer divers used both still

and video cameras, as well as field notes, to record the timing, behavior, and other pertinent details of spawning by individual organisms. Observational efforts have focused on the seventh through 10th evenings following a full moon. Dive times for the 20–30 participating divers were staggered to ensure continuous observation of the activity throughout the entire spawning period for each night.

Spawning dates were predicted based on published lunar phases and observations made in previous years at the Flower Gardens and elsewhere. Our previous observations indicated that, when full moons occurred during the morning or afternoon hours, most of the spawning took place on the evening of the seventh calendar day following the full moon (i.e., the eighth evening following a full moon). When a full moon occurred during the evening hours, spawning was observed on the eighth calendar day and eighth evening following the full moon.

Since 7 Aug. 1990, seawater bottom temperatures have been recorded every 2 hr using HoboTemp, StowAway (Onset Instruments) or Ryan TempMentor thermographs. The daily light attenuation coefficient k (m⁻¹) on the East Flower Garden reef was evaluated using solar irradiance data collected between 1995 and 1997 with a Licor LI-193SA spherical quantum light sensor and LI-1000 datalogger (Dokken et al., 1998). Hourly irradiance measurements of photosynthetically active radiation (PAR, 400–700 nm waveband), recorded in $\mu\text{mol}/\text{sec}/\text{m}^2$, were taken from 0800–1800 hr simultaneously both on the reef (24 m) and atop Mobil's HI-A389-A gas production platform less than 1 mile away.

We characterized sea state at the Flower Gardens by reporting the mean, minimum, and maximum monthly significant wave height (H_s) as acquired hourly by the National Data Buoy Center from 1990 to 1997 at C-MAN Buoys GBLC1, located 60 km to the south (27.37°N, 93.80°W; 1990–1991), and 42019, located 160 km due west (27.92°N, 95.35°W; 1990–1997) (NOAA, National Weather Service, Tallahassee, FL). Significant wave height was defined as the average of the highest one-third of the waves.

RESULTS

Species participation and behavior.—Between 1990 and 1998, each of the coral species that participated in the annual spawning episodes at the Flower Gardens exhibited remarkable consistency with regard to behavior and timing of

gamete release (Table 1; Gittings et al., 1992a, 1994). For the most part, gamete bundles released by the simultaneous hermaphrodites were protected by a thin, strong, mucus sheath. In *Colpophyllia natans*, however, the bundles were bound by an extremely fragile sheath that did not withstand handling. Furthermore, although gamete bundles for most species tended to remain intact for several minutes at the surface, bundles released by *C. natans* ruptured upon contact with the sea surface.

Babcock et al. (1986) described three broadcast spawning behaviors, all of which have been observed at the Flower Gardens in one form or another. In Type I behavior, a brief "setting period" transpired in which gamete bundles were readily visible below a distended oral disk. The bundles were then gradually released through the polyp mouth over the entire surface of the colony for anywhere from 5 to 50 min. This spawning behavior was first observed in *Diploria strigosa* at the Flower Gardens (Gittings et al., 1992a). *Colpophyllia natans* also exhibited a form of Type I spawning, but differed in that the release of gamete bundles was much slower, with only a few polyps in the colony releasing bundles at any one time. Two of the three hermaphroditic *Montastraea* species, *M. faveolata* and *M. franksi*, have consistently exhibited a variation of the Type I spawning behavior (see also van Veghel, 1994). Although similar, observations of spawning by *M. annularis* have not been consistent enough to warrant inclusion at this time. Both *M. faveolata* and *M. franksi* exhibited the "setting phase" (gamete bundles discernible under distended oral discs) and the squeezing of bundles through the polyp mouth typical of Type I spawning (i.e., Babcock et al., 1986). The timing and release of the gamete bundles, however, were different. Whereas *D. strigosa* exhibited several pulse-like releases of bundles from either specific regions or the entire colony over periods of up to 30 min, bundle release by these *Montastraea* spp. was sudden and synchronized throughout most of the colony (in some instances proceeding in a wave across the colony surface). Typically, bundles were rapidly extruded through individual polyp mouths, but without an immediate departure from the colony surface. Shortly thereafter, the bundles were slowly carried away as they became entrained in the water flowing over the colonies.

Another prominent broadcaster, the gonochoric species *M. cavernosa*, displayed Type II spawning in which gametes (or bundles) were forcefully ejected from polyp mouths more or less randomly over the entire colony surface

(Gittings et al., 1992a). Type III spawning behavior was described by Babcock et al. (1986) as the passive release of gametes from open polyp mouths. This behavior was only recently observed in *Stephanocoenia intersepta* at the Flower Gardens. One of the authors (SRG) noted that the release of eggs by female *S. intersepta* colonies was visually similar to champagne bubbles freely flowing out of the colonies. Sperm release from male colonies, however, appeared forceful or more similar to that of the Type II spawning behavior.

Timing.—The most concentrated spawning activity took place on the eighth and 10th evenings after an August or September full moon (Table 1). Although less intense and highly variable, spawning by *D. strigosa* and *M. franksi* has also been consistently observed on the seventh and ninth evenings. Other coral species, including *M. cavernosa* (males), *S. intersepta*, and *C. natans* (ninth evening), occasionally spawned during these "off nights." In addition, spawning by a few individuals has also been witnessed 1 mo prior and 1 mo following the main spawning period during the same lunar phases.

On the eighth evening following full moon, the first of two observed spawning periods began roughly 30 min after sunset (around 20:30 CDT) and lasted approximately 2 hr. This was when *D. strigosa*, *M. cavernosa*, *M. franksi* (Table 1), and several other invertebrate species, including *Spirobranchus giganteus* (Christmas tree worms) and *Ophioderma rubicundum* (ruby brittle stars), spawned most prolifically. Spawning by male colonies of *M. cavernosa* began 30 min before female colonies, with several observations of males spawning as much as 3 hr (18:00 CDT) before females. This first spawning interval was then followed by a transitional period in which early and late spawners occasionally overlapped. At the sea surface, this transition was clearly delineated by changes in the coloration of the gamete slick from the pinkish *D. strigosa* and light orange *M. cavernosa* and *M. franksi* eggs to a much richer reddish-orange of *M. annularis* and *M. faveolata* eggs. Male and female colonies of a third species, *S. intersepta*, also spawned during this period. The most prolific spawning during this second interval was between 3 and 4 hr after sunset (23:00–00:00 CDT; Table 1).

The 10th evening after the full moon was similarly divided into two spawning periods. Spawning by *C. natans* began within 30 min of sunset and lasted up to perhaps 75 min (Table 1). This was followed approximately 1 hr later

TABLE 1. Spawning date(s) and times for each of the seven coral species participating in the annual mass spawning at the Flower Gardens. Bold times indicate peak spawning activity for those species. Times reported as central daylight time (CDT). In typical years, spawning occurs following the first August full moon. In 1993 there were two full moons in August, with the resultant spawning taking place almost exclusively after the second full moon. In 1995, a normal multiday spawning period occurred following the first full moon, and a second, shorter, but intense spawning period occurred on the eighth night after the second full moon.

Species	Years observed	Evenings after first August full moon				Evenings after subsequent full moons (1993 and 1995)	
		7	8	9	10	7	8
<i>Colpophyllia natans</i>	1994–1995, 1997–1998			20:40–21:20 21:40	20:15 20:30–21:15 21:15–21:30		
<i>Diploria strigosa</i>	1991–1998	21:30–23:00	20:30–22:30	20:40–21:50 21:10	20:00	21:40–22:05	20:00–22:30
<i>Montastraea annularis</i>	1992, 1997		23:50, 00:15				
<i>Montastraea faveolata</i>	1992, 1994–1995, 1997–1998		23:15–00:40	22:55–23:35			21:40–22:10
<i>Montastraea franksi</i>	1991–1998	21:20–23:00	21:00–22:30 23:00	20:40–22:20	22:10	21:40–22:05	20:45–22:30
<i>Montastraea cavernosa</i> (male)	1990–1998	dusk 21:30	later afternoon 20:45–22:00	21:00			late afternoon 21:00 21:30–22:00 21:30–22:00
<i>Montastraea cavernosa</i> (female)	1991–1995, 1997	21:30–22:00	21:20–22:15				
<i>Stephanocoenia intersepta</i> (male)	1992–1993, 1997–1998	23:45–00:05	23:30–23:55	21:30, 22:30	22:15–22:30		21:30–22:00
<i>Stephanocoenia intersepta</i> (female)	1993, 1997– 1998	23:45–00:05	23:30–23:55		22:35–22:50		21:30–22:00
Surface spawn slick	1990–1998	21:00 21:15–23:00	20:10–20:50 21:15–23:00 23:30–23:55	21:05–21:50 (sparse)	20:10–20:50 21:00–22:00		20:00–20:30 21:00–22:20 23:00

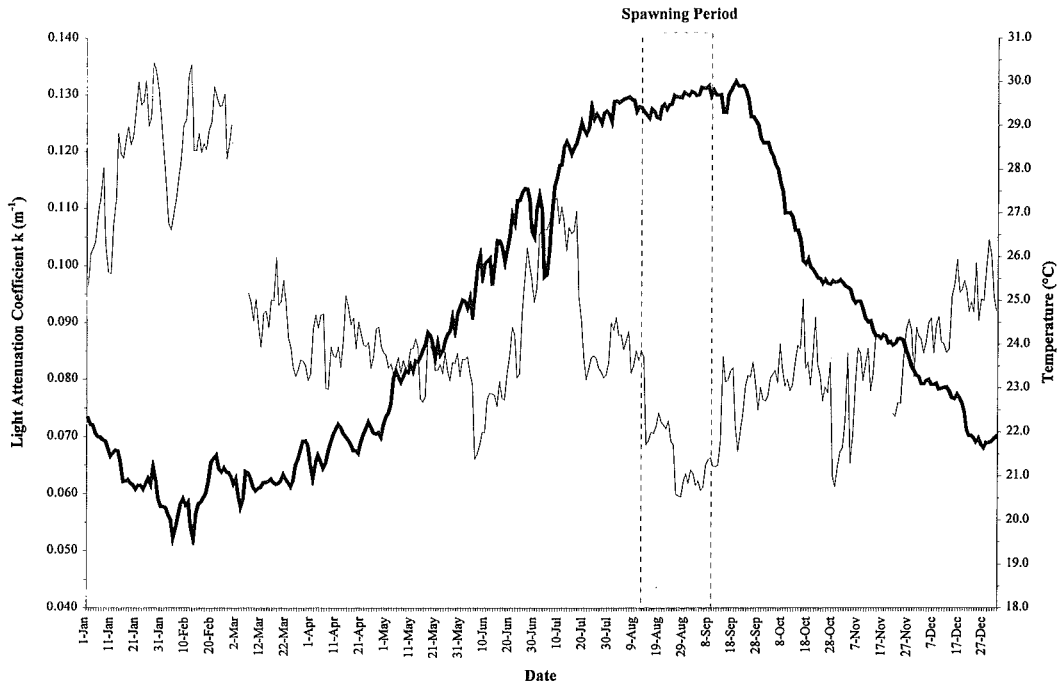


Fig. 1. Annual seawater temperature and light attenuation coefficient values for the East Flower Garden Bank reef cap at a depth of 24 m. The darker line represents the mean daily seawater temperature determined between 1990 and 1997 (temperature peaks in late July/early August). The lighter line represents mean light attenuation determined between 1995 and 1997 (minimum attenuation occurred between mid-August and mid-September). The spawning period (mid-August to mid-September) is indicated by the rectangular region.

by spawning of both male and female colonies of *S. intersepta*, with males generally spawning up to 30 min before females.

Environmental factors: Lunar periodicity, temperature, light attenuation, and sea state.—The most intense coral spawning occurred in the late summer following the first full moon after the annual seawater temperature was at or near maximum (note boxed region, Fig. 1). Spawning also coincided with a period of minimum light attenuation (Fig. 1). This period generally occurs when the sea state is at its lowest and least variable (Fig. 2, 3). During years with multiple or early full moons in August, such as 1993 (a blue moon August) and 1995, the initial spawning periods were not as well defined as in other years or as intense as the spawning following the subsequent full moon those same years. We suspect that this was due in part to the absence of summer maximum water temperatures prior to the August full moon, which seldom occur before the second week in August. In 1995, low levels of spawning were witnessed each night between 16 Aug. and 22 Aug. following a 10 Aug. full moon, with a

much more intense spawning on 16 Sept. following the subsequent full moon.

In years when full moons slightly preceded maximum water temperatures, spawning was not only less intense, but also less synchronous, spread out over several evenings and over consecutive full moons. Spawning in Aug. 1998 was much like that observed in 1995, with spawning by several species spread out over several evenings. However, the spawning was more intense than that observed in Aug. 1995. With the large number of reports of bleaching throughout the Caribbean and the rest of the world's tropical seas during 1998 (bleaching archive: <http://coral.aoml.noaa.gov>), it is possible that the Flower Gardens experienced abnormal temperatures prior to the spawning period, possibly contributing to the intense, earlier-than-normal spawning. Temperature records for 1998 have not yet been analyzed to evaluate this. No observations were attempted around the predicted September date in 1998 due to the presence of tropical storms in the northwestern Gulf.

The timing of the annual spawning episodes coincided with a period of minimum light at-

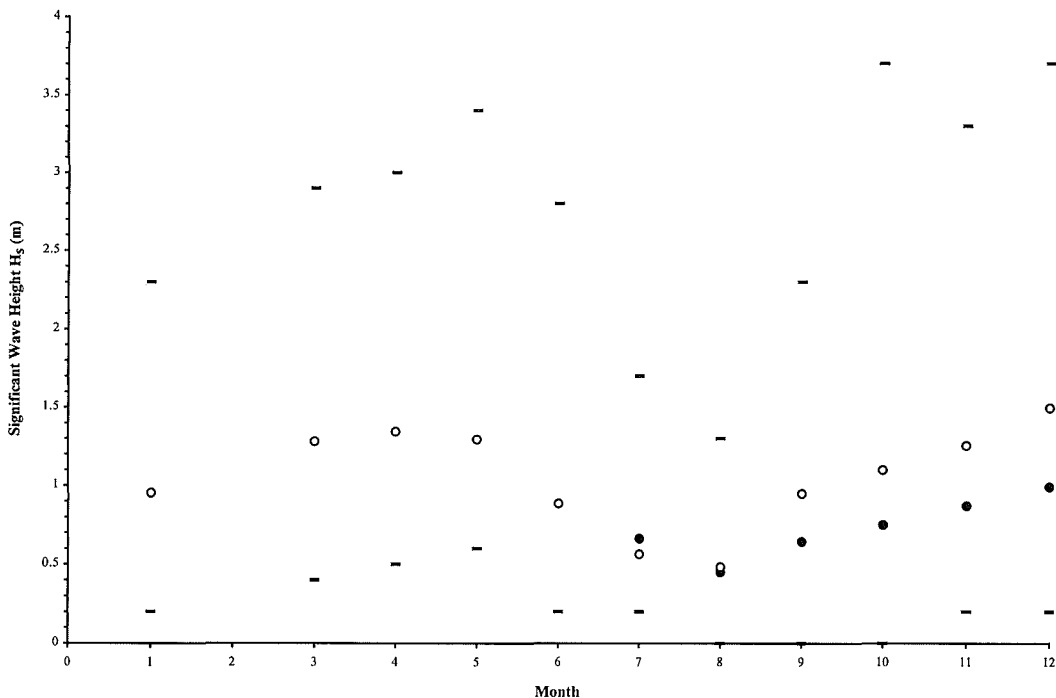


Fig. 2. Mean, maximum, and minimum significant wave height H_s (m) measured at the C-MAN Buoy GBCL1 (27.37°N, 93.80°W) in 1990 and 1991. Dark circles represent mean values from 1990. Open circles represent mean values from 1991. The dash marks on either side of dark and open circles are monthly significant wave height maxima and minima.

tenuation (Fig. 1). During at least 3 yr, spawning was preceded by a month or so of higher light attenuation caused by recurrent algal blooms or nutrient-rich surface water (upper 15 m) that reduced visibility from 20–40 m to 10–15 m (M/V *Fling* and M/V *Spre* ship logs, 1988–1997, Rinn Boats, Inc., Freeport, TX). Plankton blooms along the northern Gulf shelf edge are common in late spring or early summer (SAIC, 1989).

DISCUSSION

Seven of the eight broadcast-spawning coral species found at the Flower Gardens were observed to release gametes into the water column for external fertilization and development in a more or less synchronous fashion at specific times and during predictable periods. In contrast, corals that brood larvae following internal fertilization do not appear to spawn in synchrony at the Flower Gardens, nor do they have buoyant offspring or appear to have predictable spawning times (some even reproduce more than once each year; Baggett and Bright, 1985).

The evolution of mass spawning is likely to

have been affected by environmental parameters that ensure high levels of fertilization success and survival of planktonic larvae (e.g., Harrison et al., 1984). Many of these parameters are reflected in the behaviors and timing of mass-spawning corals at the Flower Gardens and elsewhere in the Caribbean. Mass spawning on most western Atlantic reefs, particularly at higher latitudes, occurs just after the third quarter moon (i.e., eight evenings after full moon) and occurs exclusively after sunset and during the warmest time of year. Some spawning also occurs up to 2 or 3 d on either side of this lunar phase. Generally speaking, tidal fluctuations, and thus tidally induced currents, tend to be minimal during neap tides, which occur around half moons. In addition, the long-term record of regional significant wave height shows that the spawning at the Flower Gardens consistently occurs during the period of calmest sea state. Separately, any of these factors are likely to reduce the rate of separation by eggs and sperm at the surface. Together, they may further increase the likelihood and duration of sperm/egg encounters (e.g., Levitan et al., 1991) and the effectiveness of sperm attractants (Coll et al., 1994). Water

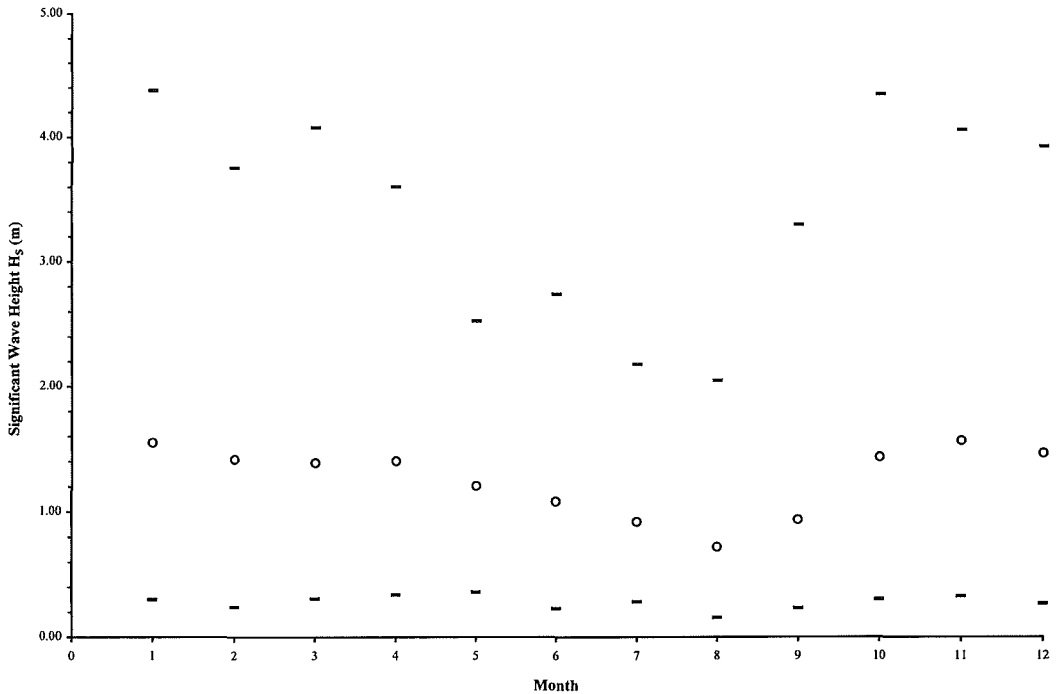


Fig. 3. Mean, maximum, and minimum significant wave height H_s (m) measured at the C-MAN Buoy 42019 (27.92°N, 95.35°W) from 1990 to 1997. Circles represent mean values. The dash marks on either side of monthly means are monthly significant wave height maxima and minima.

temperatures during this period also promote rapid larval development (e.g., Michael, 1981), as well as sperm motility and longevity (Appell and Evans, 1977).

Nocturnal spawning would reduce the potentially negative effects of UV radiation on development (Jeffrey, 1990a,b) and reduce predation by visual predators (Babcock et al., 1986; Westneat and Resing, 1988). Under laboratory conditions, exposure to UV for periods of up to 3 d caused significant levels of mortality in *Montastraea* sp. larvae (G. Wellington, pers. comm.). Gamete buoyancy reduces the capture rate by potential benthic invertebrate predators (e.g., brittle stars). These same influences likely also influence the timing of spawning by many nonscleractinian invertebrate species associated with coral reefs (Giese, 1959; Hendler and Meyer, 1982; Brazeau and Lasker, 1989; M.L.J. van Veghel, unpubl. data), including *Ophioderma rubicundum* and *Spirobranchus giganteus* at the Flower Gardens.

Corals at the Flower Gardens probably do not experience perceptible tidal variation. They are in water more than 20 m deep in an area with mixed diurnal tidal ranges of less than 0.5 m. Nevertheless, spawning and lunar phase appear to be closely correlated. It is like-

ly that these corals have retained a lunar rhythm evolutionarily acquired by shallow-water ancestors in places where it had adaptive value. This would explain consistent timing among corals on shallow and deeper reefs and those in different tidal regimes (Hayashibara et al., 1993; Babcock et al., 1994).

Although it is clear that warmer water temperatures are more favorable for fertilization and development of reef invertebrates and fish, it is important to note that significant variation exists worldwide with regard to the timing of broadcast spawning relative to water temperature. Spawning on the Great Barrier Reef occurs during the austral spring, a period of rapidly rising seawater temperature (Harrison et al., 1984). Spawning in the Arabian Gulf, Red Sea, and Ryukyu Islands also occurs during the spring (Fadlallah, 1996). But on the western coast of Australia, southern Japan, and in the Caribbean, annual mass spawnings occur in late summer, following seawater temperature maxima (Szmant, 1986; Harrison and Wallace, 1990; Gittings et al., 1992a, 1994; van Veghel, 1994; van Woeseik, 1995). In Taiwan, populations at the southern end of the island spawn during spring, and northern populations spawn 2 mo later during the summer

(Dai et al., 1992). Furthermore, the initiation of gametogenesis appears to be triggered by temperature signals (e.g., Szmant, 1991). Thus, the importance of water temperature in the reproductive process of reef invertebrates is evident, but not clearly understood (see also Harrison and Wallace, 1990).

That temperature and lunar phase work together to influence broadcast spawning at the Flower Gardens is evident when one evaluates observations made during years when full moons occurred before temperature maxima (i.e., in early August). During such years, spawning events tended to be split over 2 mo (August and September; see also Willis et al., 1985). The most dramatic spawning took place when full moons occurred during or after temperature maxima (Fig. 1), suggesting that temperature maxima and lunar phase act as dual stimuli for gamete release. Where annual temperature ranges are minimal (e.g., low latitudes), multiple annual spawning events are not uncommon (Harrison and Wallace, 1990; van Veghel, 1994).

The effect of water column productivity at the Flower Gardens on gamete production is unknown. There is some evidence suggesting annual nutrient pulses over the banks that last for several weeks in early summer. During these periods, light attenuation in the water column increases (Fig. 1), and organic matter may become available during gametogenesis. How this influences the level of gamete production and other aspects of reproduction has yet to be determined (but see Ambrose and Renaud, 1997; Company and Sarda, 1997; Ohga and Kitazato, 1997).

Synchronous spawning could promote gamete wastage caused by hybridization. Yet, within the limited time frame for broadcast spawning at the Flower Gardens, closely related coral species appear to have different release times. More distantly related species are more likely to spawn together. The latter is the case for *Diploria strigosa* and *Montastraea franksi*. Although these species spawn together, siblings such as *M. franksi* and *M. faveolata* broadcast gametes at least 1 hr apart. This, combined with probable physiological barriers to cross-fertilization between the two species (Hagman et al., 1998), reduces the likelihood for hybridization.

Harrison and Wallace (1990) noted a higher degree of asynchrony among gonochoric broadcasters than hermaphroditic species. Observations at the Flower Gardens support this. *Montastraea cavernosa* and *S. intersepta* have been much less predictable than other species

participating in mass spawning. Spawning by these two species has been observed between the sixth and 10th evenings following full moon. In addition, *M. cavernosa* may spawn a month before or after the primary event. Our observations suggest that fertilization of eggs in these species may be largely internal. Males generally spawn up to 30 min before females for both *M. cavernosa* and *S. intersepta*. Eggs collected by divers upon release show evidence of fertilization exceeding 95% (Hagman et al., 1998). Therefore, although some degree of coordination between males and females is required to ensure success, timing relative to lunar and tidal rhythms does not appear to be as critical as for externally fertilizing species.

Corals that broadcast gametes have evidently adapted in a convergent manner in response to conditions that favor reproductive success (see review by Harrison and Wallace, 1990). Their behaviors and physiological adaptations minimize hybridization and predation and ensure high fertilization levels. Although most individuals of each species spawn synchronously on the same night, invariably some individuals spawn on other nights or at unexpected times, such as during the day (based on one observation of sperm release by a male *M. cavernosa*). This "bet-hedging" behavior (e.g., Stanton, 1992) may be beneficial in the event of poor conditions (e.g., unusually heavy rains; Harrison et al., 1984) or changing climate, may provide a mechanism for adaptive drift in reproductive timing, and could reduce interbreeding among closely related species, such as *M. annularis*, *M. faveolata*, and *M. franksi*.

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