

Seasonal reproduction in equatorial reef corals

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Summary

Populations of broadcasting reef corals often exhibit marked reproductive seasonality and spawning synchrony. Within speciose coral assemblages there is often considerable overlap of spawning periods among species, resulting in multi-species spawning events (or “mass coral spawning”). Earlier geographical comparisons of reproductive synchrony suggested a reduction in the extent of mass spawning with proximity to the equator. In contrast, recent studies have revealed that reproductive seasonality and spawning synchrony within and among species are features of coral assemblages on equatorial reefs. Here we review the proposed causes of synchronous spawning among reef corals and discuss how recent findings about reproduction of corals from Singapore’s equatorial reefs shed light on these various theories. Sexual reproduction in broadcasting corals requires external fertilization, so reproductive seasonality (leading to spawning synchrony) within populations is probably highly adaptive because synchrony increases the chances of gametes meeting, enhances the possibility of outbreeding and may swamp opportunistic predators. No coastal location is truly aseasonal, with even equatorial reefs experiencing marked (albeit less pronounced) rhythmic changes in sea surface temperature. Consequently, if species respond similarly but independently to timing cues to synchronize reproduction within populations, mass spawning is just as likely to occur in equatorial coral assemblages as it is at higher latitudes.

Key words: Coral reef, mass spawning, synchrony, equatorial, seasonality, Singapore

Introduction

For much of the last century it was assumed that the primary reproductive mode for scleractinian corals was internal brooding followed by release of planula larvae

(vivipary) (e.g., Marshall and Stephenson, 1933; and see review by Harrison and Wallace, 1990). However, this premise was based on limited studies of certain brooding species and was eventually questioned by a

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number of authors (e.g., Connell, 1973; Stimson, 1978; Rinkevich and Loya, 1979a).

In the 1980s, several studies revealed that the dominant reproductive mode for scleractinian corals is broadcast spawning of gametes, followed by external fertilization (e.g., Szmant-Froelich et al., 1980; Kojis and Quinn, 1981a, 1981b, 1982; Harriot, 1983; Krupp, 1983; Babcock, 1984; Harrison et al., 1984; Wallace, 1985; Sclesinger and Loya, 1985; Babcock et al., 1986; Heyward et al., 1987; Heyward, 1988). Broadcasting species are either hermaphroditic or gonochoric (Harrison, 1985) and mature colonies usually breed annually (Babcock et al., 1986) or in some cases bi-annually (Stobart et al., 1992). For broadcasters, spawning often occurs during short predictable periods and it is common for many species to spawn during “mass spawning” events (e.g., Harrison et al., 1984; Simpson, 1985; Babcock et al., 1986; Heyward, 1986; Willis et al., 1985; Hayashibara et al., 1993; Bermas et al., 1992; Dai et al., 1992; Richmond and Hunter, 1990; Hagman et al., 1998; Guest et al., 2002). Compared to other cnidarian groups, sexual reproduction among the Scleractinia has received considerable attention (Harrison and Wallace, 1990). Each year, studies on coral reproduction appear from different regions and for new species. Some robust generalizations can be made based on the current available data, but there are still many gaps in our knowledge. For the majority of hermatypic scleractinian species we still have only rudimentary data (Harrison, 1985; Richmond and Hunter, 1990); and few studies are available from low latitude and equatorial reefs in the Indo-West Pacific (Bermas and Alino, 1994). These regions are of particular interest because they contain some of the least studied, most biologically diverse and most endangered coral communities in the world (Bryant et al., 1998).

The ranges and amplitudes of many environmental variables believed important in regulating marine invertebrate reproductive cycles (e.g., sea temperature, photoperiod, solar radiation) become less extreme with proximity to the equator (Nieuwolt, 1973). For marine invertebrates with wide latitudinal distributions, this is thought to lead to more protracted breeding seasons, presumably because conditions are suitable for reproduction for a greater part of the year, and/or there are a lack of suitable seasonal reproductive cues close to the equator (Orton, 1920; Giese and Pearse, 1974; Rinkevich and Loya, 1979b). For example, latitudinal comparisons of reproductive seasonality in the coral reef sea urchin, *Diadema setosum*, revealed longer breeding seasons at lower latitudes, with apparently “continuous” reproduction close to the equator in Singapore (1°10'N) (Pearse, 1970; Hori et al., 1987), although

even on low latitude reefs in Kenya (3°55'S) Muthiga (2003) found some seasonal variation in reproductive effort in *D. setosum*, with gonad indices negatively correlated with sea temperature and solar radiation.

The environmental causes of reproductive timing, in particular the putative role of sea temperature, have been discussed by many authors (e.g., Babcock et al., 1986, 1992; Oliver et al., 1988). In this paper we review and examine the various theories proposed to explain reproductive seasonality, spawning synchrony and “mass spawning” in broadcasting corals in the light of recent studies from equatorial coral reefs (defined here as reefs between 10°N and 10°S). We also briefly discuss the possible role of sea temperature in regulating reproductive cycles in corals. The review focuses on Indo-Pacific reefs and, in particular, we summarize a series of studies carried out to examine the seasonal patterns and reproductive synchrony of broadcasting corals on the equatorial reefs of Singapore (Guest, 2004; Guest et al., 2002, 2005). We also present some new data in the form of species lists documenting corals witnessed spawning in Singapore during field trips carried out in March 2002 and April 2003 (see Tables 2 and 3) (see Guest et al., 2002, 2005, for description of methods).

Regulation of Timing and Seasonality of Reproduction in Broadcast Spawning Corals

Broadcasting corals usually exhibit spawning synchronization within populations (i.e., simultaneous release of gametes among conspecifics) (Harrison et al., 1984). Despite the common misconception that spawning is synchronized on a single night over a large scale, spawning within populations is more commonly “split” over consecutive nights or lunar months (Babcock et al., 1986; Willis et al., 1985; Baird et al., 2002; Wolstenholme, 2004). Nonetheless, broadcast spawning corals exhibit marked reproductive seasonality (concentration of reproductive output to certain parts of the year), usually with a single annual gametogenic cycle, although biannual spawning has been documented for two *Montipora* species at Magnetic Island on the Great Barrier Reef (Stobart, 1992). It is important to distinguish between synchrony and seasonality in corals. Marked seasonality may not lead to spawning synchrony; similarly, coral populations that have extended breeding seasons may still spawn synchronously within short time windows based on the lunar and diel cycles. To maintain seasonal rhythms the processes of gametogenesis and spawning must be regulated by similar individual responses to a range of environmental factors which interact to cause a distinct

breeding season and a well-defined spawning period (Campbell, 1974).

Various hypotheses have been proposed to explain the causes of reproductive seasonality and spawning synchrony in marine invertebrates (see Baker, 1938; Giese and Pearse, 1974; Clark, 1979; Olive, 1992, 1995, 2000; Lewis et al., 2003) and in reef corals (see Harrison et al., 1984; Babcock et al., 1986, 1992; Oliver et al., 1988). It is useful to make a distinction between the environmental regulatory mechanisms directly responsible for seasonal patterns and the potential adaptive significance of these patterns (the so-called “proximate” and “ultimate” factors, respectively) (Baker, 1938). Because corals are incapable of aggregating and broadcast spawning results in external fertilization, probably the most plausible explanation for spawning synchrony within coral populations is that synchrony maximizes fertilization rates by increasing the chance of the gametes of conspecific individuals meeting in the water column (Oliver and Babcock, 1992; and see discussions in Babcock et al., 1992; Olive, 1992). Oliver and Babcock (1992) found fertilization rates in the water column were significantly higher for *Montipora digitata*, *Platygyra sinensis* and *Favites pentagona* on their principle spawning night compared to nights when fewer colonies spawned, presumably because of rapid dilution of gametes on those nights (Oliver and Babcock, 1992). There may also be further adaptive benefits of synchronous spawning gained through outbreeding (the benefits of sex, e.g., Bell, 1982), or if opportunistic predators are swamped (Harrison et al., 1984).

It is often implied in explanations of reproductive seasonality and synchrony that there must also be strong selection for spawning at a particular time, i.e., when conditions are most likely to be favourable for fertilization and/or larval survival (Babcock et al., 1986, 1992; Oliver et al., 1988; and see Olive et al., 2000). For example, spawning may be timed to coincide with periods when sea temperatures are “optimal” for gametogenesis and/or fertilization (Babcock et al., 1986); when planktonic food is most abundant (as is the case for some temperate polychaete worms, Watson et al., 2003); or to avoid periods of inclement weather (e.g., heavy rainfall; Mendes and Woodley, 2002). Similarly, spawning at certain periods of the tidal cycle may be beneficial. For example, spawning at low tide may decrease sperm dilution, whereas spawning during a period of slack water may provide sufficient time for gametes to meet before being dispersed by tidal currents (Babcock et al., 1986). Finally, spawning at night may have adaptive significance, as predation by planktivorous organisms that rely heavily on vision may be reduced (Babcock et al., 1986).

Furthermore, nocturnal spawning may reduce the damaging effects of UV radiation during the initial period of embryo development (Jeffry, 1990).

Synchronization may be maintained by similar responses to a range of environmental signals working in concert to regulate gamete maturation and spawning (Babcock et al., 1986). While progress has been made in establishing the final proximate controls of spawning time (i.e., those that define the night and time of spawning) (Babcock, 1984; Hunter, 1988; Gorbunov and Falkowski, 2002), the distal proximate cues (i.e., those that regulate the onset of gametogenesis and/or maturation of gametes) are more contentious, particularly in regard to the role of sea temperature (Simpson, 1985; Kojis, 1986; Penland et al., 2004; Mendes and Woodley, 2002). Because seawater has a high heat capacity, sea temperatures often vary rhythmically throughout the year, providing corals with a reliable cue to synchronize reproduction (Giese and Pearse, 1974). Considerable correlative evidence indicates that changes in sea temperature provide a seasonal cue for reproduction of a number of broadcasting corals (e.g., Szmant-Froelich et al., 1980; Kojis and Quinn, 1981a, 1981b; Krupp, 1983; Babcock et al., 1986; Van Veghel, 1994; Fan and Dai, 1995; Mendes and Woodley, 2002). On the Great Barrier Reef, spawning is one month earlier on inner reefs than outer reefs and this correlates with a delay in sea temperature rise (Willis et al., 1985; Babcock et al., 1986). There is one example of an experiment demonstrating that spawning times in broadcasting corals can be altered by manipulating the ambient sea temperature (Hunter, 1988). Hunter (1988) showed that spawning was precluded in colonies of *Montipora verrucosa* ($n = 4$) and *M. dilatata* ($n = 2$) maintained at winter seawater temperatures (approx 22°C) during the normal spawning period for these species in Hawaii (June–August). One experimental colony of *M. verrucosa* and both colonies of *M. dilatata* spawned approximately 1 month after seawater temperatures were returned to ambient levels (26.4°C) (Hunter 1988). Further experimental evidence is needed to establish the role of sea temperature in regulating coral reproductive cycles; this information is of particular importance in the light of predicted rises in global sea temperatures and concerns over the observed declines in the health of coral reefs.

Spawning in many scleractinians studied to date reveals the main annual spawning period at the time of year when temperatures are rising or at the annual maxima (Fadlallah, 1983; Babcock et al., 1986; Harrison and Wallace, 1990; Richmond and Hunter, 1990; Hayashibara et al., 1993; Mendes and Woodley, 2002). However, spawning of conspecific coral populations at different locations often occur at different periods

within seasonal sea temperature cycles (Simpson, 1985; Hayashibara et al., 1993; Stobart et al., 1992; Fan and Dai, 1995; Sclesinger and Loya, 1985; Babcock et al., 1994). Populations of certain corals on the east and west coasts of Australia spawn predominantly in different seasons, despite experiencing similar annual temperature regimes (Simpson, 1985). This disparity led Simpson (1985) to suggest that spawning times are a genetic legacy of timing selected for in ancestral populations. The original adaptive value may have been lost in the descendants, but the inherited spawning rhythm will remain the same, providing that the new regime does not exert a selective pressure to counteract the genetic legacy (Babcock et al., 1994). Furthermore, if the genetic connection between reefs remains high, this may inhibit the ability of the population to adapt to the new conditions. Some of these disparities may be resolved by investigating spawning patterns over a complete annual cycle in these locations, and recent data from Scott Reef in Western Australia revealed that many broadcasting coral species spawned in both March/April and October/November (i.e., at the same time as those on the Great Barrier Reef) (J. Gilmour, pers. comm.).

The apparent inconsistency in the relationship between spawning times and changes in annual sea surface temperatures have led some authors to suggest that other environmental factor(s) may be important e.g., rainfall (as an ultimate factor) (Mendes and Woodley, 2002) or insolation (potentially as both an ultimate and a proximate factor) (Penland et al., 2004). Attempts to understand the role of temperature (or any other seasonal environmental variable for that matter) are confounded because of the difficulty in decoupling non-independent climatic processes and the inability to imply cause based on correlation alone (Olive, 1995).

One major barrier to the acceptance of sea temperature as the primary, seasonal timing signal for reproduction in corals is rooted in the assumption that annual variations in sea temperature in equatorial locations (i.e., between 10°N and 10°S) are insufficient to provide a reliable cue for reproduction. If this assumption were true, there would either be a progressive latitudinal breakdown in reproductive synchrony (particularly between species) (Oliver et al., 1988; Richmond and Hunter, 1990; Kenyon, 1995); or if seasonal reproduction does occur, then some factor(s) other than temperature must regulate reproductive seasonality and synchrony in equatorial corals (Mendes and Woodley, 2002; Penland et al., 2004). Alternatively, the assumption is simply wrong and the “myth” of the benign equatorial tropics is exactly that. Indeed, marked reproductive seasonality is a feature of many equatorial coral assemblages (Edinger et al., in

Tomascik et al., 1997; Baird et al., 2001, 2002; Guest et al., 2002, 2005; Penland et al., 2004), and there are adequate proximate cues for seasonal reproduction, including marked changes in sea temperature associated with the monsoons (Nieuwolt, 1973, and see below).

“Mass” Coral Spawning

One of the most remarkable features of reef coral assemblages is the phenomenon of multi-species synchronous spawning, or “mass” coral spawning (Harrison et al., 1984; Willis et al., 1985; Babcock et al., 1986). During the mass spawning period on parts of the Great Barrier Reef, at least 140 scleractinian species spawn over eight nights in late spring and at least 31 species have been documented spawning simultaneously on one reef. Following mass spawning events, gametes form slicks on the surface that can be a few kilometers in length, making them visible from the air (Oliver and Willis, 1987). Multi-species spawning has also been documented among other invertebrate and algal assemblages on coral reefs (Babcock et al., 1992; Alino and Coll, 1989; Clifton, 1997) and in Irish sea lochs (Minchin, 1992). Mass coral spawning events have been observed in coral assemblages over a wide geographical range, including eastern and western Australia (Harrison et al., 1984; Simpson, 1985; Willis et al., 1985; Babcock et al., 1986; Babcock et al., 1994; Wilson and Harrison, 2003); Bermuda (Wyers et al., 1991); the Central Pacific (Richmond and Hunter, 1990); Curacao (Van Veghel, 1993); the Gulf of Mexico (Hagman et al., 1998); Hawaii (Heyward, 1986); Indonesia (Edinger et al., in Tomascik et al., 1997); Japan (Heyward et al., 1987; Hayashibara et al., 1993; van Woesik, 1995); the Maldives (pers. obs.; A. Azeez, pers. comm.; Loch et al., 2002); Palau (Penland et al., 2004); the Philippines (Bermas et al., 1992); Singapore (Guest, 2004; Guest et al., 2002, 2005); the Solomon Islands (Baird et al., 2001); Taiwan (Dai et al., 1992); and Yap (Kenyon, 1995). Indeed, multi-species spawning among broadcasters is a probably a feature of all speciose coral assemblages. Early comparisons of reproductive patterns between the Red Sea and the Great Barrier Reef led Schesinger and Loya (1985) to assert that Red Sea corals exhibit “temporal reproductive isolation” (i.e., no overlap in spawning periods among species), a contention that was upheld by Schesinger et al. (1998). However, this assertion is based on incomplete sampling of broadcasting assemblages (i.e., a small proportion of the species assemblage from distantly related families) from only one location in the northern Red Sea (Eilat). Their data actually indicate marked reproductive seasonality, with the majority of broadcasting species reproducing over

a period of 3 to 4 months in the summer (Schlesinger et al., 1998). The six sampled *Acropora* species spawned within a 2-month period (Schlesinger and Loya, 1985; Schlesinger et al., 1998). With at least 42 *Acropora* species present in the Red Sea (Wallace, 1999), it would be surprising if there were truly no overlap in spawning periods among species. Sampling that is representative geographically, taxonomically and temporally is required to establish the extent of reproductive seasonality and synchrony among broadcasting corals elsewhere in the Red Sea.

The reasons why many coral species might spawn together are not clear. Indeed, some authors have suggested that there may be a number of potential disadvantages to this strategy, e.g., the production of non-viable inter-species hybrids (Hodgson, 1988) and competition among larvae for settlement space (Schlesinger and Loya, 1985). A number of explanations for the existence of mass spawning have been proposed (see Harrison et al., 1984; Harrison and Wallace, 1990; Babcock et al., 1986, 1992; Oliver et al., 1988) and are synthesized here.

(1) Multi-species spawning is itself an adaptive strategy, i.e., species gain some advantage by timing spawning to occur when other species are spawning (e.g., predator satiation). Species may have co-evolved short, overlapping spawning periods; too ephemeral to rely on as source of food and of large enough scale to swamp opportunistic predators. The other explanations take into consideration the fact that most of the documented “mass spawning” species are closely related or have very similar reproductive strategies and larval development patterns. Thus, it is plausible that these species have responded in a similar, but independent way to regulating factors, resulting in brief overlapping spawning periods. This can happen in at least three ways (none of which are mutually exclusive).

(2) Allocation of resources to reproduction is limited to certain times of the year as a direct result of the amount of energy available.

(3) Species respond to, or are entrained by, specific seasonal, lunar and diel “cues” (i.e., transducible environmental timing signals) to (a) increase the chances of fertilization and outbreeding within populations and/or (b) spawn at the time of the year when environmental conditions are likely to be “optimal” for successful fertilization, larval development, survival and/or settlement.

Reproductive Seasonality and Spawning Synchrony on Equatorial Reefs

As previously stated, in equatorial regions where the range and amplitude of sea temperature and other

environmental variables are often less pronounced, it was predicted that little reproductive synchrony among species would occur (Oliver et al., 1988; Richmond and Hunter, 1990; Kenyon, 1995). Furthermore, on reefs experiencing small sea temperature ranges, it was expected that initiation of gametogenesis would be more frequent (Oliver et al., 1988). Studies of reproductive timing and seasonality of some marine invertebrate species suggest that breeding seasons are longer at low latitudes (e.g., *Diadema setosum*) (Pearse, 1970; Hori et al., 1987; Muthiga, 2003; and see Orton, 1920; Giese, 1959; Giese and Pearse, 1974). Similarly, in brooding corals that have been studied over a wide latitudinal range, breeding seasons appear to become more protracted at lower latitudes. *Acropora palifera* was reported to spawn only once a year on the southern Great Barrier Reef (Heron Island 23°S), but year round in the northern Great Barrier Reef (Lizard Island 14°S) and in Papua New Guinea (7°S) (Kojis, 1986). Release of planulae among certain pocilloporids (*Pocillopora damicornis*, *Seriatopora hystrix*, *Stylophora pistillata*) occurs seasonally on parts of the southern Great Barrier Reef (Heron Island 23°S) (Tanner, 1996) but year round in Palau (7°N) (Atoda, 1947a, 1947b, 1951). It is important to note, however, that comparisons among different marine invertebrate taxa or even between brooding and broadcasting corals may not be appropriate when attempting to make generalizations, as contrasting life histories and reproductive strategies may result in quite different reproductive patterns.

For populations of the broadcasting species *Acropora formosa* and *A. hyacinthus*, Oliver et al. (1988) reported reduction in spawning synchrony and evidence of biannual spawning at Madang on the northern coast of Papua New Guinea (5°S) compared to populations on the Great Barrier Reef. Apart from this single study (Oliver et al., 1988), there was no other evidence to support the hypothesis of a latitudinal breakdown in synchrony or multiple annual gametogenic cycles for broadcasting species at the equator. Indeed, it has now emerged that multi-species synchrony does occur in coral assemblages at low latitudes. In the Karimunjawa Islands (central Java Sea), where sea temperature ranges between 27.5°C and 29°C, Edinger et al. (cited in Tomascik et al., 1997) observed 22 scleractinian species spawning over three nights following the full moon in October 1995. Similarly, in the Solomon Islands (8°N) where there is little fluctuation in annual temperature or tidal amplitude, Baird et al. (2001) found that 28 of 41 *Acropora* species contained mature eggs in the week prior to the full moon in November 1999. Results from one study in Palau (7°30'N) lend support to both ideas (i.e.,

multi-species synchrony and longer breeding seasons on an equatorial reef) (Penland et al., 2004). Penland et al. (2004) observed a large number of coral species spawning synchronously in April 2002 and considered this event to be the most extensive for that year. However, further studies revealed four subsequent mass spawning events in May, August and September 2002 and February 2003, involving a total of 47 broadcasting species (Penland et al., 2004).

Reproduction of Corals in Singapore

Singapore is a small island nation situated at the southern most tip of Peninsula Malaysia, approximately 137 km north of the equator, between latitudes 1°09'N and 1°29'N, and longitudes 103°36'E and 104°25'E. Despite extensive coastal reclamation over the past four decades, relatively diverse coral assemblages are found around many of the islands south of mainland Singapore (Chou, 1996). Singapore's equatorial location and the accessibility of its reefs make it an ideal location for reproductive studies. Here we summarize the results of an investigation carried out between 2001 and 2003 to examine the seasonal timing of reproduction and extent of synchrony among corals on Singapore's reefs (see Guest, 2004; Guest et al., 2002, 2005, for full details).

We investigated the gametogenic cycles of two common broadcasting scleractinian corals from different families with contrasting reproductive modes. A gonochoric broadcaster, *Porites lutea* (Poritidae), and a hermaphroditic broadcaster, a morphospecies of *Platygyra* (Faviidae), were sampled monthly over 14 months between March 2001 and April 2002 (Guest, 2004). Histological analysis revealed markedly similar seasonal gametogenic cycles with maturation of gametes and spawning occurring predominantly in March and/or April (Guest, 2004). There was some evidence of biannual spawning in both species with the second spawning between September and November, with <20% of colonies containing mature eggs at this time compared to 100% of colonies in April (Guest, 2004). These findings suggest that the majority of colonies spawn during the main spawning season (i.e., around March/April), although some of these colonies undergo a second annual gametogenic cycle that culminates between September and November (Guest, 2004). The length of the oogenic and spermatogenic cycles of *Porites lutea* (4–6 months and 1–3 months, respectively) were found to be similar to three other studies of this species between latitudes 23° and 29°N, indicating that the length of the gametogenic cycle is relatively constant within this species throughout its range (Table 1) (Guest, 2004).

To see if the seasonal reproductive patterns were similar (i.e., March/April spawning) for other scleractinian species, we noted the presence of ripe gametes (based on egg colour) in an assemblage of *Acropora* over 15 months between March 2002 and May 2003 (Guest et al., 2005). This method allowed us to sample large numbers of colonies and to ascertain the reproductive season and the extent of synchrony (in terms of gamete maturation) within and among species. At a seasonal level there was marked reproductive synchrony among species in the *Acropora* assemblage, with the majority appearing to spawn in March and April (Guest et al., 2005). In March 2002 and April 2003, 68% (n = 19) and 79% (n = 14), respectively, of species had colonies containing mature gametes (Guest et al., 2005). Around half of the colonies sampled in March 2002 (48.5%, n = 113) and April 2003 (47.4%, n = 98) were ready to spawn (inferred from the presence of pigmented eggs) (Guest et al., 2005). Populations of at least two species (*Acropora hyacinthus* and *A. digitifera*) were split over at least 2 months (Guest et al., 2005). A few colonies (<5%) were ready to spawn in October and November (Guest et al., 2005). Two tagged colonies of *A. humilis* contained mature eggs in October/November 2002 and again in April 2003, suggesting that some colonies may spawn bi-annually (Guest et al., 2005). Within species, the proportions of colonies that contained mature gametes varied considerably. Some populations were highly synchronous, for example 86% of *Acropora humilis* (n = 7) and 75% of *A. digitifera* (n = 16) were ready to spawn in the same month (April 2003) (Guest et al., 2005). Other species had moderate or low levels of population synchrony or population fecundity during the main spawning season. For example, only 42% of *A. hyacinthus* colonies (n = 12) and 12% of *A. tenuis* colonies (n = 8) were mature at the same time (Guest et al., 2005). It is not clear why many of the colonies were not fecund during the spawning season. It is possible that some individuals spawn at other times of the year (although we failed to find fecund colonies in months outside of the main spawning season), or not at all in some years (i.e., some colonies may skip a year altogether). Reproductive output may also be reduced by environmental stressors, such as chronic fragmentation (Wallace, 1985), bleaching (Baird and Marshall, 2002) or decreased water quality (Ward and Harrison, 2000). Long-term studies following individual colonies and populations through time are required to understand the reproductive patterns of these species on Singapore's reefs.

We carried out nighttime observations *in situ* to see whether corals in Singapore participate in mass spawning events similar to those described by Willis et al.

Table 1. Comparison of the gametogenic cycle *Porites lutea* from four studies between latitudes 23°S and 29°N

Location	Reproductive strategy	Length of gametogenic cycle (months)	Month of spawning	Reference
Eilat, Israel, N. Red Sea (29°N)	Gonochoric, some male polyps found in predominantly female colony	♀ 5, ♂ 2	July	Schlesinger et al., 1998
Singapore (1°N)	Gonochoric	♀ 4–6, ♂ 1–3	Predominantly March and April	Guest, 2004
Lizard Island, GBR (14°S)	Gonochoric	♀ 4–6, ♂ 1–2	November–January	Harriot, 1983
Heron Island, GBR (23°S)	Gonochoric	♀ ♂ approx. 4	mid-January–early February	Kojis and Quinn, 1981a

(1985) on the Great Barrier Reef (Guest, 2004; Guest et al., 2002). Many scleractinian species, including *Acropora* spp., spawned in the weeks following the full moons of March 2002 and April 2003 during 2-h periods between approximately 20:00 h and 22:00 h (Guest, 2004; Guest et al., 2002). Between 5 and 12 species were seen spawning simultaneously on each night (Guest, 2004; Guest et al., 2002). Spawning of at least 18 scleractinian species from five families (Acroporidae, Faviidae, Merulinidae, Oculinidae and Pectiniidae) was documented at one reef (Raffles Lighthouse) between the third and the fifth nights after the full moon in March 2002 (Table 2, Fig. 1) (Guest, 2004; Guest et al., 2002). Similarly, in April 2003 at least 13 scleractinian species from five families (Euphyllidae, Faviidae, Merulinidae, Oculinidae and Pectiniidae) spawned between the third and sixth nights after the full moon at another reef (Pulau Hantu) (Table 2, Fig. 1) (Guest, 2004). We also fractured polyps of a range of other coral species prior to the spawning event in April 2003 and found that a further 13 species from four families (Favidae, Merulinidae, Mussidae and Euphyllidae) contained pigmented gametes (Table 3) (Guest, 2004), although it is possible for some of these species that gametes may become pigmented two or more months prior to spawning.

Clearly marked reproductive seasonality and spawning synchrony within and among species are characteristics of Singapore's corals. While the majority of reproductive effort appears to be concentrated during a single seasonal mass spawning period in Singapore, many colonies may spawn at other times of the year or not spawn at all in some years (Guest, 2004; Guest et al., 2005). This is not evidence of a latitudinal breakdown in synchrony. The situation is, in fact, very similar to that on the Great Barrier Reef where many species and colonies spawn outside the main mass spawning periods, or not at all in some years. In a 2-year study of nine sympatric *Acropora*

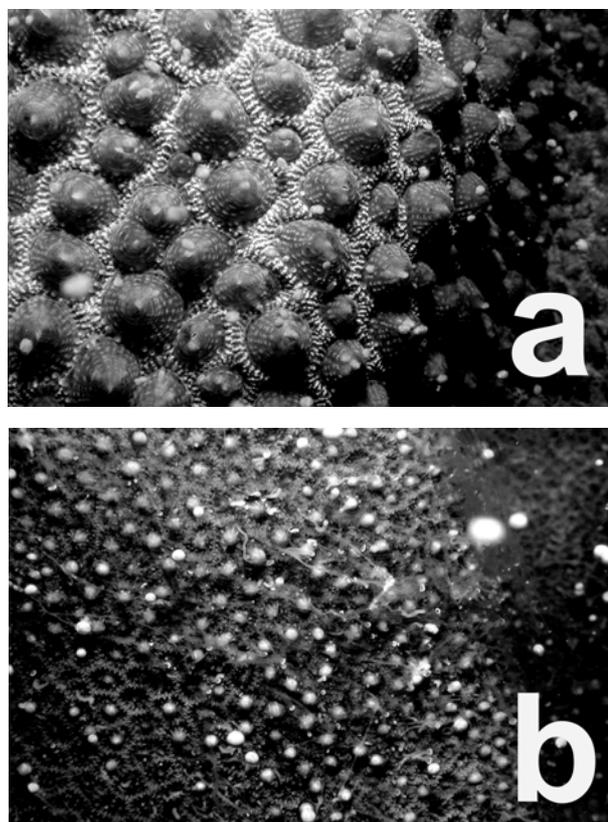


Fig. 1. Corals spawning in Singapore following the full moon in March 2002. a, *Favites* sp.; b, *Goniastrea minuta*.

species at Big Broadhurst Reef (18°55'S), Wallace (1985) found that colonies of *Acropora granulosa* spawned in late summer (i.e., approximately 4 months after the main spawning period); colonies of *A. sarmentosa* were mature in February, August and November; and colonies of *A. horrida* were never found to contain mature gametes (Wallace, 1985). In a study to compare latitudinal variation in spawning synchrony among the *Acropora*, Baird et al. (2002) found that

Table 2. List of corals observed spawning in 2002 and 2003

Family and species	Mode	Number of nights after full moon March 2002	N	Number of nights after full moon April 2003	N
Family Acroporidae					
<i>Acropora millepora</i>	H	3–5	3	—	—
<i>Acropora hyacinthus</i>	H	5	2	—	—
<i>Acropora</i> sp. 1	H	3–5	3	—	—
Family Faviidae					
<i>Echinopora lamellosa</i>	H	5	1	5	1
<i>Echinopora</i> sp.	H	4	1	1	1
<i>Favia</i> sp.	H	4	1	—	—
<i>Favites halicora</i>	H	3	1	—	—
<i>Favites</i> sp. 1	H	3	>5	5	1
<i>Favites</i> sp. 2	H	4	1	—	—
<i>Goniastrea minuta</i>	H	3–5	3	3	1
<i>Goniastrea pectinata</i>	H	3	1	—	—
<i>Oulophyllia benettae</i>	H	—	—	3	1
<i>Oulophyllia</i> sp. 1	H	—	—	3	1
<i>Platygyra ryukyuensis</i>	H	3–4	>5	3–5	2
<i>Platygyra sinensis</i>	H	3–4	>5	—	—
<i>Platygyra</i> sp. 1	H	3–5	>5	6	1
Family Merulinidae					
<i>Merulina ampliata</i>	H	5	>5	3–6	>5
<i>Scapophyllia cylindrica</i>	H	3	1	—	—
Family Oculinidae					
<i>Galaxea fascicularis</i>	G*	4–5	>5	3–6	>5
<i>Galaxea astreata</i>	G*	4	1	—	—
Family Pectiniidae					
<i>Echinophyllia</i> sp.	H	5	1	—	—
<i>Pectinia lactuca</i>	H	—	—	4–5	2
<i>Pectinia paeonia</i>	H	4	>5	3–6	>5
Family Euphyllidae					
<i>Euphyllia ancora</i>	G	—	—	4–6	3

Reproductive mode: H, hermaphrodite; G, gonochoric; G*, pseudo-gynodioecous. Full moons dates were March 29th 2002 and April 17th 2003. N = number of colonies observed spawning. Observations began on the day of the full moon and continued until the 5th night after full moon in 2002 and the sixth night after the full moon in 2003.

high synchrony in gamete maturity among colonies for most of the *Acropora* species studied at Lizard Island (14°S), Pelorus Island (18°40'S) and Lady Elliot Island (23°45'S) was the exception, rather than the rule. Similarly, in a study of five species and seven morphospecies from the *Acropora humilis* group at Lizard Island, Wolstenholme (2004) found that a second substantial spawning event occurs 3 months after the main mass spawning, with all but one of the study species participating in both events. For example, colonies of *A. samoensis* spawned 1, 2 and 3 months after the main mass spawning period; the majority of colonies of *A. digitifera* spawned three months after the mass spawn; and colonies of *A. gemmifera* were highly variable in their spawning times with mature colonies present over a period of 4 months. Finally, Hughes et al. (2000) found that

some colonies of *A. hyacinthus*, *A. cytherea* and *A. millepora* did not contain eggs during the main spawning period in one year in both the northern and southern Great Barrier Reef, suggesting that some colonies miss one or more years, or spawn in other months.

Cause of Multi-species Spawning Synchrony on Equatorial Coral Reefs

In the absence of manipulative experiments, it is only possible to speculate about which environmental factor(s) in Singapore have caused marked reproductive seasonality among and within broadcasting coral populations. However, despite Singapore's equatorial position, distinct and predictable seasonal patterns of sea surface temperature do occur because of

Table 3. Coral species, number of colonies sampled and egg colours from fractured polyps just before the full moon in April 2003

Family and species	N	Colour
Family Faviidae		
<i>Diploastrea heliopora</i>	2	Red/orange
<i>Favia</i> sp. 1	2	Blue/green
<i>Favia</i> sp. 2	1	Blue/green
<i>Favia</i> sp. 3	1	Blue/green
<i>Favites abdita</i>	3	Orange
<i>Favites complanata</i>	1	Blue/green
<i>Platygyra pini</i>	1	Red
Family Merulinidae		
<i>Merulina scabricula</i>	1	Orange
Family Mussidae		
<i>Lobophyllia hemprichii</i>	2	Orange
<i>Symphyllia agaricia</i>	1	Orange
<i>Symphyllia radians</i>	1	Orange
<i>Symphyllia recta</i>	2	Orange
Family Euphyllidae		
<i>Euphyllia divisa</i>	1	Red

the southeast Asian monsoon (Tham, 1973; Gin et al., 2000). There is a marked and predictable rise in sea temperature (3–4 °C) following the northeast monsoon, as a result of changes in the net transport of water through the Singapore Strait (Tham, 1973; Gin et al., 2000). Sea temperature gradually rises from 27–28 °C in January/February to a maximum of 30–31 °C in April/May during the inter-monsoon period (Tham, 1973). Thus, it is plausible that this rise provides the most suitable seasonal cue for gamete maturation, while lunar and diel cycles regulate the nights and times of spawning. In support of this, we found that the majority of oocyte and testes development in *P. lutea* and *Platygyra* sp. occurred during this period of sea water warming and the main spawning period occurs when sea temperatures are close to the annual maxima (Guest, 2004).

Two other factors — seasonal changes in solar irradiance and changes in the time of sunrise and sunset — may be important in regulating gametogenic cycles of equatorial corals. Insolation varies seasonally as a result of changes in effective solar altitude, with annual insolation maxima occurring around the equinoxes (March and September). This knowledge led Penland et al. (2004) to suggest that insolation may be a better predictor of spawning times for corals in the Indo-West Pacific than sea temperature. Photoperiod (day length) varies by less than 10 min throughout the year in Singapore (Tham, 1973) and remains constant at the equator. However, the time of the earliest and

latest sunrise varies by nearly 30 min each year (Aslaksen and Teo, 2004). The largest changes occur around the equinoxes and coincide with the maturation of gametes and spawning of corals in Singapore. Indeed, this factor explains and predicts the annual synchronous flowering of trees in equatorial rainforest trees (Brochert et al., 2005).

In Singapore, sea temperature and solar irradiance remain within ranges that are suitable for spawning of corals to occur elsewhere (e.g., Hayashibara et al., 1993; Babcock et al., 1994; Penland et al., 2004). In other words, conditions are suitable for breeding year round, so it seems unlikely that the timing of reproduction in any scleractinian is limited to certain times of the year by resource availability.

It is not clear whether there is an adaptive (ultimate) advantage to spawning when environmental conditions are likely to be “optimal” for fertilization, larval development, survival and settlement. However, it is conceivable that a 3 °C increase in ambient seawater temperature may confer a significant advantage (e.g., maximizing fertilization success because of increased sperm motility, increasing larval development rate, or affecting the duration of the planktonic phase), causing spawning at the warmest time of the year in Singapore to be adaptive.

Because broadcasting corals require external fertilization, responding similarly to specific environmental signals to ensure conspecific reproductive synchrony (in the order of minutes; e.g., Levitan et al., 2004) is probably of prime importance to ensure high fertilization rates. Thus, one of the most plausible hypotheses explaining multi-species spawning is that species respond similarly but independently to timing cues to synchronize spawning within populations — resulting in many species having short overlapping spawning periods. No coastal location is truly aseasonal, even equatorial reefs experience marked (albeit less pronounced) rhythmic changes in sea surface temperature. Consequently, mass spawning is just as likely to occur on equatorial reefs as it is at higher latitudes; indeed, this remarkable phenomenon is probably a feature of all speciose coral assemblages.

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