

New insights into patterns of coral spawning on Western Australian reefs

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Abstract On reefs around Australia, coral mass spawning typically occurs during the austral spring (October/November) on the east coast, and during autumn (March/April) on the west coast. However, to investigate the incidence of a secondary spawning event in spring on the west coast, the reproductive state of corals was assessed on two reefs. The results indicated that of the 29 species of *Acropora* investigated, multiple colonies of 11 species spawned in late spring or in early summer, in contrast to previous reports of spawning during autumn. Additionally, of four species that were followed through time at one reef, two spawned in both spring and autumn, however, individual colonies had only one gametogenic cycle. Within a single site, conspecific colonies were reproductively isolated and may not interbreed, potentially representing the initial stage of sympatric speciation in these populations.

Keywords Coral reproduction · Biannual spawning · Reproductive isolation · Barrow Island · Dampier Archipelago

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Introduction

Most corals around the world broadcast spawn their gametes for external fertilization and development, and many participate in mass spawning events (Harrison and Wallace 1990). Mass spawning was originally defined as the synchronous release of gametes by many species of corals, in one evening between dusk and midnight (Willis et al. 1985). Implicit in this definition of mass spawning is the involvement of both many species and a high proportion of colonies within species, in contrast to instances of multi-specific spawning that involve some species and a lower proportion of colonies. Since the discovery of the phenomenon, mass spawning or multi-specific spawning events have been documented on an increasing number of reefs around the world (see Penland et al. 2004; Guest et al. 2005a; Carroll et al. 2006), and are probably a feature of many speciose coral assemblages (Guest et al. 2005a).

On many reefs, there is a primary spawning event each year in which the largest proportion of corals and species participate, while a smaller proportion of colonies and species spawn at other times of the year, which may vary among years (e.g., Wallace 1985; Baird et al. 2002; Wolstenholme 2004; Guest et al. 2005b; Carroll et al. 2006; Mangubhai and Harrison 2006; Nozawa et al. 2006). Most research has focused on the participation of corals in the primary spawning, with comparatively little work detailing the times of spawning for other individuals and species. Additionally, very little is known about variation in spawning among years, and whether individuals and species spawn at different times of the year do so consistently.

Differences in the time of spawning among species and morphs on the same reef can lead to reproductive isolation and genetic differentiation (Fukami et al. 2003). In some instances, species and/or morphs spawn in different months,

either in consecutive months or different seasons, (e.g., Penland et al. 2004; Wolstenholme 2004; Guest et al. 2005b; Mangubhai and Harrison et al. 2006) while in other instances spawning in different hours on the same night is sufficient to prevent colonies from interbreeding (e.g., Knowlton et al. 1997; Fukami et al. 2003). Where there are consistent differences in the times of spawning among conspecific colonies over years, the differences are evident in patterns of genetic variation and/or morphological features (Stobart and Benzie 1994; Dai et al. 2000; Wolstenholme 2004). If reproductive isolation arising from differences in the time of spawning is a permanent feature of the life histories of conspecific colonies, then it will lead to fixed genetic differences and sympatric speciation (Coyne 1992).

On coral reefs around Australia, mass spawning occurs predominantly on the east coast in the austral spring (October/November), and on the west coast in autumn (March/April; Harrison et al. 1984; Willis et al. 1985; Simpson 1991; Babcock et al. 1994). More recently on the east coast, some species have been found to spawn outside the mass spawning period (e.g., Wolstenholme 2004) with some individuals participating in two spawning events a year (e.g., Stobart et al. 1992). Similarly on some reefs off north Western Australia, recent observations of mature eggs in colonies and slicks of spawn suggested a second multi-specific spawning during spring at a similar time to that on the east coast.

The aim of this study was to investigate the extent to which a second spawning was occurring in spring in species of *Acropora* on two Western Australian reefs, based on the stages of gamete development within colonies. Additionally, at one reef, individuals of four species of *Acropora* were re-sampled through time to determine the proportion spawning during spring and/or autumn, and whether individuals had more than one gametogenic cycle each year.

Materials and methods

This study was conducted around Barrow Island (21°46'S, 115°28'E) and in the Dampier Archipelago (20°28'S, 116°37'E), Western Australia (Fig. 1). At Barrow Island, branches from 142 randomly selected colonies from 28 species of *Acropora* were sampled on the 11 September 2005, approximately 6–8 weeks prior to the predicted dates of spawning in spring (6–10 nights after the full moon in October) to ascertain their reproductive status. At the Dampier Archipelago, 15–20 colonies of *Acropora samoensis*, *Acropora millepora*, *Acropora hyacinthus*, and 6 colonies of *Acropora cytherea*, were tagged along a fixed transect and re-sampled in October 2002, February 2003 and October 2003, approximately 1–2 weeks prior to the predicted dates of spawning in spring and autumn (6–10 nights after the full moon in March) to determine whether individuals were spawning in both periods. A skeletal sample of all species was bleached and sent to the Museum of Tropical Queensland for identification.

Samples consisted at least three branches from each colony and were fixed in 10% formalin:seawater for a minimum of one week before decalcifying in solutions of 5% HCl. At least five polyps from each sample were dissected and viewed under a stereomicroscope (Wallace 1985). Egg size was measured using a graticule slide and calculated as the geometric mean (square root of the maximal x medial diameter; Wallace 1985). In the *Acropora*, egg sizes range between 200 and 600 μm within 8 weeks of spawning, testes become visible microscopically in dissected samples 4–8 weeks prior to spawning, and egg diameter prior to release ranges from 300–945 μm (Wallace 1985; Szmant 1986; Kenyon 1992; Wallace 1999; Vargas-Angel et al. 2006).

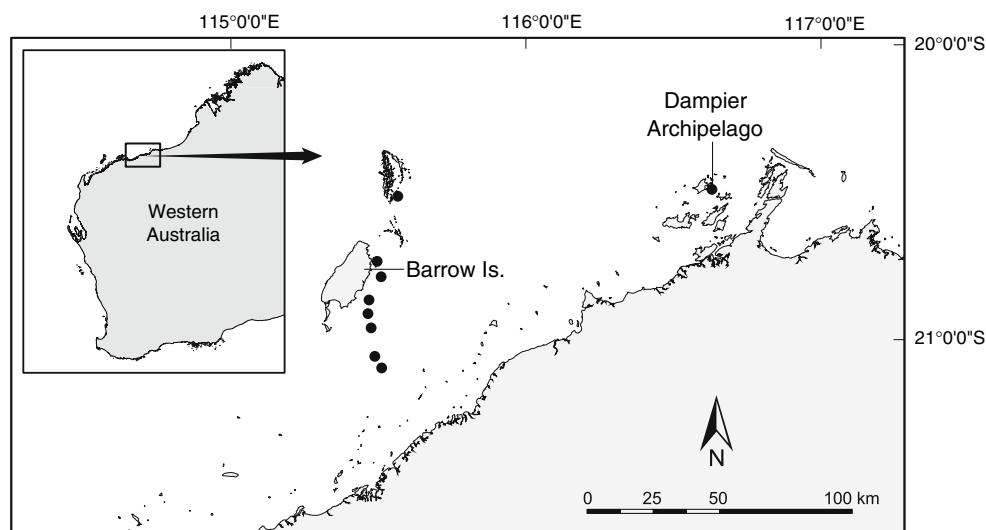


Fig. 1 Location of study sites of north Western Australia

In each colony, the time of spawning was inferred from egg size, pigmentation (in Dampier Archipelago only), and the presence or absence of testes (Harrison et al. 1984). Colonies with “large” eggs had well developed testes present, eggs were pigmented and/or their diameter was >350 µm and spawning was predicted within 4–6 weeks; those with “medium” eggs did not have testes, egg diameter was 200–350 µm and spawning was predicted within 8–12 weeks; those with “small” eggs did not have testes, egg diameter was <200 µm and spawning was predicted within 6–7 months; no inference about the time of spawning was drawn from colonies without visible eggs.

Results and discussion

The proportion of species and colonies spawning in spring

In 11 of the 29 species of *Acropora* sampled from either Barrow Island or the Dampier Archipelago, spawning was inferred to occur during spring or early summer (October–December) based on the presence of testes and/or large eggs (Table 1). Of these 11 species, 7 have been previously

documented to participate in the autumn spawning on Western Australian reefs (Table 1) (Simpson 1985; Babcock et al. 1994).

At the Dampier Archipelago, 7 (64%) colonies of *A. samoensis* and 4 (80%) colonies of *A. cytherea* contained pigmented eggs and visible testes when sampled in October 2002 and 2003. At Barrow Island, 2 (100%) colonies of *Acropora humilis*, 2 (25%) colonies of *Acropora latistella*, 1 (50%) colony of *Acropora cf muricata* and 2 (25%) colonies of *A. samoensis*, had visible testes and large eggs with a mean diameter of 440 µm (range 390–510 µm; Table 1) when sampled in September 2005. Based on the presence of testes, the diameter of the eggs and rates of egg development in *Acropora* (Wallace 1985; Vargas-Angel et al. 2006) all five species were inferred to spawn following the full moons in October 2002, 2003 and 2005.

In addition to the species predicted to spawn in October 2005 at Barrow Island, 8 species of *Acropora* had 1–2 (8–25%) colonies without visible testes but with mean egg sizes of between 220 and 300 µm when sampled in September (Table 1). Based on rates of egg development in *Acropora* (Wallace 1985; Vargas-Angel et al. 2006), these colonies were predicted to spawn following the full moon

Table 1 Colonies sampled at Barrow Island in September 2005; showing the percentage (%) of colonies containing eggs in different developmental stages, their mean diameter (µm) and their predicted time of spawning

Species	N	Egg Size				Time of Spawning (inferred)					
		Large % (mean diam.)	Medium % (mean diam.)	Small %	None %	Spring Oct.	Nov.	Summer Dec.	Jan.	Feb.	Autumn Mar./Apr.
<i>A. cf muricata</i> *	2	50 (510)	0	0	50	■					
<i>A. humilis</i>	2	100 (430)	0	0	0	■					
<i>A. latistella</i> *	8	25 (410)	13 (300)	50	12	■	■				■
<i>A. samoensis</i>	8	25 (390)	25 (240)	50	0	■	■				
<i>A. digitifera</i> *	8	0	13 (220)	87	0		■	■			
<i>A. florida</i> *	7	0	14 (250)	43	43		■				
<i>A. nasuta</i> *	8	0	25 (235)	62	13		■				
<i>A. spicifera</i> *	13	0	8 (225)	38	54		■	■			
<i>A. subulata</i>	10	0	10 (270)	70	20		■				
<i>A. valida</i> *	5	0	20 (270)	60	20		■				
<i>A. "kosurini like"</i>	2	0	0	100	0						
<i>A. acuminata</i>	1	0	0	100	0						
<i>A. austera</i>	8	0	0	62	38						
<i>A. cerealis</i>	7	0	0	71	29						
<i>A. divaricata</i>	1	0	0	100	0						
<i>A. donei</i>	1	0	0	100	0						
<i>A. glauca</i>	11	0	0	64	36						
<i>A. hyacinthus</i>	10	0	0	80	20						
<i>A. intermedia</i>	4	0	0	75	25						
<i>A. millepora</i>	3	0	0	100	0						
<i>A. muricata</i>	3	0	0	0	100						
<i>A. papillare</i>	2	0	0	100	0						■
<i>A. polystoma</i>	1	0	0	100	0						
<i>A. sarmentosa</i>	3	0	0	100	0						
<i>A. secale</i>	3	0	0	100	0						
<i>A. selago</i>	7	0	0	100	0						
<i>A. vaughani</i>	2	0	0	50	50						
<i>A. verweyi</i>	2	0	0	50	50						

* Species observed to spawn in autumn in Western Australia (Simpson 1985; Babcock et al. 1994)

A *Acropora*

in November and/or December 2005, 8–12 weeks after being sampled.

For all of the other species sampled at either Barrow Island or the Dampier Archipelago, the developmental stages of eggs suggested their participation in the autumn spawning in approximately 6 months time. Assuming that the small eggs within colonies developed to maturation, most of the colonies (>60%) and species (93%) that were sampled probably spawned in autumn at the same time as at least 146 other species of corals on Western Australian reefs (Simpson 1991; Babcock et al. 1994), supporting the existing evidence that the largest mass spawning occurs during autumn.

Studies of *Acropora* assemblages from around the world suggest that spawning patterns and seasonality vary in different regions. On the Great Barrier Reef (GBR), several *Acropora* species have been recorded spawning 1–3 months after the mass spawning period (Wolstenholme 2004), while in Kenya, 17 species of *Acropora* have been found to spawn over a 7 month period (Mangubhai and Harrison 2006). In Singapore most *Acropora* species and colonies have been observed to spawn in March/April with a small proportion spawning in October/November (2.1 and 3.8% of species respectively; Guest et al. 2005b). The pattern of spawning of *Acropora* on north Western Australian reefs most closely resembles that of Singapore. By comparison, however, the secondary spawning reported here for the *Acropora* involved a larger proportion of species (38%) and colonies within species (8–100%; median 25%).

The species of *Acropora* sampled through time at the Dampier Archipelago had pigmented eggs and testes present during both spring and autumn. Of the 53 colonies sampled, *A. samoensis* contained large pigmented eggs in October 2002 (64%), and in February and October 2003 (36 and 50% respectively); as did colonies of *A. cytherea* in October 2002 (80%) and in February and October 2003 (20 and 80% respectively). However, in individuals, mature eggs were only observed once each year (suggesting 1 gametogenic cycle), and the size of the eggs suggested colonies consistently spawned during the same season over consecutive years. Similarly, in a sympatric population of *Mycedium elephantotus* that spawned during two distinct periods on Taiwanese reefs, individual colonies had only one annual gametogenic cycle (Dai et al. 2000). These results are in contrast to other instances of bi-annual spawning where some colonies have been found to have two gametogenic cycles and participate in both events, such as in three species of *Montipora* on the GBR (Stobart et al. 1992), two species of *Platygyra* off Kenya (Mangubhai and Harrison 2006) and one species of *Acropora* off Singapore (Guest et al. 2005b). Optimal conditions may well be required for colonies to participate in two spawning events a year, with some colonies reabsorbing eggs that were

initiated in a second cycle, while others kept in favorable conditions spawned year round (Harrison and Wallace 1990). Longer and more intensive sampling is required to determine whether colonies on some Western Australian reefs are capable of initiating two gametogenic cycles and/or participating in two spawning events during years when conditions are suitable.

Colonies of *A. samoensis* and *A. cytherea* that spawned during different seasons were located at the same site, even adjacent to each other along a single transect. If these patterns of reproductive isolation are consistent through time, then colonies at the same site are unlikely to interbreed, providing a mechanism for sympatric speciation. Genetic differentiation among conspecific colonies, and potentially the early stages of speciation, have been reported for populations of *Mycedium* and *Acropora* that spawn at different times (Dai et al. 2000; Wolstenholme 2004). As with these examples, a variety of hypotheses may explain the patterns of spawning reported here for Western Australian reefs. Conspecific colonies spawning during spring and autumn may reflect the legacy of dispersal of immigrants from different reefs where spawning occurs at each of these times. Alternately, the species have responded differently to pressures underlying reproductive success during these seasons, and/or against spawning during mid to late summer. As with the reefs of Taiwan where a similar pattern of reproduction has been described for *M. elephantotus*, some of the most severe disturbances on Western Australian reefs are cyclones, heavy rainfall and bleaching episodes that occur during mid to late summer, and there may be selective advantages to not spawn and recruit during this period (Dai et al. 2000).

The magnitude of genetic differentiation between conspecific colonies spawning at different times on Western Australian reefs remains to be determined, and may provide insights into whether or not the patterns had been consistent over many years, or whether colonies could switch their times of spawning or periodically participate in two spawning events each year. Nevertheless, the spawning during two different seasons suggests conditions for much of the year are suitable for gametogenesis, spawning, larval settlement and post-settlement survival, for multiple species of *Acropora* on Western Australian reefs.

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