

## Mass spawning of corals on a high latitude coral reef

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**Abstract.** Evidence is presented that at least 60% of the 184 species of scleractinian corals found on reefs surrounding the Houtman Abrolhos Islands (Western Australia) participate in a late summer mass spawning. These populations are thus reproductively active, despite most species being at the extreme southern limit of their latitudinal range (28°–29°S). In the present study, coral mass spawning occurred in the same month on both temperate (Houtman-Abrolhos) and tropical (Ningaloo) reefs of Western Australia, despite more than two months difference in the timing of seasonal temperature minima between the two regions. This concurrence in the month of spawning suggests that temperature does not operate as a simple direct proximate cue for seasonal spawning synchrony in these populations. Seasonal variation in photoperiod may provide a similar and more reliable signal in the two regions, and thus might be more likely to synchronize the seasonal reproductive rhythms of these corals. Also there is overlap in the nights of mass spawning on the Houtman Abrolhos and tropical reefs of Western Australia, despite significant differences in tidal phase and amplitude between the two regions. This indicates that tidal cycle does not synchronize with the night(s) of spawning on these reefs. Spawning is more likely to be synchronised by lunar cycles. The co-occurrence of the mass spawning with spring tides in Houtman Abrolhos coral populations may be evidence of a genetic legacy inherited from northern, tropical ancestors. Micro-tidal regimes in the Houtman Abrolhos region may have exerted insufficient selective pressure to counteract this legacy.

to the large number of species which breed at the same time, as well as the brevity and predictability of the breeding period (Willis et al. 1985), although similar phenomena have been described in temperate communities (Minchin 1993). Many of the species involved in the mass spawnings have wide biogeographic distributions, thereby allowing inter-regional comparisons of spawning behaviour. Such comparisons provide a means of identifying common factors which may synchronize the spawnings and assist in isolating the underlying causes (ultimate factors) and mechanisms (proximate cues) responsible for the coral mass spawning.

Comparisons of community spawning patterns among geographic regions for which we currently have data suggest that the presence or absence of coral mass spawning may reflect regional variations in environmental cycles. The highly synchronized coral spawning along most of the Great Barrier Reef (see Oliver et al. 1988) is thought to involve at least three proximate cues (temperature, moonlight and daylight) operating on successively finer time scales (Babcock et al. 1986). The ultimate factors determining the timing of spawning within species at each of these scales (physiology, enhanced fertilization and predator avoidance respectively) have been discussed by Oliver et al. (1988). Regardless of the timing of spawning some degree of synchrony within a species is vital if gametes are to be fertilized. Multispecific spawning synchrony, or mass spawnings, are more difficult to explain. It has been suggested that the most likely explanation for between-species spawning synchrony on the Great Barrier Reef (GBR) is that many species have independently, but similarly, responded to strong selective pressures promoting reproductive success (Oliver et al. 1988). The lack of mass spawning in regions with less pronounced variations in temperature or tidal regimes, such as the Red Sea and the Caribbean, suggests that variation in temperature and/or tidal cycles may exert insufficient pressure for the evolution of spawning synchrony (Shlesinger and Loya 1985; Szmant 1986). Other explanations, which have been advanced to explain the absence of mass spawning in the Red Sea include temporal partitioning of the breed-

### Introduction

Spawning patterns in many Indo-Pacific and Western Australian coral communities are unique with respect

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ing season, either to reduce competition among juveniles or to reduce gamete wastage due to hybridization (Shlesinger and Loya 1985). However, it is difficult to resolve how such biotic factors could select against mass spawning in the Red Sea but not on the Great Barrier Reef. Observations that reproductive synchrony breaks down in Papua New Guinea (Oliver et al. 1988) and Micronesia (Richmond and Hunter 1990), where variation in seasonal temperature and/or tidal cycles is minimal, support the hypothesis that seasonal environmental cycles strongly influence community spawning patterns.

Evidence exists, however, which apparently contradicts the importance of environmental cycles in the evolution of synchronous spawning in corals. Two Caribbean species, *Montastrea annularis* and *M. cavernosa*, exhibit strong reproductive synchrony despite minimal variations in temperature and tidal amplitudes in the Caribbean (Szmant 1991). This suggests that proximate cues for spawning synchrony are available in the absence of strong temperature or tidal signals. The role of temperature, as either a proximate or an ultimate factor for spawning synchrony in coral communities, has been questioned by Simpson (1985, 1987) because of the six-month difference in the seasonal timing of the mass spawning between east and west coast tropical reefs of Australia, despite very similar seasonal temperature cycles in these regions. It is clear that further information on spawning patterns from geographic regions having different seasonal or synodic environmental cycles will provide additional evi-

dence with which to evaluate hypotheses concerning the role of environmental cycles in the evolution of coral mass spawning.

The presence of well-developed subtropical reefs off the coast of Western Australia (WA) provides an opportunity to examine spawning patterns which have evolved under a suite of temperature and tidal cycles that contrast with those already studied. The Houtman Abrolhos Islands and their surrounding reefs are the southernmost reefs in the Indian Ocean (Fairbridge 1950) lying between 28 °C and 29 °S on the edge of the continental shelf, about 60 nm off the coast of Western Australia (Fig. 1). Luxuriant coral communities are present, particularly in the lagoons and on the leeward slopes of the reefs. Coral diversity is high for this latitude with 183 species of hermatypic scleractinians, representing 42 genera (Veron and Marsh 1988). Sea temperatures are relatively low on Houtman Abrolhos reefs, with smoothed monthly mean temperatures ranging from a maximum of 23.5 °C in February/March to a minimum of 19.8 °C in September/October (Pearce 1986). On northern tropical reefs in the Dampier Archipelago, the sea temperature ranges from 23.2 °C to 29.6 °C. The Abrolhos Islands are located in the south-western Australian tidal zone (mixed diurnal/semi-diurnal, microtidal patterns) and tidal cycles have a maximum spring amplitude of about 1 m (Easton 1970). The relationship between tidal and lunar cycles at the Abrolhos differs substantially from that on the northern coast of WA or the GBR where semi-diurnal, macro-tidal tides prevail.

In 1986, corals from the Abrolhos Islands were sampled in the week prior to the date predicted for spawning on Ningaloo Reef and tropical reefs in Western Australia (Simpson and Masini 1986). Corals from both the Abrolhos and Ningaloo had large pigmented eggs and well-developed testes (Simpson, unpublished data), indicating that corals from both locations were approaching reproductive maturity at the same time. An expedition was mounted to monitor and observe coral spawning in the Abrolhos during March 1987 in order to explore correlations between spawning patterns and the suite of temperature and tidal cycles. Approximately 70% of scleractinian species at the Abrolhos are at the southernmost limit of their distributions (Veron and Marsh 1988). Therefore this site had additional interest in terms of determining whether gametogenesis and spawning occurred on a high latitude reef (see Yonge 1940; Veron 1974) and whether these corals, living at the extremes of their ranges, were represented by 'pseudo-populations' (*sensu* Yamaguchi 1987), unable to complete gametogenesis.

## Methods

Observations were carried out at Beacon Islands in the Wallaby Group of the Houtman Abrolhos Islands between the 11th and 27th of March 1987. Colonies were tagged and sampled on varying dates beginning on the 11th, and all were re-sampled on the 27th. A number of colonies were sampled repeatedly over the period of the study, 422 colonies from 107 species were sampled two times or more over the period of the study. Numerous single random samples were also collected. The reproductive status of the corals was determined either from in situ observations of broken sections, microscopic

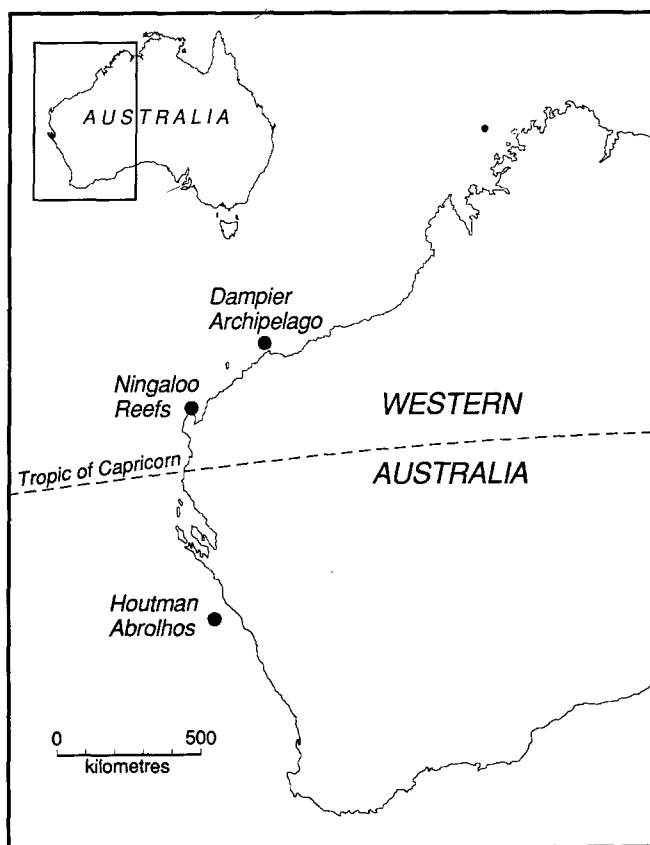


Fig. 1. Location map of Western Australia

examinations of live material at a shore-based laboratory, dissections of preserved material, or by a combination of these methods. The stage of sperm development (as described by Harrison et al. 1984) was monitored daily from a range of colonies in order to gauge the imminence of spawning. Possible spawning nights were predicted based on observations of sperm development and activity, as well as predictions of major spawning dates for tropical reefs in WA in 1987. Accordingly night dives were conducted from the 22nd to the 26th March (7–11 nights after the full moon) between approximately 1900 and 2230 h. In situ tagged colonies, transplanted tagged colonies and any other nearby colonies at the dive site were monitored on each night. Colonies of selected species were also kept in aquaria to provide additional observations of spawning. A data logger recording instantaneous measurements of sea temperature and depth, every 15 minutes, was deployed at a depth of about 2 m at the study site from the 11th to the 27th of March.

## Results

### Sperm development

Daily observations of sperm development and motility revealed that, at the commencement of observations on March 11th, those species that were approaching reproductive maturity (mainly species of *Acropora* and faviids) possessed immature spermatids with round heads and low motility. In samples examined on March 16th, nuclear material in the sperm of the *Acropora* species had begun to condense and sperm heads were more triangular or irregular. On the 17th and 18th sperm nuclei in several

favid species had begun to condense. From the 18th until the 22nd both the proportion of condensed sperm and their degree of activity continued to increase. From the 22nd until the night of spawning (March 24–26) sperm continued to develop but daily changes were less marked as peak numbers and activity of sperm were approached.

### Spawning observations

Of the 107 species sampled during the study (Appendix 1) there was evidence of mass spawning from 58 (54%), based on in situ and aquarium observations (31 of the 58) and laboratory examination of preserved sequential samples. A further 36 species (34%) probably spawned during or immediately after the main spawning period as assessed from gamete maturity in random live samples. Colonies of these species were found to possess ripe testes with condensed sperm, or coloured eggs, indicating that spawning was imminent. For the remaining 13 coral species (12%) there was no indication of developed gametes and it was impossible to make any inference concerning mode or timing of reproduction.

Of the 58 species in which spawning was confirmed, 16 (28%) had some proportion of colonies that did not spawn despite containing mature gametes. For the 14 species where the number of tagged colonies was 5 or more, the proportion of tagged colonies that spawned

**Table 1.** Field spawning observations, Abrolhos Islands: hour and date of spawning, March 1987

Species	n	March date		
		24	25	26
		Hour of spawning		
<i>Cyphastrea microphthalmia</i>	3	2040	2110	
<i>C. serailia</i>	3	1950–2010	2055	
<i>Montipora capricornis</i>	2	2020	2005–2020	
<i>Acanthastrea echinata</i>	1		2150	
<i>Acropora aculeus</i>	1		2025	
<i>A. cerealis</i>	1		2235	
<i>A. glauca</i>	6		2025–2110	
<i>A. latistella</i>	>4		2110–2115	2115–2210
<i>A. nasuta</i>	1		2230	
<i>A. spicifera</i>	9		2145–2230	2045–2220
<i>A. tenuis</i>	2		2230	2015–2230
<i>A. valida</i>	9		2230–2250	2105–2305
<i>A. willisae</i>	4		2140–2155	2220
<i>Echinophyllia aspera</i>	3		2050	2100
<i>Galaxea fascicularis</i>	2		2200	
<i>Montipora grisea</i>	1		2040	
<i>M. hoffmeisteri</i>	1		2010	
<i>M. turgescens</i>	2		2020–2035	
<i>Oxypora lacera</i>	1		2105	
<i>Acropora anthocercis</i>	1			2250
<i>A. aspera</i>	2			2000–2020
<i>A. florida</i>	1			2130
<i>A. formosa</i>	2			2205–2220
<i>A. grandis</i>	4			2145–2250
<i>A. selago</i>	>2			2105–2115
<i>A. stoddarti</i>	1			2215
<i>Goniastrea australiensis</i>	1			2120
<i>Favia fava</i>	1			2230

ranged from 100% for *A. spicifera* ( $n=25$ ) and *A. grandis* ( $n=15$ ) to 11% for *A. stoddarti* ( $n=9$ ) with an overall mean of approximately 70% (Table 1). In 23 of the 58 species with definite spawning records, a proportion of the population sampled did not contain gonads. These colonies may have been non-reproductive or have spawned at some other time of the year. There were 11 spawning species in which some colonies still contained gametes at the end of the study on March 27, though based on examinations of gametes, spawning in these colonies was imminent. In addition to partial spawning of populations, partial spawning of individual colonies was observed in three species, *Astreopora myriophthalma*, *Lobophyllia hemprichii* and *Merulina ampliata* (Appendix 1).

### Timing of Spawning

Spawning was observed in the field and aquaria on three nights, the 24th, 25th and 26th of March. These dates correspond to the ninth, tenth and eleventh nights after the full moon (15th of March). Four species were recorded spawning on the 24th, 24 species on the 25th, and 19 species on the 26th (Fig. 2). Daily samples from 9 species common on the Beacon Island reef flat ( $n=31$  colonies) confirmed that the tenth and eleventh nights after full moon were the major spawning nights as only *A. grandis* (one colony) spawned on the 24th, 7 species (12 colonies) spawned on the 25th, and 6 species (16 colonies) spawned on the 26th. Colonies of *A. aspera*, *A. grandis*, *A. spicifera*, *A. valida* and *A. florida* all spawned on the nights of the 25th and 26th. *A. grandis* spawned on all three nights. One colony each of *A. aspera* and *A. grandis* had not spawned when observations finished on the morning of March 27th.

Although more species were recorded spawning on the 25th, the two most abundant species on Beacon Island reefs, *Acropora grandis* and *A. spicifera*, spawned at

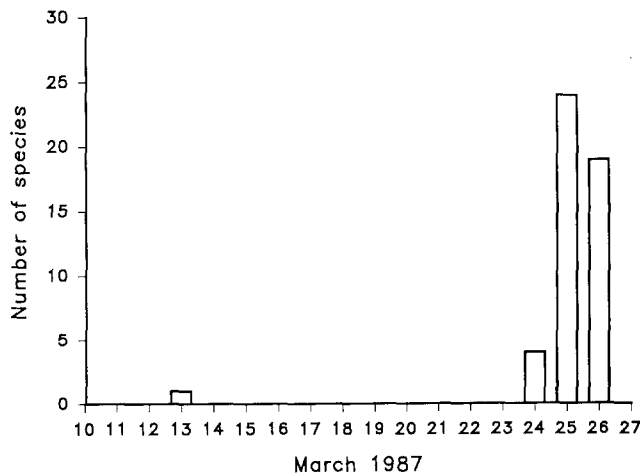


Fig. 2. Frequency of coral spawning at the Houtman Abrolhos Islands reefs (March 1987). Data include only those species either directly observed to spawn on the night indicated, or inferred to spawn on that night on the basis of sequential daily sampling of tagged colonies. Full moon March 15

approximately 2300 h on the 26th, producing extensive slicks of gametes on the surface between 2300 h and midnight. Winds at this time were about  $5 \text{ m s}^{-1}$  from the southwest. Winds increased to over  $10 \text{ m s}^{-1}$  during the night and no slicks were observed by the following morning. Despite lighter winds on the night of the 25th, no slicks were observed. All spawning observed in the field occurred between 1950 and 2305 h (Table 1).

Although all of the direct observations and most of the inferred records of spawning were made towards the end of the period of study, there were three species (*Acropora aspera*, *A. nasuta* and *Turbinaria peltata*) in which one tagged colony each was inferred by sequential samples to spawn around the time of the full moon (Fig. 2, Appendix 1). In the case of *Acropora aspera* the sequential samples were only one day apart, which placed the date of spawning on the 14th (the day before the full moon), eleven to twelve days before the majority of the population spawned. Although only three colonies of *A. nasuta* were recorded spawning, a similar pattern was also evident in this species. In *T. peltata*, the only colony which could positively be determined to spawn did so between the 13th and 16th of March.

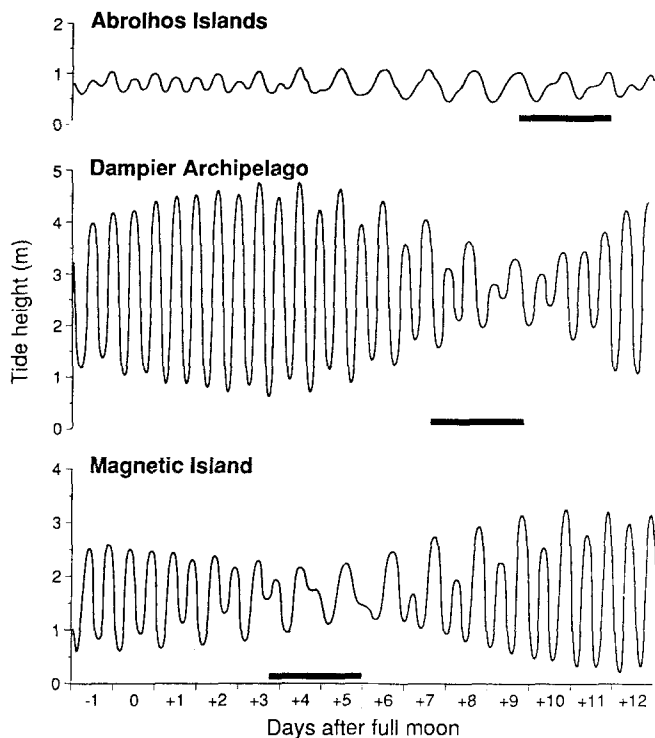
### Environmental data

Seawater temperatures recorded by us during the period of the study ranged from  $21.5^\circ\text{C}$  to  $24.1^\circ\text{C}$  with a mean temperature of  $23^\circ\text{C}$  between March 11 and 27.

### Discussion

We have presented evidence that 94 of the 107 scleractinian species sampled from the Houtman Abrolhos Islands reefs during this study spawned either immediately after the March full moon or 9 to 11 nights thereafter. A further 18 species present at the Abrolhos but not observed during this study have been recorded as spawners or probable spawners at other Western Australian coral reefs (Simpson 1985, 1987, 1988). Thus, at least 60% of the 184 species of Scleractinia which have been recorded to occur on reefs surrounding the Houtman Abrolhos Islands are likely to breed during a one week period. Given the number of species involved and the shortness of the breeding period, the spawning at the Abrolhos Islands reefs may be classified as a mass spawning of similar magnitude to the mass spawnings which occur on the GBR (Harrison et al. 1984) and on tropical West Australian Reefs (Simpson 1985). Despite the high latitude of the Houtman Abrolhos reefs, coral populations do not constitute 'pseudo-populations' such as have been found at the extreme of the ranges of other tropical reef-dwelling organisms (Yamaguchi 1987), as evidenced by the large numbers of eggs and testes observed in the colonies sampled and their release as mature gametes.

With the exception of two endemic or temperate species (*Acropora spicifera*, *A. stoddarti*) all species spawning on the Houtman Abrolhos reefs commonly participate in either the Western Australian or Great Barrier Reef mass



**Fig. 3.** Tidal patterns at three locations in Australia. Periods of main mass spawning are shown (line). Western Australia: Abrolhos, March 1987; Dampier, March 1986. Great Barrier Reef: Magnetic Island, October 1986

spawnings. Thus, any variation in the timing of the mass spawning among the three locations is unlikely to be attributable to taxonomic differences among the participating species and should provide insights into the selective pressures which operate to synchronize the mass spawnings at these three sites.

#### Monthly patterns

Mass spawning on both the Great Barrier Reef and tropical reefs in Western Australia occurs around the time of neap tides. Spawning on the temperate Houtman Abrolhos reefs, however, was observed well after neap tides and in fact took place just after spring tides (Fig. 3). Although variations in tidal amplitude are minimal in the Abrolhos region, the timing of the spawning suggests that either the tidal cycle per se does not provide the proximate cue to synchronize the night of spawning on these reefs, or that the corals respond to the tidal cycle differently in different locations. We suggest that the former conclusion is more appropriate for the following reasons.

A more likely interpretation of the available information is that variation in moonlight intensity provides the timing indicator to entrain lunar rhythms and synchronize the night of spawning within populations (e.g. Hauenschild 1960; Kennedy and Pearse 1975). This is supported by the similarity in the lunar timing of spawning on tropical and temperate reefs in Western Australia. Mass spawning has consistently occurred between the 8th and 10th nights after the March full moon at Ningaloo

and other tropical reefs of Western Australia (Simpson 1988). In the present study, spawning at the Houtman Abrolhos islands took place 9–11 nights after the March full moon. In the following year, the majority of corals at the same site in the Houtman Abrolhos spawned on the 8th–10th nights after the full moon (K. Nardi personal communication).

Babcock et al. (1986) have argued that enhanced fertilization during neap tides is the ultimate factor underlying lunar mass spawning synchrony in these corals. This hypothesis was supported by the observation that mass spawning coincides with neap tides on both tropical reefs of Western Australia and the Great Barrier Reef, despite differences in timing with respect to the lunar night at the two locations (8–10 versus 4–6 nights after the full moon respectively). We suggest that the co-occurrence of the mass spawning with spring tides on Houtman Abrolhos reefs may still be consistent with this hypothesis if two assumptions are made.

First, if it is assumed that coral populations on Houtman Abrolhos reefs have been established through larval dispersal from northern tropical reefs, then Houtman Abrolhos corals may have inherited mechanisms to cue their spawning from their tropical ancestors (i.e. a “genetic legacy” *sensu* Oliver et al. 1988). Secondly, the retention of this timing may not provide evidence against the role of neap tides as the underlying ultimate factor for within-population spawning synchronization, if it is assumed that the micro-tidal conditions on Abrolhos reefs have not exerted enough selective pressure to shift the timing of spawning away from the inherited lunar rhythm. Thus, in the absence of a tidal regime that could exert selective pressure strong enough to alter the lunar timing of the spawning, corals on Houtman Abrolhos reefs may have retained the spawning patterns of their tropical ancestors. Alternatively, it may be that not enough time has elapsed for the Houtman Abrolhos populations to have diverged from their source populations in relation to monthly lunar rhythms used to cue the spawnings.

With respect to the first assumption, it is highly probable that northern tropical populations have supplied most of the larval recruits to the Houtman Abrolhos coral populations. Veron and Marsh (1988) found that the suite of scleractinian species recorded from the Abrolhos reefs was more similar to those recorded from northern, tropical reefs than to those found on nearby temperate coastal reefs. Simpson (1985) has discussed further evidence that the transport of larvae in poleward currents connects coral populations in the Houtman Abrolhos with northern populations. In particular, the Leeuwin current intensifies in the austral autumn and begins to flow strongly southward ( $0.2 \text{ m s}^{-1}$ , Cresswell 1991) along the coastline of Western Australia at approximately the time that the mass spawning occurs (Cresswell and Golding 1980). It is 600 km to Ningaloo (just north of the Tropic of Capricorn), the nearest major tract of coral reef north of the Abrolhos Islands. Calculations suggest that at these current speeds, it would take larvae approximately 35 days to reach the Houtman Abrolhos from northern reefs. It has been shown that coral larvae can be transported at rates faster than would be calculated on the basis of current speed

alone, due to surface-driven effects on buoyant reproductive propagules (Willis and Oliver 1990). Even if transport from the tropics to the Abrolhos took 30 to 40 days, this time period is well within the maximum longevity of 91 days reported for planulae of some externally fertilized corals (reviewed in Harrison and Wallace 1990).

With respect to the second assumption, phylogenetic or historical constraints on phenology have long been recognised in plant populations (Kochmer and Handel 1986; Fox 1989). The implicit corollary is that local environmental variables are not strong enough to overcome the inherited historical/phylogenetic constraints. An additional brake on divergence, of particular importance to marine organisms with external fertilization, is the need to maintain spawning synchrony as a method of ensuring adequate levels of fertilization (Oliver and Babcock 1992). The potential importance of post-spawning events to the survival of early life history stages may be subsumed by this requirement for spawning synchrony (Colin and Clavijo 1988). It is not known what proportion of annual recruits originate from local spawnings versus spawnings on northern reefs, however, the ongoing input of larvae from tropical reefs would further tend to retard rates of divergence in coral populations in the Houtman Abrolhos.

#### Seasonal patterns

The similarity in the timing of the mass spawning between the Abrolhos reefs and tropical reefs in Western Australia, despite marked differences in temperature regimes in the two regions (Fig. 4), provides further evidence (Simpson 1985) that there is not a simple, direct, proximate relationship between temperature and spawning in corals (Harrison et al. 1984). Mean monthly sea temperatures peaked one or two months before spawning at both locations, but absolute values differed by 5–7 °C. In addition, the timing of both the winter minima and the spring rise in sea temperature differed by three months between the two locations.

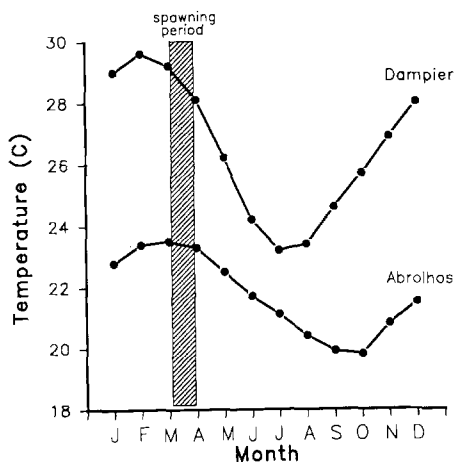


Fig. 4. Mean monthly sea temperatures (°C) for the Dampier Archipelago (1982–83) and the Abrolhos Islands (1970–80). (From Pearce 1986)

Seasonal variation in daylength (photoperiod) may provide an alternative cue to trigger various stages of gamete maturation and synchronize the month or season of breeding. Unlike the seasonal temperature patterns described already, seasonal photoperiod patterns are similar (with respect to the timing of seasonal maxima and minima) at the two locations. Variation in daylength has been shown to be used by a wide variety of organisms for synchronizing breeding seasons, particularly plants (Salisbury 1961) and terrestrial invertebrates (Saunders 1981; Hoffman 1978), but also by a variety of marine invertebrates (Pearse and Ernisse 1982). Experimental studies with corals have demonstrated that they do adjust the timing of their gamete or planulae release in response to diurnal (daylight) or lunar (moonlight) phase-shifts (Babcock 1984; Jokiel et al. 1985; Hunter 1988). As light cues are involved in synchronizing the hour and night of spawning, it is possible that photoperiod cues are involved in synchronizing the month of spawning. Kojis (1986) found that variation in the reproductive seasonality of *Acropora palifera* between the north coast of Papua New Guinea (7°S) and Heron Is. (23°S) was greater than could be explained by temperature alone, and suggested that the photoperiod may play a more important role than temperature in influencing gametogenic cycles. More recent studies of mass spawning coral species in northern Papua New Guinea (Oliver et al. 1988) have demonstrated that on low latitude reefs, characterized by minimal seasonal variation in photoperiod (or temperature), spawning is spread over at least 6 months. Although there is no direct evidence that the photoperiod operates to synchronize annual reproductive rhythms in corals, the topic merits further investigation in view of our finding that spawning times are the same on tropical and temperate reefs in Western Australia, despite substantial differences in the timing of annual temperature maxima and minima between the two regions. However, if photoperiod does function as a proximate cue for annual reproductive synchrony, then the six-month difference in the mass spawnings between the Great Barrier Reef and reefs of Western Australia would suggest that corals respond to this cue in different ways on the east and west coasts of Australia.

The ultimate evolutionary factors responsible for differences in the seasonal timing of spawning between corals on West Australian reefs and the Great Barrier Reef are difficult to deduce from present information. The seasonal 'turn-on' of southward flowing currents, such as the Leeuwin in WA, or monsoonal, wind-driven coastal currents on the Great Barrier Reef in October–November, have been suggested to selectively disperse larvae of corals which breed at these times of year southward from equatorial regions (Simpson 1987, 1991). Thus, coral populations on the east and west coasts of Australia may have inherited different genetic legacies with respect to mechanisms for synchronizing spawning seasonality. Throughflow from the equatorial Pacific via Indonesia (Murray and Arief 1988) is considered to be a major component in the dynamics of the Leeuwin current (Cresswell 1991). However, the finding of Oliver et al. (1988) that equatorial corals generally do not have a single, discrete spawning period sheds doubt on this hypo-

thesis. Further assessment of these ideas will have to await more detailed data on specific reproductive patterns for equatorial populations, as well as studies of long-distance larval dispersal in these regions.

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**Appendix 1**

Confirmed spawning records for corals sampled during March 1987 at the Houtman Abrolhos Islands. a: direct field observations of spawning; b: direct aquarium observations of spawning; c: spawning inferred from sequential samples; p: partial spawning of a colony inferred from sequential samples; \*: ripe gametes present but colony did not spawn; n: no gametes present, did not spawn; [---c, p, \*, n---]: indicates the period over which sequential samples were taken; these records are placed on the day of spawning, where samples were taken daily. Where samples were separated by more than one day the record is placed at the middle of that period, unless precise dates of spawning could be determined for other members of the population, in which case the records are placed together. +: random sample possessing ripe gonads; -: random sample lacking ripe gonads.

Species	n	Number of colonies observed in March:																	
		Date	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
<b>Acroporidae</b>																			
<i>Acropora</i>																			
<i>abrolhosensis</i>	1																		[-----1c-----]
<i>aculeus</i>	1																		1a
<i>anthocercis</i>	3																		1a2b
<i>aspera</i>	>8				[1c]														[1c-- >2a4c-]
<i>cerealis</i>	1																		1a
<i>digitifera</i>	5																		[-3c---1b1c-]
<i>florida</i>	3																		[-1c--1a1c-]
<i>formosa</i>	4																		[-----2a2c-]
<i>glauca</i>	9																		[-6a2c1c-----]
<i>grandis</i>	15																		[-1c--1c--4a9c-]
<i>latistella</i>	>5																		[-2a->2a2c1c*]
<i>nasuta</i>	3																		[[-----1c-----]]
<i>pulchra</i>	5	2+ 2+																	-----1c-----]
<i>selago</i>	>2																		>2a
<i>solitaryensis</i>	5																		[-3c1*1n-----]
<i>spicifera</i>	25																		[-3a-6a16c-]
<i>stoddarti</i>	11	2+																	[-1a1*7n-]
<i>tenuis</i>	2																		2a
<i>valida</i>	21																		[-3a-6a10c2*]
<i>willisae</i>	11																		[-3a--1a7c-]
<i>Astreopora</i>																			
<i>myriophthalma</i>	7	1+																	-----1c2p2+-----]
<i>Montipora</i>																			
<i>capricornis</i>	4																		[-1a2c-1a-----]
<i>grisea</i>	4																		[-1a1c1*1n-----]
<i>hoffmeisteri</i>	1																		1a
<i>turgescens</i>	4																		[-2a2n-----]
<b>Faviidae</b>																			
<i>Cyphastrea</i>																			
<i>microphthalma</i>	6																		[1-----1a---2a1*1n-----]
<i>serailia</i>	5																		[-2a---2a1c-----]
<i>Favia</i>																			
<i>complanata</i>	2																		[-1c1n-----]
<i>favus</i>	7	3+																	[-1a3c--]
<i>maritima</i>	2																		[-1c1n-----]
<i>maxima</i>	1																		[-1c-----]
<i>pallida</i>	2																		[-2c-----]
<i>Favites abdita</i>	2	1+																	[-1c-----]
<i>F. c.f.</i>																			
<i>bennettiae</i>	5	1+																	[-3c1n-----]
<i>flexuosa</i>	2																		[-2c-----]
<i>halicora</i>	6																		[-6c-----]
<i>russelli</i>	3																		[-2c-----1+-----]
<i>Goniastrea</i>																			
<i>australiensis</i>	7	1+																	[-1a5c--]
<i>pectinata</i>	7	2+ 1-																	[-4c-----2a2n-----]

<i>Montastrea curta</i>	7	[1 + 2 - ----- 3c1n-----]		
<i>Montastrea magnistellata</i>	3	2+ [------ 1c-----]		
<i>Platygyra lamellina</i>	4	1- [------ 1 + - 1 + - 1c - -]		
<i>Plesiastrea versipora</i>	3		1 +	2b
<b>Poritidae</b>				
<i>Alveopora gigas</i>	14	1+ [------ 6c2*5n-----]		
<i>A. verriliana</i>	12	2+ [------ 3c1*5n----- 1 +-----]		
<i>Goniopora djiboutiensis</i>	1	[------ 1c-----]		
<b>Mussidae</b>				
<i>Acanthastrea echinata</i>	3	1+	1 +	1a
<i>Lobophyllia hemprichii</i>	5	2+ [------ 2c1p-----]		
<i>Blastomussa wellsii</i>	5		2 +	3b
<b>Dendrophylliidae</b>				
<i>Turbinaria mesenterina</i>	18	1+ 1 + 1- [------ 1 + - 1 + - 4 + 4 - 3c1*1n-----]		
<i>T. peltata</i>	2	[------ 1c-----]		1 -
<b>Pectiniidae</b>				
<i>Echinophyllia aspera</i>	10	[------ 3a7c-----]		
<i>Mycedium elephantotus</i>	3	2+ [------ 1c-----]		
<i>Oxypora lacera</i>	8	1 + 2 -		1a4c
<b>Agaricidae</b>				
<i>Pachyseris speciosa</i>	5	[------ 2c2*1n-----]		
<b>Merulinidae</b>				
<i>Merulina ampliata</i>	4	[------ 3c1p-----]		
<b>Oculinidae</b>				
<i>Galaxea fascicularis</i>	11	1 + 1 -	[- - - 2 - ----- 2a2c1*2n - - -]	
<b>Caryophyllidae</b>				
<i>Euphyllia divisa</i>	2	[------ 1b - - 1b - - -]		

Probable spawners; Colonies of these species were sample only before the main spawning nights and found to possess ripe testes with condensed sperm, or coloured eggs, indicating that spawning was imminent. Brackets indicate number of colonies sampled.

Acroporidae: *Acropora cytherea* (1), *A. horrida* (4), *A. millepora* (2), *A. nobilis* (1), *Astreopora gracilis* (2), *Montipora aequituberculata* (3), *M. danae* (2), *M. informis* (2), *M. mollis* (2), *M. turtlensis* (1). Faviidae: *Barabattoia amicornum* (2), *Favia lizardensis* (2), *F. veroni* (1), *Favites chinensis* (2), *Moseleya latistella* (1), *Platygyra daedalea* (2). Poritidae: *Alveopora tizardi* (1), *Goniopora columna* (3), *G. fenestrata* (1), *G. stutchbryi* (1), *Porites lutea* (2). Mussidae: *Acanthastrea hillae* (3), *Lobophyllia corymbosa* (1), *Symphyllia wilsoni* (1). Dendrophylliidae: *Turbinaria bifrons* (2), *T. frondens* (7), *T. radicalis* (1), *T. reniformis* (2). Pectiniidae: *Oxypora glabra* (2). Agaricidae: *Leptoseris explanulata* (2), *Pavona varians* (2). Merulinidae: *Hydnophora pilosa* (4), *Scapophyllia cylindrica* (1). Siderastreidae: *Coscinarea marshae* (1). Fungiidae: *Fungia repanda* (1).

For the remaining 13 coral species there were no indications of developed gametes and it was impossible to make any inference concerning mode or timing of reproduction. Brackets indicate

number of colonies sampled. Acroporidae: *Acropora donei* (1), *Montipora foliosa* (1), *M. hispida* (1), *M. undata* (2). Faviidae: *Goniastrea palauensis* (1). Poritidae: *Alveopora allingi* (2), *A. spongiosa* (4). Mussidae: *Blastomussa merletti* (1). Pectiniidae: *Echinophyllia orpheensis* (1). Agaricidae: *Leptoseris hawaiiensis* (2), *L. mycetoserioides* (1). Siderastreidae: *Psammocora contigua* (1), *Psammocora superficialis* (2). Astrocoeniidae: *Stylocoeniella guentheri* (1).

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