Latitudinal variation in the reproduction of *Acropora* in the Coral Sea.

A. H. Baird[1,2], P. A. Marshall[3], J. Wolstenholme[1]

Abstract Most comparisons available suggest that synchronous spawning of numerous species of scleractinian corals is restricted to regions with large variations in environmental cycles, such as temperature and tides, with a progressive breakdown in seasonality and synchrony of reproduction towards the equator. Here we compared the reproductive condition of *Acropora* at 4 locations in the Coral Sea with contrasting environmental cycles. In the Solomon Islands (SI) where environmental conditions varied little, mature oocytes were found in 28 of the 38 *Acropora* species sampled. This was similar to the pattern on the Great Barrier Reef (GBR) and indicates that synchronous spawning is a feature of coral assemblages in the absence of major environmental fluctuations. In 8 widespread and abundant species the proportion of the population with mature oocytes was 2-4 times lower in the SI, and a higher proportion of colonies had immature oocytes. These data are consistent with an extended reproductive season in the SI when compared to the GBR. Some asynchrony of gamete release was evident in most species at all locations. In addition, a high number of colonies with no visible gametes suggests that colonies of species which typically participate in mass spawning episodes on the GBR, may miss one or more years, or spawn at other times of the year.

Keywords Coral, Life history, Mass spawning

Introduction

The annual mass spawning of scleractinian corals on the Great Barrier Reef (GBR) is one of the most spectacular of natural phenomena. Over 130 species spawn synchronously in the week following a full moon in late spring over much of the GBR (the mass spawning period *sensu* Willis et al. 1985) and more than 30 species have been recorded spawning within hours on the same night at a single location (Babcock et al. 1986; Willis et al. 1985). Some populations on inshore reefs spawn one lunar month before offshore reefs and in some years, when the full moon occurs in first half of October, spawning is split over two months with some colonies releasing gametes one month before the remainder of the population (Willis et al. 1985).

A number of hypotheses have been proposed to explain the mass coral spawning on the GBR, the most likely of which is that species have independently, but similarly, responded to strong selective pressure promoting reproductive success (reviewed in Harrison and Wallace 1990). The selective pressure is hypothesized to result from large fluctuations in environmental cycles, in particular seawater temperatures and tidal amplitude, which create a brief period when conditions for fertilization and survival of gametes are optimal (Harrison and Wallace 1990). In the absence of large fluctuations in environmental cycles the prediction is for an extended breeding season and less synchrony between species (Richmond and Hunter 1990). The available comparisons of coral community spawning patterns generally support this prediction. For example, in regions where the environmental parameters are relatively constant the coral spawning period extends for several months and gamete release occurs during many lunar phases (Red Sea, Shlesinger and Loya 1985; Caribbean, Szmant 1986; Micronesia, Richmond and Hunter 1990; Japan, Hayashibara et al. 1993). Similarly, closer to the equator, synchrony of spawning between species is reduced and some corals may breed throughout the year (Papua New Guinea (PNG), Oliver et al. 1988; Palau, Kenyon 1995). However, recent observations of 12 coral species spawning in synchrony following the full moon in October 1995 in the Java Sea, challenge the idea that mass spawning is restricted to regions with large fluctuations in environmental variables (Edinger et al. in Tomascik et al. 1997).

The length and time of the reproductive season is also strongly influenced by environmental variables (Harrison and Wallace 1990). On the GBR most broadcast spawning species have an annual gametogenic cycle, and the release of gametes is usually restricted to one or a few nights each year, and tends to occur synchronously over a wide geographic area (see review by Harrison and

[1] Department of Marine Biology, James Cook University, Townsville, Qld 4811, Australia.
[2] Present address: Department of Chemistry, Biology and Marine Sciences, University of the Ryukyus, Senbaru 1, Nishihara, Okinawa 903-0123, Japan. e-mail: andrewbaird@ozemail.com.au
[3] Great Barrier Reef Marine Park Authority, Townsville, Q 4811, Australia.

Wallace 1990), although some degree of split spawning within populations has been recorded (Wallace 1985; Willis et al. 1985). In contrast, *Acropora* populations closer to the equator apparently release gametes for an extended period and some colonies may have two gametogenic cycles per year (Oliver et al. 1988). A similar latitudinal pattern in reproduction is evident in brooding corals, many of which have an extended reproductive season near the equator. For example, pocilloporids breed throughout the year at Palau (Atoda 1947 a & b, 1951) whereas on the GBR breeding is seasonal (Harriott 1983, Tanner 1996). Similarly, *Acropora palifera* releases planulae throughout the year in PNG but only in the summer months on the southern GBR (Kojis 1986).

The aim of this study was to examine latitudinal variation in the reproduction of the *Acropora*. In particular, we wanted to determine the proportion of these populations with oocytes in various states of maturity in order to examine how the length of the reproductive season and the number of species spawning in synchrony varied between 4 sites separated by 15 ^{O} latitude within the Coral Sea.

Methods

The reproductive condition of *Acropora* colonies were examined at 4 sites in the Coral Sea separated by over 15 degrees of latitude: the Solomon Islands (8^{O} 06' S, 156^{O} 51' E); Lizard Island in the northern GBR (14 ^{O} 39' S, 145 ^{O} 27 'E); Pelorus Island in the central GBR (18 ^{O} 40' S, 146 ^{O} 32' E); and Lady Elliot in the southern GBR (23^{O} 45' S, 152^{O} 23' E). All sites were visited 1-2 weeks before the expected mass spawning period of corals on the GBR (i.e. 2-7 days following the full moon on 23 November 1999).

The reproductive condition of colonies was established by breaking coral branches below expected sterile zones (Wallace 1985) to expose the developing oocytes (after Harrison et al. 1984). The degree of synchrony in the maturation of gametes between polyps within a colony is generally high (Wallace 1985). However, not every fracture of the branch will penetrate a polyp. Consequently, up to 3 branches were broken per colony and colonies were only scored as empty if all 3 branches were empty. All the available evidence indicates that colonies will release eggs following the full moon subsequent to their maturation (Willis et al. 1985; Babcock et al. 1986; Oliver et al. 1988) which is indicated by pigmentation in the oocytes and is readily recognisable underwater (Harrison et al. 1984). While some *Acropora* may release white/pale cream eggs (Harrison pers. comm.) this would not appear to be the typical pattern.

Three reproductive conditions were defined based on the colour of the oocytes: mature - oocytes pigmented; immature – oocytes white (if the oocytes are pale but visible it indicates that they are close to maturity and likely to spawn within 1-3 months); empty - oocytes too small to see or absent (this indicates either that the colony has recently spawned, or is unlikely to do so for at least 3 months). Corals were sampled haphazardly except on Lizard Island, where corals of the *Acropora humilis* group were targeted as part of a separate research program, and on Lady Elliot Island where only 8 species were sampled.

Two environment variables considered to be important influences on the reproduction of corals were examined to see how they differed between the locations: tidal amplitude and seawater temperature. Variation in tidal amplitude was expressed as the difference between Mean High Water Spring and Mean Low Water Spring where tides were semi-diurnal (Lizard Island Pelorus Island and Lady Elliott) and the difference between Mean Higher High Water and Mean Lower Low Water where tides were diurnal (Solomon Islands and Lizard Island). Data on tidal amplitude were obtained from The Australian National Tide Tables 1999. Sea surface temperature (SST) variation was estimated as the difference between the annual maximum monthly mean SST minus the annual minimum monthly mean. For sites on the GBR this figure was calculated from monthly mean surface temperatures collected between the years 1903-1994 (Lough 2000). In the Solomon Islands this figure was calculated from monthly mean SST collected between the years 1995-98 supplied by ICLARM Coastal Aquaculture Center, Gizo, Solomon Islands.

Results and Discussion

The mean annual temperature range was 2.5 to 3.5 times greater at sites on the GBR when compared to the Solomon Islands, ranging from 2 ^{o}C in the Solomon Islands to 5.4 ^{o}C at Lady Elliot Island (Table 1). The mean annual temperature varied predictably with latitude, ranging from 28.0 ^{o}C in the Solomon Islands to 24.0 ^{o}C at Lady Elliott Island (Table 1). Tidal variation was 2 to 2.5 times higher on the GBR ranging from 0.8 m in the Solomon Islands to 2.1 m at Pelorus Island and Lady Elliot Island (Table 1). Tidal range varied little between the three sites on the GBR (Table 1). If the magnitude of fluctuations in these variables are important determinants of the length of the reproductive season and spawning synchrony between species the expectation would be for a longer breeding season and for less synchrony between species in SI when compared to the sites on the GBR.

Table 1. Sea Surface Temperature (SST) and tidal variation at four sites in the Coral Sea. The temperature range is the difference between the annual monthly maximum and annual monthly minimum for the years 1903-1997 on Lizard Island, Pelorus Island and Lady Elliot and the years 1995-1998 for Solomon Islands. The mean is the mean annual temperature. Tidal range is the difference between the MHHW and MLLW where tides are diurnal (Gizo, Solomon Islands and Lizard Island) and between MHWS and MLWS where tides are semi-diurnal (Pelorus Island and Lady Elliot).

location	Latitude	Temperature range ^{O}C	Mean Annual Temperature ^{O}C	Tidal range (metres)
Solomon Islands	8^{O} 06'	2.0	28.9	0.8
Lizard Island	14 ^{O} 39'	4.6	27.2	1.9
Pelorus Island	18 ^{O} 40'	5.1	26.1	2.1
Lady Elliot Island	23 ^{O} 45'	5.4	24.4	2.1

In 8 widespread and abundant species the proportion of the colonies with oocytes was typically 2-4 times lower in SI than at sites on the GBR (Table 2). The exception was *A. digitifera*, in which no colonies on Lizard Island had visible oocytes, compared to 34% of colonies in SI (Table 2). The proportion of colonies with oocytes was generally high at the three GBR sites and greater than 50% in all these species except *A. muricata* (Table 2). The proportion of the populations with oocytes varied little between sites on the GBR with the exception of *A. humilis* where a high proportion of colonies had oocytes at Lizard Island (Table 2). These data indicate that the reproductive output of these *Acropora* is more concentrated at this time of year on the GBR than in the SI.

Table 2. The proportion of colonies (%) with visible oocytes in 8 common species at the four study sites in the Coral Sea. Blank cells indicate that less than five colonies were sampled at that location.

Species	Solomon Islands	Lizard Island	Pelorus Island	Lady Elliot
Acropora cytherea	17		83	80
Acropora digitifera	34	0	78	
Acropora muricata	0		44	50
Acropora humilis	14	93	51	60
Acropora hyacinthus	47		100	80
Acropora millepora	48	92	88	70
Acropora nasuta	45	89	94	100
Acropora tenuis	0	75	82	90

The proportion of all colonies with immature oocytes was six times higher in the SI (6%) than at sites on the GBR (1%) (Table 3-5). Furthermore, the majority (58%) of colonies in SI had no visible gametes (Table 3) suggesting they had spawned recently, may spawn at another time of year or may not spawn not at all. Either way, these data are consistent with the fact that the reproductive season of the *Acropora* is extended at lower latitudes.

There was evidence for asynchrony of spawning between individual colonies in most species. If only the well sampled species are considered (n>5) there were only 7 instance where all colonies were in a similar reproductive condition. At Lizard Island all 7 *A. monticulosa* colonies had mature oocytes (Table 4), at Pelorus all 16 *A. hyacinthus* colonies contained mature oocytes (Table 5) and similarly, all 10 *A. nasuta* colonies at Lady Elliot contained mature oocytes (Table 6). No oocytes were visible in *A. intermedia*, *A. muricata* and *A. tenuis* colonies in SI (Table 3), and similarly at Lizard Island all 6 *A. digitifera* colonies appeared empty. In all other instances the population included colonies with oocytes at different stages of maturity. For example, in the SI 8 species had colonies with mature oocytes, colonies with immature oocytes and colonies with no visible oocytes (Table 3), indicating that gametes would be released over at least 2 months. Similarly species with colonies in all 3 reproductive conditions were found at all sites on the GBR (Table 4-6). These data suggest that some asynchrony in the release of gametes between colonies can be a feature of the reproductive biology of the *Acropora* at these sites.

Table 3. The proportion of colonies (%) in each species containing mature, immature or no visible oocytes (empty) in the Solomon Islands (n = the number of colonies sampled).

species	mature	immature	empty	n
Acropora anthocercis	80	0	20	10
Acropora brueggemanni	25	0	75	8
Acropora cerealis	10	0	90	10
Acropora clathrata	17	0	83	6
Acropora cytherea	17	0	83	6
Acropora digitifera	34	0	66	29
Acropora divaricata	33	11	56	9
Acropora gemmifera	29	43	29	21
Acropora granulosa	20	0	80	5
Acropora humilis	5	9	86	22
Acropora hyacinthus	44	3	54	39
Acropora intermedia	0	0	100	14
Acropora latistella	60	0	40	5
Acropora loripes	60	20	20	5
Acropora microclados	65	0	35	17
Acropora millepora	48	0	52	21
Acropora monticulosa	10	40	50	10
Acropora muricata	0	0	100	14
Acropora nasuta	35	10	55	20
Acropora plumosa	44	0	56	9
Acropora robusta	53	0	47	19
Acropora sarmentosa	40	0	60	5
Acropora secale	88	9	3	32
Acropora sp_a	60	0	40	5
Acropora tenuis	0	0	100	7
Acropora valida	21	0	79	19
Acropora acuminata	33	0	67	3
Acropora austera	25	0	75	4
Acropora caroliniana	0	100	0	1
Acropora florida	0	0	100	4
Acropora horrida	0	0	100	3
Acropora jacquelineae	0	0	100	1
Acropora kimbeensis	100	0	0	2
Acropora lutkeni	67	0	33	3
Acropora nana	0	0	100	4
Acropora palmerae	0	0	100	3
Acropora selago	25	25	50	4
Acropora spicifera	0	0	100	1
Acropora valenciennesi	0	0	100	3
total	36	6	58	403

One possible reason that spawning was asynchronous in many species is the phenomenon of split spawning (Willis et al. 1985). In years when the full moon falls early in October the spawning of many species on reefs in the Central GBR is split over two months (Willis unpublished data). Similarly, Wallace (1985) found evidence for split spawning in *Acropora nobilis*, and Babcock et al. (1986) observed *A. latistella* spawning in October and November. Consequently, colonies without visible oocytes in November may have spawned in October. However, in 1999 the October full moon occurred on the 25th and split spawning at the sites at Pelorus was therefore unlikely. At Lizard Island extensive sampling in October (JW) found no colonies with mature oocytes. Another possible reason that colonies lacked visible oocytes is that they may spawn 3 or more months later. Finally, not all colonies may release oocytes every year. There is some evidence to indicate that this may be a feature of *Acropora* reproductive biology. For example, mature gametes were never found in *Acropora horrida* in a two year study in the central GBR (Wallace 1985) and Hughes et al. (2000) collected monthly samples of coral tissue from adult colonies of *A. hyacinthus, A. cytherea* and *A. millepora* on reefs in both the northern and southern GBR, and found that a proportion of these colonies did not release eggs one year. These data suggest that colonies of species which typically participate in the mass spawn on the GBR may miss one or more years, or spawn at other times of the year. However, many other factors may influence the reproductive output of coral colonies such as competition (e.g. Tanner 1997) and various forms of stress (Harrison and Wallace 1990). For example, Baird and Marshall (unpublished data) recorded a 50% reduction in the proportion of *Acropora hyacinthus* colonies with oocytes following bleaching. Consequently, spatial variation in the proportion of the population gravid may reflect differences between locations in the prevalence of competition or stress. Further detailed studies of the population biology of *Acropora* are required to fully define the length of the reproductive season and the timing of gamete release at all these locations.

Table 4. The proportion of colonies (%) in each species containing mature, immature or no visible oocytes (empty) at Lizard Island, Northern Great Barrier Reef (n = the number of colonies sampled).

species	mature	immature	empty	n
Acropora sarmentosa	40	0	60	5
Acropora digitifera	0	0	100	6
Acropora monticulosa	100	0	0	7
Acropora tenuis	75	13	13	8
Acropora nasuta	89	0	11	9
Acropora samoensis	0	69	31	16
Acropora millepora	92	0	8	24
Acropora humilis	89	4	7	54
Acropora gemmifera	60	6	33	108
Acropora aspera	0	0	100	1
Acropora cerealis	33	0	67	3
Acropora cytherea	0	0	100	2
Acropora florida	0	0	100	1
Acropora grandis	0	0	100	3
Acropora horrida	100	0	0	1
Acropora hyacinthus	50	0	50	2
Acropora intermedia	0	0	100	1
Acropora latistella	25	0	75	4
Acropora longicyathus	0	0	100	1
Acropora loripes	33	0	67	3
Acropora lutkeni	100	0	0	1
Acropora muricata	0	0	100	1
Acropora nana	0	0	100	2
Acropora pulchra	0	0	100	1
Acropora selago	100	0	0	2
Acropora valida	100	0	0	1
total	62	1	37	267

The number of *Acropora* species with mature oocytes, which were therefore expected to spawn following the next full moon, varied between the locations. Mature oocytes were present in 28 (71%) species in the SI (Table 3), 15 (58%) species at Lizard Island (Table 4) and 19 (86%) species at Pelorus Island (Table 5). The number of species with mature oocytes at Lizard Island is likely to have been underestimated because of the small number of colonies sampled in many of the species (Table 4). These data indicate that a high proportion of the *Acropora* species spawn in synchrony at this time of year at all these sites. In particular, the high number of *Acropora* spawning in synchrony in the SI indicates that mass spawning is a feature of coral assemblages even in absence of major fluctuations in environmental variables.

Table 5. The proportion of colonies (%) in each species containing mature, immature or no visible oocytes (empty) at Pelorus Island, Central Great Barrier Reef (n = the number of colonies sampled).

species	mature	immature	empty	n
Acropora cerealis	29	0	71	7
Acropora cytherea	83	0	17	12
Acropora digitifera	78	0	22	9
Acropora donei	56	0	44	9
Acropora elseyi	85	0	15	13
Acropora humilis	38	13	50	8
Acropora hyacinthus	100	0	0	16
Acropora intermedia	83	0	17	12
Acropora millepora	88	0	12	17
Acropora muricata	44	0	56	9
Acropora nasuta	94	0	6	17
Acropora secale	80	0	20	5
Acropora tenuis	82	0	18	11
Acropora valida	29	0	71	17
Acropora austera	100	0	0	1
Acropora florida	100	0	0	1
Acropora gemmifera	67	0	33	3
Acropora latistella	0	0	100	1
Acropora lutkeni	0	100	0	1
Acropora robusta	100	0	0	1
Acropora samoensis	0	0	100	1
Acropora spathulata	100	0	0	4
total	72	1	27	175

Table 6. The proportion of colonies (%) in each species containing mature, immature or no visible oocytes (empty) at Lady Elliot Island, southern Great Barrier Reef (n = the number of colonies sampled).

Species	mature	immature	empty	n
Acropora tenuis	80	10	10	10
Acropora muricata	50	0	50	10
Acropora humilis	60	0	40	10
Acropora secale	90	0	10	10
Acropora cytherea	80	0	20	10
Acropora hyacinthus	80	0	20	10
Acropora nasuta	100	0	0	10
Acropora millepora	70	0	30	10
total	76	1	23	80

Acknowledgements The study would not have been possible without the support and encouragement of TP Hughes. We thank the staff at Pelorus and Lizard Island Research Stations for their assistance and Evi and Lau from the ICLARM Coastal Aquaculture Center, Gizo, Solomon Islands. Susan Dance of ICLARM kindly provided the SST temperature data for the Solomon Islands. This is publication number 187 of the Coral Ecology Group at James Cook University.

References

Atoda K (1947a) The larva and postlarval development of some reef building corals. II *Stylophora pistillata* (Esper). Sci Rep Tohoku University, 4th Ser 18: 48-64

Atoda K (1947b) The larva and postlarval development of some reef-building corals. I. *Pocillopora damicornis cespitosa* Dana. Scient Rep Tohoku Univ Ser 4 18: 24-47

Atoda K (1951) The larvae and postlarval development of some reef building corals. V. *Seriatopora hystrix* Dana. Sci Rep Tohoku University 4th Ser 19: 33-39

Babcock RC, Bull GD, Harrison PL, Heyward AJ, Oliver JK, Wallace CC, Willis BL (1986) Synchronous spawnings of 105 scleractinian coral species on the Great Barrier Reef. Mar Biol 90: 379-394

Harriott VJ (1983) Reproductive ecology of four scleractinian species at Lizard Island, Great Barrier Reef. Coral Reefs 2: 9-18

Harrison PL, Babcock RC, Bull GD, Oliver JK, Wallace CC, Willis BL (1984) Mass spawning in tropical reef corals. Science 223: 1186-1189

Harrison PL, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinzky, Z. (eds.) Ecosystems of the world: Coral Reefs. Elsvier, Amsterdam, p. 133-207

Hayashibara T, Shimoike K, Kimura 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

Hughes T. P., Baird A. H., Dinsdale E., Moltschaniwskyj, N., Pratchett, M., Tanner, J. & Willis, B.(2000). Supply-side ecology works both ways: the link between benthic adults and larval recruits. *Ecology* 81 (8): 2241-2249

Kenyon J (1995) Latitudinal differences between Palau and Yap in coral reproductive synchrony. Pac Sci 49: 156-164

Kojis BL (1986) Sexual reproduction in *Acropora (Isopora)* (Coelenterata: Scleractinia) II. Latitudinal variation in *A. palifera* from the Great Barrier Reef and Papua New Guinea. Mar Biol 91: 311-318

Oliver JK, Babcock RC, Harrison PL, Willis BL (1988) The geographic extent of mass coral spawning: Clues to ultimate causal factors. Proc 6th Int Coral Reef Symp 2: 803-810

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

Shlesinger Y, Loya Y (1985) Coral community reproductive patterns: Red Sea verses the Great Barrier Reef. Science 228: 1333-1135

Szmant AM (1986) Reproductive ecology of Caribbean reef corals. Coral Reefs 5: 43-54

Tanner JE (1996) Seasonality and lunar periodicity in the reproduction of pocilloporid corals. Coral Reefs 15: 59-66

Tanner JE (1997) Interspecific competition reduces fitness in scleractinian corals. J Exp Mar Biol Ecol 214: 19-34

Tomascik T, Mah A J, Nontij A, Moosa M K (1997) The Ecology of the Indonesian Seas Part One. Periplus Hong Kong 642p

Wallace CC (1985) Reproduction, recruitment and fragmentation in nine sympatric species of the coral genus *Acropora.* Mar Biol 88: 217-233

Willis BL, Babcock RC, Harrison PL, Oliver JK, Wallace CC (1985) Patterns in the mass spawning of corals on the Great Barrier Reef from 1981 to 1984. Proc 5th Int Coral Reef Symp 4: 343-348