

Spawning patterns of scleractinian corals at the Solitary Islands — a high latitude coral community in eastern Australia

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ABSTRACT: The timing and synchrony of reproduction in scleractinian corals varies greatly among geographic locations, along latitudinal gradients, and among regions. On the east coast of Australia, there are extensive subtropical coral communities within the Solitary Islands Marine Park (30° S). From 1994 to 1996, the pattern of reproduction was studied in 27 species from 10 genera of broadcast spawning scleractinian corals. Spawning periods were determined directly from observations of 4 species that spawned in aquaria, and indirectly from repeated sampling of 236 tagged field colonies by noting the disappearance of mature gametes. Evidence of sexual reproduction was observed in 24 coral species, and gametes were released annually from December to April. Spawning periods were staggered among species and among colonies within some species. Spawning in massive species was generally more synchronous and predictable than for acroporid species. Massive coral species spawned from 8 to 12 nights after a full moon, whereas there was no obvious lunar periodicity of spawning among acroporid corals. This asynchronous pattern of reproduction contrasts with the highly synchronous spawning of more than 140 coral species during mass spawning periods on the Great Barrier Reef (GBR) in October to December each year. The delay in the timing of coral spawning at the Solitary Islands compared with the GBR coincides with the delayed rise in sea temperatures in the subtropics. In addition, the highly variable nature of sea temperatures at the Solitary Islands around the time of gamete maturation and spawning may account for the less synchronous pattern of reproduction in this high-latitude coral community.

KEY WORDS: Coral · Spawning · Subtropical reef · Reproductive synchrony

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INTRODUCTION

On the east coast of Australia, a number of subtropical coral communities exist south of the Great Barrier Reef (GBR). The southernmost limit of extensive coral communities along this coast is found 700 km south of the GBR within the Solitary Islands Marine Park on the north coast of New South Wales at 30° S. A total of 90 species from 28 scleractinian genera have been recorded in surveys by Veron et al. (1974) and Harriott et al. (1994). This unexpectedly high diversity of corals results from the location of the Solitary Islands within a biogeographical overlap zone, between the northern tropical and southern temperate marine provinces.

The coral assemblage comprises mostly tropical species at the southern limit of their distribution, with a smaller number of subtropical and temperate species that dominate the community in terms of percentage cover (Veron 1993, Harriott et al. 1994).

Although corals contribute up to 50% of the benthic cover, there is no true coral reef development at the Solitary Islands. A number of factors have been proposed to explain the absence of coral reefs in subtropical latitudes including water temperature, light availability, competition with macroalgae and reduced growth rates (reviewed by Harriott & Banks 2002). In particular it has been suggested that cooler water temperatures experienced at these regions inhibit sexual reproduction of

corals, and therefore maintenance of coral populations will be dependent on the influx of recruits from tropical regions (Wells 1957, Veron 1974). As the coral communities at the Solitary Islands are 700 km south of the GBR, and 100 to 200 km from the nearest subtropical communities, it is important to determine whether or not these coral communities are sexually reproductive. A number of recent studies have shown that coral communities at other high latitude locations are sexually reproductive: Tarut Bay, Arabian Gulf (26° N) (Fadlallah 1996); Kuwait, Arabian Gulf (29° N) (Harrison 1995); Houtman Abrolhos, Western Australia (29° S) (Babcock et al. 1994); Lord Howe Island, eastern Australia (31° S) (authors' unpubl. data); and Shikoku Island, Japan (32° N) (van Woessik 1995).

The most common form of sexual reproduction among scleractinian corals is broadcast spawning (cf. brooding) (Harrison & Wallace 1990, Richmond & Hunter 1990). Synchronous spawning among colonies of the same coral species is necessary for successful reproduction, as most species do not self-fertilise (Heyward & Babcock 1986, Harrison & Wallace 1990, Willis et al. 1997). The timing and degree of spawning synchrony within and among coral species varies widely among coral communities in different locations.

On the GBR, over 140 broadcast spawning coral species reproduce during annual mass spawning events over 4 to 5 d periods, a few nights after the full moon in the austral spring or early summer (Harrison et al. 1984, Babcock et al. 1986, Harrison & Wallace 1990, Harrison 1993). Spawning is generally predictable and is highly synchronous among colonies and species. It has been proposed that a range of environmental factors act as proximate cues to synchronise the timing of these spawning events. Maturation of gametes is associated with an increase in water temperatures in the months prior to spawning, and the main nights of spawning coincide with neap tide periods when tidal currents are minimal, thus enhancing the chance of fertilisation (Babcock et al. 1986).

Mass coral spawning has also been recorded in Western Australia, where corals at both tropical and subtropical latitudes spawn in late summer (Simpson 1991, Babcock et al. 1994). In southern Japan, mass coral spawning occurs on reefs at Akajima Island, although spawning is less synchronous than on the GBR, with the main period of spawning extending over 2 to 3 lunar months in some species (Hayashibara et al. 1993). In the Caribbean, coral spawning usually occurs from July to September each year with corals on northern reefs tending to spawn earlier than corals on southern reefs. Spawning is concentrated during periods from 2 to 9 nights after full moons (nAFM), and some multispecific spawning on the same night within a site has been recorded (Szmant 1986, Richmond & Hunter

1990, Soong 1991, Gittings et al. 1992, Van Veghel 1993, 1994, Steiner 1995). At Eilat in the northern Red Sea, spawning within each species is synchronised at particular lunar phases each year; however, spawning among species is asynchronous and is staggered over a 4 mo period (Schlesinger & Loya 1985). Extended reproductive seasons with less synchrony of spawning among coral species have also been recorded in Hawaii, the Gulf of Mexico and the central and eastern Pacific (reviewed in Harrison & Wallace 1990, Richmond & Hunter 1990, Kenyon 1992, Glynn et al. 1994). In these locations, there is often less variation in the environmental cues (e.g. temperature, tidal range) thought to synchronise coral spawning on the GBR (Oliver et al. 1988, Harrison & Wallace 1990).

Preliminary studies at the Solitary Islands in 1992 and 1993 showed that mature gametes were present in some species of coral in January to April, and spawning was recorded for 4 *Acropora* species and 1 *Acanthastrea* species during February 1993 (P. L. Harrison unpubl. data). The aim of this study was to document the pattern, timing and degree of synchrony of spawning in a range of coral species at the Solitary Islands Marine Park.

MATERIALS AND METHODS

Study sites. The Solitary Islands Marine Park is located on the mid-north coast of New South Wales between 29 and 30° S (Fig. 1). Well-developed coral communities exist on rocky reefs around the offshore islands within the Marine Park. Studies of coral reproduction were carried out at North Solitary and North West Solitary Islands, as these reefs have the highest diversity and cover of coral within the Marine Park (Harriott et al. 1994).

Timing of spawning. In 1994 and 1995, 236 coral colonies of 27 species were tagged, including a range of tropical and subtropical coral species. A total of 86 colonies were tagged at North Solitary Island and 150 at North West Solitary Island. These colonies were sampled intensively during the spawning season (December to April) in 1994, 1995 and 1996 to assess the maturity and presence or absence of gametes in polyps. Small samples (approximately 3 to 6 cm long or in diameter) were taken from mature regions of each colony, and subsequent samples were taken from other areas of the colony to avoid resampling damaged areas. Care was taken to sample relatively large coral colonies (>50 cm diameter) to minimise any stress to the colony. Mature eggs usually become pigmented close to the spawning period and are visible in broken sections of coral (Harrison et al. 1984). Maturity of spermatozoa was assessed by dissecting spermaries

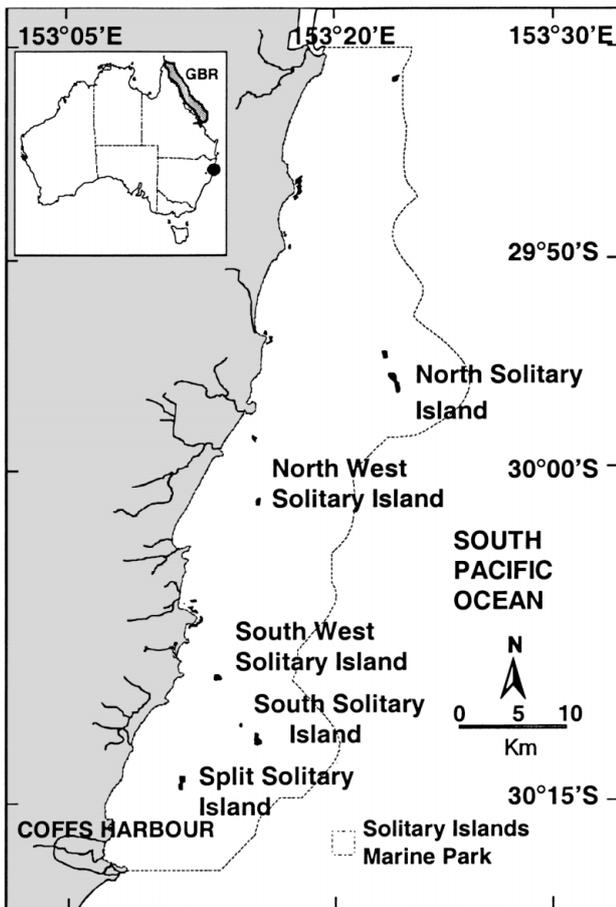


Fig. 1. Map showing location of Solitary Islands Marine Park

from broken sections of corals and examining sperm under a high power microscope (Harrison et al. 1984). Colonies were sampled approximately every 2 wk until signs of reproductive maturity (i.e. pigmented eggs and sperm with a flagellum and a condensing head) were evident, then colonies were sampled every few days, where possible, until gametes disappeared. Spawning was inferred from the presence or absence of mature gametes in these sequential samples.

The timing of spawning was also obtained from observations of corals collected from the study sites and maintained in aquaria. Portions of colonies with mature gametes were collected from North and North West Solitary Islands and transported to the Arrawarra Field Station, where they were kept in aquaria or 50 l plastic containers. Water quality was maintained using either flowthrough seawater, mechanical filtration or $\frac{1}{3}$ water exchange twice daily. Coral colonies were kept under a natural light and dark photoperiod regime, and were monitored each evening for signs of spawning. Details of the timing and behaviour of spawning were noted. In order to determine whether laboratory

observations reflected the timing of spawning in field populations, tagged colonies of the same species were sampled in the field within 24 to 48 h of spawning being observed in aquaria. In this paper the date of spawning is expressed as nAFM.

RESULTS

Of the 27 species of scleractinian coral sampled, gametes were seen in 24 species, and spawning was observed or inferred in 21 of these species including 15 acroporids, 3 faviids, 2 mussids and 1 dendrophylliid. A list of coral species and the synodic months in which mature gametes were seen over the 3 yr study is shown in Table 1. Gametes were not observed in broken sections of tagged colonies of *Acropora humilis* (1 colony), *A. robusta* (1 colony), and *Pavona minuta* (1 colony) examined with a dissecting microscope during the spawning season of other coral species.

Studies from 1994 to 1996 showed that there was an extended period of coral spawning at the Solitary Islands from December to April each year. Spawning was staggered both among and within coral species over this period, with the main period of coral spawning in January and February (Table 1). The timing of spawning for every colony sampled in 1994, 1995 and 1996 is shown in Fig. 2 (acroporid species) and Fig. 3 (massive species). Although each colony was sampled on multiple occasions, only the dates of the last gravid sample and the subsequent sample when colonies had no gametes present are shown, to demonstrate the spawning period of each coral colony.

January was the main spawning month for *Acropora solitaryensis*, *A. glauca*, *A. cytherea*, *A. hyacinthus*, *A. florida*, *Cyphastrea serailia* and *Montastrea curta*, while *A. valida*, *A. lutkeni*, *A. divaricata*, *A. nasuta* and *Acanthastrea lordhowensis* spawned mainly in February. Most colonies of *A. digitifera*, *A. lovelli* and *Goniastrea australensis* spawned between March and April. The spawning period of the coral community was also extended by asynchrony of spawning among colonies of some species, which resulted in spawning periods extending over 1 to 4 mo. For example, some colonies of *A. solitaryensis* released gametes in December, and others between March and April (Fig. 2).

Acroporidae

Acroporid corals released gametes between December and April each year. Spawning was largely asynchronous among colonies within each species, although for most species, a proportion of the population released gametes around the same period.

Table 1. Synodic months in which gametes were seen in 24 species of scleractinian coral at the Solitary Islands Marine Park from 1994 to 1996; +: mature gametes present, +^: gametes present but maturity not assessed, *: only 1 colony sampled, #: subtropical species

Species	Synodic month					
	Nov	Dec	Jan	Feb	Mar	Apr
Family: Acroporidae						
<i>Acropora solitaryensis</i> #		+	+	+	+	+
<i>Acropora glauca</i> #		+	+	+	+	
<i>Acropora valida</i>		+	+	+	+	
<i>Acropora hyacinthus</i>		+	+			
<i>Acropora lutkeni</i>			+	+	+	+
<i>Acropora cytherea</i>		+	+			
<i>Acropora nasuta</i>			+	+	+	+
<i>Acropora divaricata</i>			+	+	+	
<i>Acropora sarmentosa</i>		+	+			
<i>Acropora florida</i>			+	+		
<i>Acropora digitifera</i>			+	+	+	
<i>Acropora lovelli</i>			+	+	+	
<i>Acropora secale</i>			+	+		
<i>Acropora polystoma</i> *				+		
Family: Faviidae						
<i>Cyphastrea serailia</i>		+	+			
<i>Montastrea curta</i>		+	+	+		
<i>Goniastrea australensis</i> #			+	+	+	+
Family: Mussidae						
<i>Acanthastrea echinata</i>		+	+	+		
<i>Acanthastrea lordhowensis</i> #			+	+		
Family: Siderasteridae						
<i>Coscinarea columna</i> *				+	^	
<i>Psammocora superficialis</i> *		+	^			
Family: Poritidae						
<i>Goniopora lobata</i> *		+	^			
Family: Dendrophyllidae						
<i>Turbinaria frondens</i> *				+	^	
<i>Turbinaria radicalis</i> *		+	^			

Acropora solitaryensis exhibited the least synchronous spawning pattern of all species studied. In addition, the release of gametes was not associated with a particular lunar phase. While many colonies of *Acropora* species released gametes around the new moon in January, some colonies released gametes around the full moon, and others released gametes during the last half of the lunar phase in February and March.

Table 2. Aquarium observations of spawning of corals from the Solitary Islands Marine Park from 1994 to 1996. *: no observations, ^: all tagged colonies in the field spawned by 12 nAFM, #: subtropical species

Species	Lunar month	nAFM		
		1994	1995	1996
<i>Montastrea curta</i>	January	10	9–11	10
<i>Cyphastrea serailia</i>	January	*	10–11	9–10
<i>Acanthastrea lordhowensis</i> #	February	9	10–12	9–13, 16^
<i>Goniastrea australensis</i> #	March	12	8–9	*

Massive species

In the massive species studied, spawning was generally synchronous within each species and occurred between 8 to 12 nAFM. However, spawning among species was staggered over 3 lunar months (Fig. 3) with *Montastrea curta* and *Cyphastrea serailia* spawning in January, *Acanthastrea lordhowensis* in February, and *Goniastrea australensis* in March. The dates when massive species were seen spawning in aquaria in each year of study are shown in Table 2. Examination of tagged colonies in the field just before and after the nights of spawning in aquaria confirmed the disappearance of mature gametes in the majority of the population during this period. An exception to this occurred in 1996, when the main spawning of *A. lordhowensis* in aquaria occurred 16 nAFM in February, but field populations had spawned by 12 nAFM in February.

Spawning in *Montastrea curta*, *Cyphastrea serailia*, *Acanthastrea lordhowensis* and *Goniastrea australensis* occurred between 1 to 4 h after sunset and was characterised by a typical 'setting' phase (Babcock et al. 1986) followed by the release of gametes from the polyp mouth. Spawning occurred over a 0.5 to 1 h period each night. *C. serailia* and *M. curta* spawned positively buoyant egg-sperm bundles. *A. lordhowensis* was observed to release clouds of sperm during spawning, but sperm were also incorporated into egg-sperm bundles. Egg-sperm bundles of these species were also positively buoyant, and floated to the surface after release. In each species, spawning occurred over 1 to 3 nights, with some colonies releasing gametes on each of 3 successive nights.

While the majority of tagged colonies of these species released gametes around these times, some colonies spawned up to 1 lunar month earlier, or later than other colonies (Fig. 3). In addition, some colonies of *Montastrea curta* released gametes over 2 lunar phases in January and February 1995 and 1996 (Fig. 3). Examination of broken sections of these colonies showed eggs at 2 stages of development, with a mixture of pigmented (mature) eggs

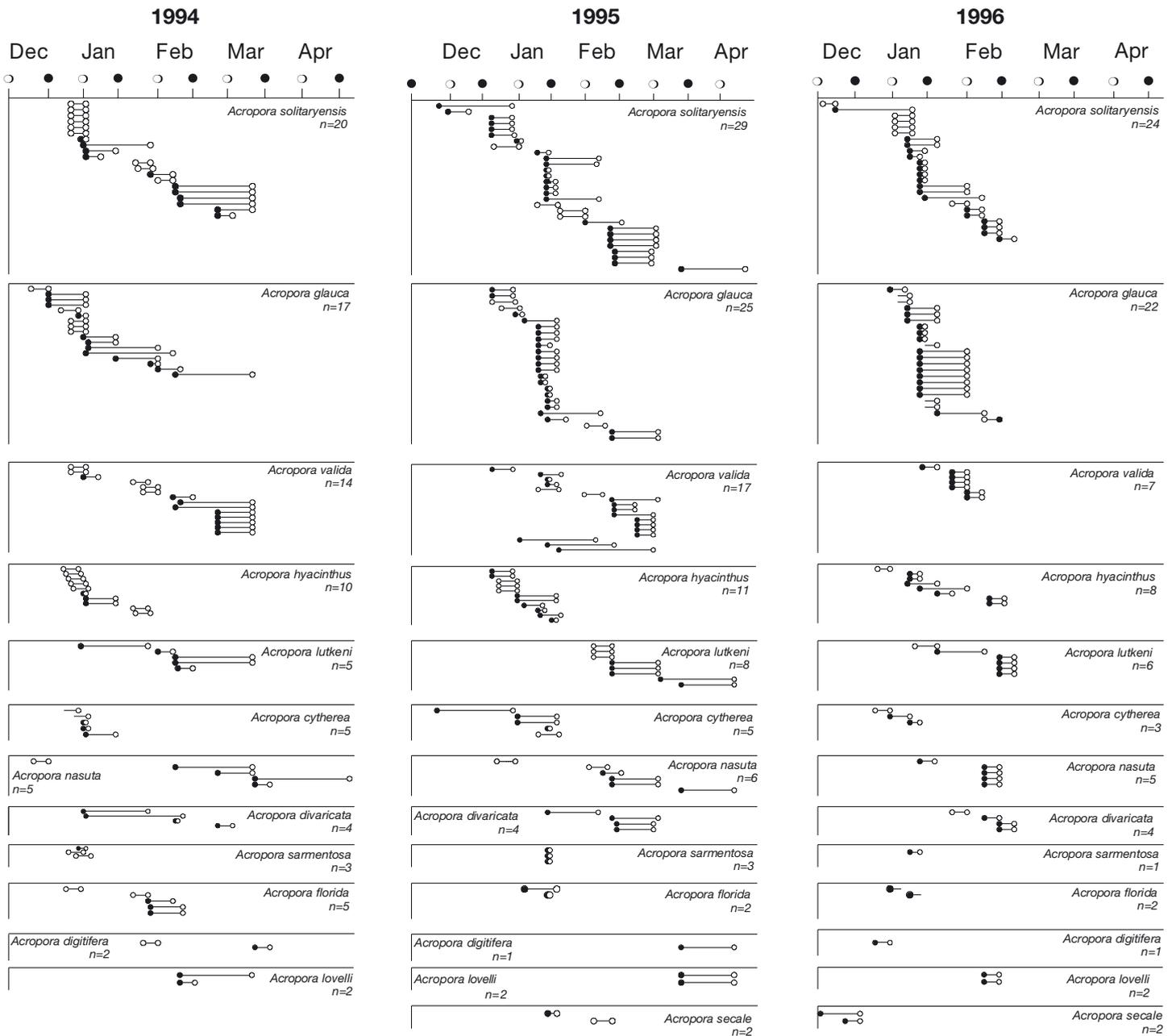


Fig. 2. Periods over which gametes disappeared in tagged colonies of acroporid coral species at North and North West Solitary Islands from 1994 to 1996 for species represented by 2 or more colonies. Each line denotes spawning records for a single colony. ○ = full moon, ● = new moon, ●—○ represents the period between the last sample date when gametes were present (closed symbol) and the subsequent sample date (open symbol) when gametes were absent, ●— represents the last date when gametes were present but the colony was not sampled again, —○ represents the situation where a colony was empty when first sampled, ●—▲—○: triangle represents the date when some of the gametes had disappeared, indicating partial spawning

and pale (immature) eggs in the same polyp. The pale eggs became pigmented and were released in the month following the release of the initially mature eggs. One colony of *Cyphastrea serailia* in 1995, and 2 colonies in 1996, also released gametes over 2 periods within the same lunar month of January (Fig. 3).

DISCUSSION

This study has shown that many scleractinian reef corals at the Solitary Islands Marine Park are sexually reproductive, and that broadcast spawning is a common form of reproduction. Mature gametes were seen

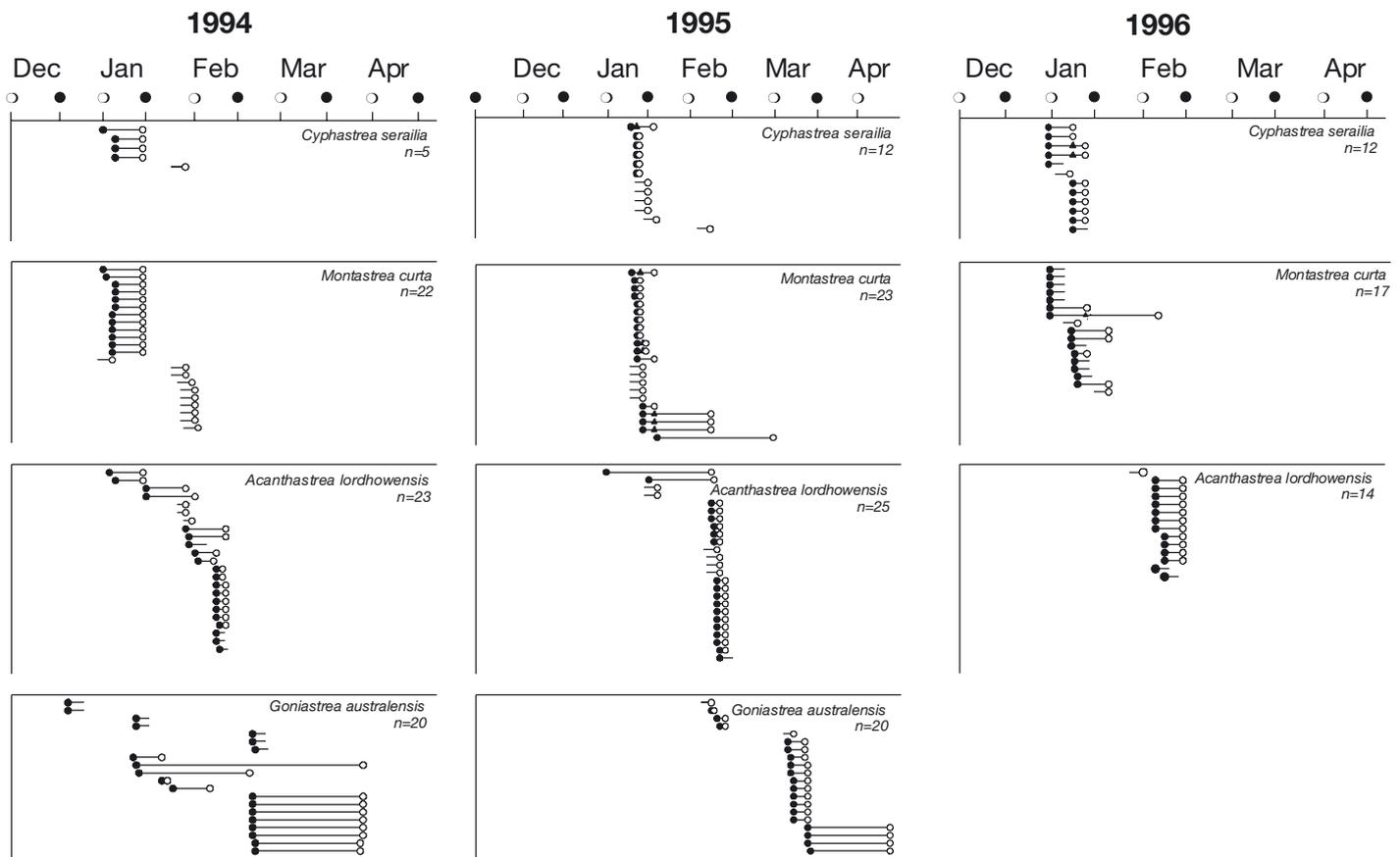


Fig. 3. Periods over which gametes disappeared in tagged colonies of massive coral species at North and North West Solitary Islands from 1994 to 1996 (For explanation of symbols see Fig. 2)

in a range of taxonomic groups (24 species from 9 genera) and in both tropical and subtropical coral species. This indicates that reproduction is not inhibited at these high latitude locations despite many species being at, or near, their southern latitudinal limit of distribution (Veron 1993).

Spawning synchrony within each species

Massive coral species exhibited a greater degree of synchrony of spawning within each species compared with acroporids. Spawning among the majority of tagged and collected colonies of *Montastrea curta*, *Cyphastrea serailia*, *Acanthastrea lordhowensis* and *Goniastrea australensis* was predictable, and occurred between 1 to 4 h after sunset, 8 to 12 nAFM in January to March.

This contrasts with acroporid species, in which mature gametes were present in the population over a period of 3 to 6 wk, and in the case of *Acropora solitaryensis*, over 4 mo. However, some colonies of the same acroporid species released gametes synchronously as gametes disappeared from a proportion of

the population between 2 sequential sampling dates. Synchronised spawning in at least part of the population is likely to be important for successful fertilisation, and field observations of spawning are required to determine the timing and degree of spawning synchrony among colonies of each coral species. During this study, spawning in most *A. solitaryensis* colonies occurred either around the new moon or between the new and full moon, although P. L. Harrison (unpubl. data) recorded synchronous spawning of 9 *A. solitaryensis* colonies at North West Solitary Island on the 3 nAFM in February 1993.

Spawning synchrony among species

In contrast to the mass coral spawning episodes reported on reefs on the GBR, in Western Australia, and some other regions (reviewed in Harrison & Wallace 1990, Richmond & Hunter 1990), coral spawning at the Solitary Islands is less synchronous and occurs over an extended period of up to 4 mo. This reproductive pattern is more similar to that described from

Japan, the Red Sea and Hawaii, where individual species spawn at different months and lunar phases over a 3 to 4 mo period (reviewed in Harrison & Wallace 1990, Richmond & Hunter 1990). The degree of spawning synchrony in coral communities varies among other high latitude reefs. Mass spawning occurs on reefs in northern Japan (van Woiesik 1995) and subtropical reefs off Western Australia (Babcock et al. 1994), while coral spawning is spread over at least 3 mo on reefs in Kuwait (Harrison 1995). Despite the extended reproductive season at the Solitary Islands, it is likely that some degree of multispecific spawning occurred among acroporid species at the Solitary Islands as colonies from up to 9 species released gametes between the same concurrent sampling dates (Fig. 2). However, in most cases, it was not possible to determine whether these colonies released gametes on the same night, as sequential samples were taken many days apart due to rough weather conditions. Also, no direct observations of spawning in the field could be made because of the logistic difficulties of night diving at these exposed study sites. Multispecific spawning within an extended reproductive season has also been reported in the Caribbean (Wyers et al. 1991, Gittings et al. 1992). The release of gametes from many species around the same time indicates that different coral species are responding independently to exogenous or endogenous cues for spawning.

Environmental factors that influence reproduction

The timing and degree of synchrony of mass coral spawning on the GBR has been linked both to seasonal changes in water temperatures and to tidal cycles. Babcock et al. (1986) suggested that the primary proximate factor in determining the month of spawning in corals on the GBR was increasing water temperature. These authors also noted that most corals spawned during neap tides when tidal currents are minimal, which is thought to maximise the chance of fertilisation success. Comparisons between the Solitary Islands and the GBR with respect to tidal variation are restricted to 4 massive species for which the nights of spawning are known. In these species from the Solitary Islands, spawning coincided with periods of minimal tidal variation; i.e. on a neap tide period a few hours prior to low tide. However,

the large variation in the timing of spawning among colonies of acroporid species at the Solitary Islands, with respect to lunar phase, makes it difficult to determine the extent of tidal influence on the timing of coral spawning in these species.

At the Solitary Islands, spawning occurs 2 to 5 mo later than on the GBR, which corresponds to the delay in the timing of the rise of maximum sea surface temperature (SST) on the SE coast of Australia (Fig. 4). Thus, the delay in spawning at the Solitary Islands compared to the GBR may simply reflect the difference in timing of the rise of sea surface temperature (SST) between the 2 regions. A similar situation has been described for high latitude populations of coral in northern Japan, where a delay in spawning of 2 mo compared to southern reefs coincides with a delay in the rise of SST (van Woiesik 1995).

However, on reefs in Western Australia, coral spawning occurs after the summer SST maxima, and the timing of mass spawning (8 to 10 nAFM) at tropical latitudes (Ningaloo Reef, 22 to 24° S) occurs in the same week as mass spawning (9 to 11 nAFM) on reefs at subtropical latitudes (Houtman Abrolhos, 29° S) (Babcock et al. 1994). This synchronous spawning pattern occurs despite marked differences in the temperature regimes between the 2 sites. At Ningaloo Reef, the SST maxima are 5 to 7°C warmer, and the timing of the winter minima and sea temperature rise occurs 3 mo earlier compared to the Houtman Abrolhos (Babcock et al. 1994). Difference in tidal regimes between

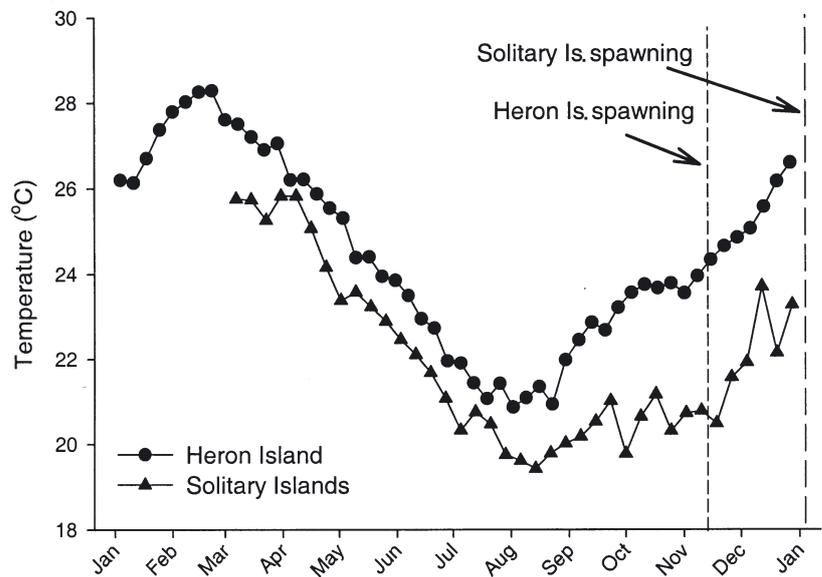


Fig. 4. Water temperatures recorded at Heron Island (Great Barrier Reef) and Solitary Islands in 1998, showing the start of spawning periods at each location. Heron Island data from Great Barrier Reef Marine Park Authority and Solitary Islands data from V. Harriott (unpubl. data)

the 2 sites means that tropical corals at Ningaloo Reef spawn on neap tides, whereas subtropical corals at the Houtman Abrolhos spawn near spring tides (Babcock et al. 1994). Babcock et al. (1994) suggested that corals at subtropical latitudes might be exhibiting a spawning pattern inherited from parent colonies on tropical reefs. Despite the high latitude location of the Houtman Abrolhos reefs, these have a strong tropical influence which can be attributed to the strength and path of the Leeuwin Current, resulting in a coral community dominated by tropical species (Babcock et al. 1994).

In contrast, environmental conditions between the GBR and Solitary Islands are substantially different and may explain the different reproductive patterns at the 2 locations. While the East Australian Current (EAC) brings warm tropical water to the Solitary Islands region, it impinges on the islands and coastline on a sporadic basis (J. Wilson & G. Cresswell unpubl. data). This probably explains the large variation in water temperatures within the Solitary Islands Marine Park, as the EAC moves on- and offshore (Fig. 4). The EAC may also transport planktonic larvae from the GBR as indicated by the large number of tropical coral and fish species at the Solitary Islands. However, in contrast to the Houtman Abrolhos, the coral community at the Solitary Islands is dominated by subtropical species, indicating that the environment is very different to tropical regions. The highly variable nature of the sea temperature regime may explain the different responses of individual corals to this stimulus and thus the extended, asynchronous and sometimes unpredictable nature of the spawning pattern observed in some acroporid corals at the Solitary Islands. In addition, factors other than temperature, such as lunar cycles and chemical cues, may be important in determining the time of spawning for at least some massive coral species which spawn synchronously at the Solitary Islands. Babcock et al. (1994) proposed that factors such as photoperiod and lunar phase were more important than an increase in SST and neap tidal phases in synchronising the timing of coral spawning at tropical and subtropical reefs in Western Australia. In addition, Olive (1995) noted that in many invertebrate species, experimental studies have shown that factors other than temperature are important in the timing of reproductive cycles.

Implications for subtropical coral communities

It is now clear that sexual reproduction is common in many species of broadcast spawning coral at the Solitary Islands, and in other high latitude locations. Therefore, the restriction of coral reefs to tropical regions cannot be explained by the absence of sex-

ual reproduction in high latitude coral communities. However, there are many factors that may affect the reproductive process between spawning and successful recruitment. The asynchronous pattern of spawning within and among some coral species may reduce fertilisation rates in the field, as most broadcast spawning species do not self-fertilise (Heyward & Babcock 1986, Willis et al. 1997). Partitioning of reproductive effort among colonies of a single species over a longer period of time may also increase the chance of larval survival and settlement in a highly variable environment, as long as a portion of the population spawn together to ensure fertilisation (Schlesinger & Loya 1985).

Wilson & Harrison (1997) have shown that planulae larvae of some species of coral from the Solitary Islands are able to develop and settle successfully in laboratory conditions on substratum and in temperatures similar to those experienced in the field. Therefore it is likely that planulae larvae are produced by broadcast spawning corals at the Solitary Islands, because spawning is synchronous among most colonies in populations of massive coral species, and in at least some colonies in populations of acroporid species. If significant numbers of competent larvae are produced at the Solitary Islands, then there is potential for these corals to contribute to the maintenance of local populations. This would greatly reduce the time required for communities to recover from damage caused by natural or anthropogenic disturbances, compared to a dependence on larvae from distant tropical reefs. Oceanographic data obtained from the Solitary Islands during the periods of coral spawning suggest that, while at times southward currents are strong and are likely to sweep larvae away from the region, at other times currents are weak and oscillate in a north–south direction along the coast (Wilson 1998). This could provide a mechanism for the retention or return of larvae produced at the Solitary Islands to the local area or to nearby reefs. It is likely, then, that coral populations at the Solitary Islands are important in the geographic distribution of scleractinian corals on subtropical reefs along eastern Australia, and act as 'stepping stones' for larval dispersal and recruitment (Wilson & Harrison 1998).

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LITERATURE CITED

- Babcock RC, Bull GD, Harrison PL, Heyward AJ, Oliver JK, Wallace CC, Willis BL (1986) Synchronous spawning of 105 scleractinian coral species on the Great Barrier Reef. *Mar Biol* 90:379–394
- Babcock RC, Willis BL, Simpson CJ (1994) Mass spawning of corals on a high latitude coral reef. *Coral Reefs* 13:161–169
- Fadlallah YH (1996) Synchronous spawning of *Acropora clathrata* coral colonies from the western Arabian Gulf (Saudi Arabia). *Bull Mar Sci* 59:209–216
- Gittings SR, Boland GS, Deslarzes KJP, Combs CL, Holland BS, Bright TJ (1992) Mass spawning and reproductive viability of reef corals at the East Flower Garden Bank, northwest Gulf of Mexico. *Bull Mar Sci* 51:420–428
- Glynn PW, Colley SB, Eakin CM, Smith DB and 5 others (1994) Reef coral reproduction in the eastern pacific: Costa Rica, Panama, and Galapagos Islands (Ecuador). II Poritidae. *Mar Biol* 118:191–208
- Harriott VJ, Banks SA (2002) Latitudinal variation in coral communities in eastern Australia: a qualitative biophysical model of factors regulating coral reefs. *Coral Reefs* 21: 83–94
- Harriott VJ, Smith SDA, Harrison PL (1994) Patterns of coral community structure of subtropical reefs in the Solitary Islands Marine Reserve, eastern Australia. *Mar Ecol Prog Ser* 109:67–76
- Harrison PL (1993) Coral spawning on the Great Barrier Reef. *Search* 24:45–48
- Harrison PL (1995) Status of the coral reefs of Kuwait. Final Report to the United Nations Industrial Development Organization and the United Nations Development Programme. UNIDO and UNDP, Vienna
- Harrison PL, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky Z (ed) *Coral reefs*. Elsevier Science, Amsterdam, p 133–207
- Harrison PL, Babcock RC, Bull GD, Oliver JK, Wallace CC, Willis BL (1984) Mass spawning in tropical reef corals. *Science* 223:1186–1189
- Hayashibara T, Shimoike K, Kinur T, Hosaka S, Heyward A, Harrison P, Kudo K, Omori M (1993) Patterns of coral spawning at Akajima Island, Okinawa, Japan. *Mar Ecol Prog Ser* 101:253–262
- Heyward AJ, Babcock RC (1986) Self- and cross-fertilization in scleractinian corals. *Mar Biol* 90:191–195
- Kenyon JC (1992) Sexual reproduction in Hawaiian *Acropora*. *Coral Reefs* 11:37–43
- Olive PJW (1995) Annual breeding cycles in marine invertebrates and the environmental temperature: probing the proximate and ultimate causes of reproductive synchrony. *J Therm Biol* 20:79–90
- Oliver JK, Babcock RC, Harrison PL, Willis BL (1988) Geographic extent of mass coral spawning: clues to ultimate causal factors. *Proc 6th Int Coral Reef Symp* 2:803–809
- Richmond RH, Hunter CL (1990) Reproduction and recruitment of corals: comparisons among the Caribbean, the tropical Pacific, and the Red Sea. *Mar Ecol Prog Ser* 60:185–203
- Schlesinger Y, Loya Y (1985) Coral community reproductive patterns: Red Sea versus the Great Barrier Reef. *Science* 228:1333–1335
- Simpson CJ (1991) Mass spawning of corals on Western Australian reefs and comparisons with the Great Barrier Reef. *J R Soc West Aust* 74:85–91
- Soong K (1991) Sexual reproductive patterns of shallow-water reef corals in Panama. *Bull Mar Sci* 49:832–846
- Steiner SCC (1995) Spawning in scleractinian corals from SW Puerto Rico (West Indies). *Bull Mar Sci* 56:899–902
- Szmant AM (1986) Reproductive ecology of Caribbean reef corals. *Coral Reefs* 5:43–54
- Van Veghel MLJ (1993) Multiple species spawning on Curaçao reefs. *Bull Mar Sci* 52:1017–1021
- Van Veghel MLJ (1994) Reproductive characteristics of the polymorphic Caribbean reef building coral *Montastrea annularis*. I. Gametogenesis and spawning behaviour. *Mar Ecol Prog Ser* 109:209–219
- van Woesik R (1995) Coral communities at high latitude are not pseudopopulations: evidence of spawning at 32°N, Japan. *Coral Reefs* 14:119–120
- Veron JEN (1974) Southern geographic limits to the distribution of Great Barrier Reef hermatypic corals. *Proc 2nd Int Coral Reef Symp* 2:465–473
- Veron JEN (1993) A biogeographic database of hermatypic corals. Australian Institute of Marine Science, Townsville
- Veron JEN, How RA, Done TJ, Zell LD, Dodkin MJ, O'Farrell AF (1974) Corals of the Solitary Islands, central NSW. *Aust J Mar Freshw Res* 25:193–208
- Wells JW (1957) Coral Reefs. *Mem Geol Soc Am* 67:609–631
- Willis BL, Babcock RC, Harrison PL, Wallace CC (1997) Hybridization among mass spawning reef corals. *Coral Reefs* 16(Suppl):S53–S65
- Wilson J (1998) Reproduction and larval ecology of broadcast spawning corals at the Solitary Islands, eastern Australia. PhD thesis, Southern Cross University, Lismore
- Wilson J, Harrison P (1997) Sexual reproduction in high latitude coral communities at the Solitary Islands, eastern Australia. *Proc 8th Int Coral Reef Symp* 1:533–538
- Wilson J, Harrison P (1998) Settlement competency periods of larvae of 3 species of scleractinian corals. *Mar Biol* 131: 339–345
- Wyers SC, Barnes HS, Smith SR (1991) Spawning of hermatypic corals in Bermuda: a pilot study. *Hydrobiologia* 216–217:109–116

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