

## Latitudinal variation in reproductive synchrony in *Acropora* assemblages: Japan vs. Australia

Andrew H. BAIRD<sup>1,2,\*</sup>, Chico L. BIRREL<sup>3</sup>, Terence P. HUGHES<sup>1</sup>, Abbi MCDONALD<sup>1</sup>,  
Satoshi NOJIMA<sup>4</sup>, Cathie A. PAGE<sup>1</sup>, Morgan S. PRACHETT<sup>1</sup>,  
and Hideo YAMASAKI<sup>2</sup>

<sup>1</sup>ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland 4812, Australia

<sup>2</sup>Centre of Molecular Biosciences (COMB), University of the Ryukyus, Nishihara, Okinawa 903–0123, Japan

<sup>3</sup>Department of Marine and Tropical Biology, James Cook University, Townsville, Queensland 4812, Australia

<sup>4</sup>Amakusa Marine Biological Laboratory, Graduate School of Kyushu University Amakusa, Kumamoto, Japan

Corresponding author: A.H. Baird

E-mail: andrew.baird@jcu.edu.au

Communicated by Makoto Tsuchiya

**Abstract** The annual mass spawning of scleractinian corals on the Great Barrier Reef (GBR), Australia, is purported to be unprecedented in terms of the taxonomic and geographical scale of spawning synchrony. Here, we compare spawning synchrony both within and among coral species in four regions spanning 10° of latitude on the GBR and compare this with four regions separated by a similar latitudinal range within the Japanese tropical and sub-tropical Archipelago. On the GBR, peak reproductive activity at all latitudes occurred in November whereas there was a clear disjunction in the period of peak reproductive activity among the four regions in Japan, with tropical locations spawning up to 3 months earlier. In Sekesei Lagoon (22°N), a high proportion of *Acropora* colonies were mature following the full moon in April; at Akajima Island (26°N) peak reproductive activity occurred in May; at Oku (28°N) peak reproductive activity occurred in June and in Amakusa (31°N), reproductive activity likely peaked in July. However, mature colonies of *Acropora* were found prior to every full moon for at least 5 months at two regions examined in detail (The Whitsundays Islands on the GBR and

Akajima Island). While these regions on GBR appear to act more homogeneously than regions over a similar latitudinal range in Japan with respect to the timing of peak reproductive activity, and the proportion of colonies mature was often higher during these peaks, the reproductive season on the GBR is much longer (5 months) than is typically appreciated.

**Keywords** coral reef, spawning synchrony, reproduction

---

### Introduction

Most scleractinian corals broadcast spawn gametes (Baird et al. 2009). Oogenic cycles in broadcast spawning species typically range from 6 to 14 months (Harrison and Wallace 1990), therefore, most colonies spawn only once per year. Fertilization success and larval survivorship is greatly reduced when few colonies spawn because of rapid gamete dilution and predation (Harrison and Wallace 1990; Oliver and Babcock 1992; Levitan et al. 2004),

resulting in lower recruitment outside peak spawning periods (Hughes et al. 2002). Therefore, spawning synchrony is likely to be highly adaptive in broadcasting species, and many corals spawn at predictable times each year (Baird et al. 2009).

In many coral assemblages, spawning is synchronized not only among colonies within a population, but also among numerous species within an assemblage. For example, during the annual “mass spawn” on the GBR (Harrison et al. 1984), up to 30 species release gametes within hours on a single reef (Willis et al. 1985) and over 130 species spawn in the weeks following the full moon in October and/or November (Willis et al. 1985; Harrison and Wallace 1990). The taxonomic and geographical extent of multi-species spawning on the GBR has long been considered to be unprecedented, because there is little apparent overlap in spawning period for species within coral assemblages in many other major reef areas. For example, ecologically dominant species at Eilat in the northern Red Sea spawn in different seasons, months and lunar phase (Shlesinger and Loya 1985; Shlesinger et al. 1998, but see Hanafy et al. 2010). Similar patterns of temporal reproductive isolation occur in parts of the Central Pacific, Hawaii, and the Eastern Pacific Ocean (Richmond and Hunter 1990; Glynn and Ault 2000, but see Kenyon 2008). In combination, patterns emerging from these early studies suggest that ‘mass spawning’, defined by Willis et al. (1985) as “the synchronous release of gametes by many species of corals, in one evening between dusk and midnight” is restricted to geographic regions with appropriate proximate cues. In particular, Oliver et al. (1988) hypothesised that mass spawning would only occur in regions where large fluctuations in environmental variables provide the necessary cues by which corals can synchronise spawning (see also Harrison and Wallace 1990). However, spawning events involving many species on one evening have since been described from over 23 locations worldwide (see review in Baird et al. 2009), including regions such as the Solomon Islands (Baird et al. 2001) and Singapore (Guest et al. 2005) which lack large seasonal variation in environmental variables. More recently, Harrison and Booth (2007) have suggested that “‘mass spawning’ is distinguished from other lesser multi-specific spawning patterns by its much larger ecological

scale”. Similarly, Mangubhai and Harrison (2009) argued the term should be “restricted to describing these (GBR) extreme synchronous multi-specific spawning events, rather than including all multi-specific spawning”. They further state that events on the GBR are “unusual in relation to their magnitude and geographic scale” (Mangubhai and Harrison 2008, p 85). Two basic features underpin the argument that mass spawning events on the GBR are unusual. Firstly, there is high spawning synchrony both within coral populations and among coral species, and this synchrony is evident over a large geographic scale.

The aim of this study was to examine these two features, and to test their generality, by quantifying reproductive synchrony in *Acropora*-dominated assemblages along a latitudinal gradient spanning nearly 10° degrees of latitude on the GBR and among regions covering a similar latitudinal gradient within the Japanese Archipelago.

## Materials and methods

### Latitudinal patterns in coral spawning synchrony on the Great Barrier Reef

In 2004, one to three mid-shelf reefs were visited in each of four sectors of the Great Barrier Reef Marine Park: the Far North (12°S), Cooktown (14°S), Townsville (18°S), and the Capricorn Bunker region in the south (22°S). At each reef, the species and reproductive condition (see below) of all *Acropora* colonies encountered during one hour swims at 0–2 m depth were recorded. All sites were visited 1–2 weeks before the expected mass spawning period (*sensu* Willis et al. 1985) on the GBR (i.e. 2–7 days following the full moon on 27 Nov 2004).

### Latitudinal patterns in coral spawning synchrony in the Japanese Archipelago

The reproductive condition of *Acropora* colonies was examined at four regions in Japan separated by nearly 10° of latitude: Sekesei Lagoon in the Yeayama Islands (22°N), Akajima in the Kerama Islands (26°N), Oku in northern Okinawa (28°N), and Amakusa in southern Kyushu (31°N). All sites were visited 0–10 days before the full moon of each month in 2001. At each region, one

to five reefs or islands were visited with one to three sites per reef or island. At each reef, the species and reproductive condition (see below) of all *Acropora* colonies encountered during one hour swims at 0–2 m depth were recorded. Each region was visited from one to three times, as outlined in Fig. 2.

### Seasonal Patterns of reproduction in *Acropora* assemblages GBR vs. Japan

Four mid-shelf reefs off the Whitsunday Islands were visited 1–2 weeks before the full moons of October, November, December, January and February in 2003. At each reef the species and reproductive condition of all *Acropora* colonies encountered during one hour swims at 0–2 m depth at three sites were recorded. In order to compare the proportion of the *Acropora* assemblage spawning in each month throughout the reproductive season on the GBR with that in Japan, we extracted data from Table 1 in Hayashibara et al. (1993) who recorded the night of spawning in 32 *Acropora* species between May to August over a three year period from 1989 to 1991.

### Establishing the reproductive condition of *Acropora* colonies

The reproductive condition of colonies was established by breaking coral branches below the apical sterile zones (Wallace 1985) to expose the developing oocytes in older, distal tissues. 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 three branches were broken per colony and colonies were only scored as empty if all three branches were empty. The available evidence indicates that almost all colonies will release eggs following the full moon subsequent to oocyte maturation (Harrison and Wallace 1990; Hayashibara et al. 1993), which is indicated by pink, red or brown pigmentation in the oocytes and is readily recognisable underwater (Harrison et al. 1984). Three reproductive conditions were defined following Baird et al. (2002) 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 three months).

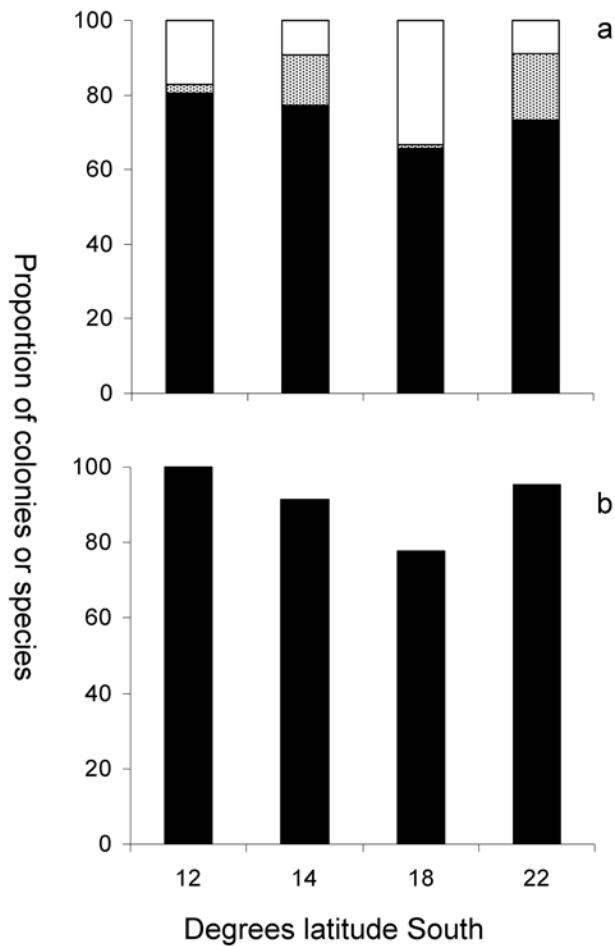
## Results

### Latitudinal patterns in coral spawning synchrony on the Great Barrier Reef

A high proportion of *Acropora* colonies were mature prior to the full moon in November 2004 at all four regions on the GBR (Fig. 1a). The proportion of mature colonies ranged from 62% on mid-shelf reefs off Townsville (18°S) to 80% on the reefs in the far North (12°S) (Fig. 1a). Importantly, there was no apparent trend in spawning synchrony with latitude (Fig. 1). Immature colonies were also recorded at all sites; the proportion ranging from 1% on the reefs off Townsville to 20% at the reefs in the southernmost region (22°S) (Fig. 1a). Empty colonies were also recorded at all sites, ranging from 5% on the reefs off Cooktown (14°S) to 30% on the reefs off Townsville (Fig. 1a). The proportion of species with at least one colony mature prior to mass spawning was high at all sites, ranging from 75% (n=18) off Townsville to 100% (n=22) in the far North (Fig. 1b).

### Latitudinal patterns in coral spawning synchrony in the Japanese Archipelago

In contrast to the patterns on the GBR, where a high proportion of colonies (62–80%) were mature at the same time at all four regions, there was clear disjunction in the time of peak reproductive activity among the four locations in the Japanese Archipelago. In Sekesei Lagoon (22°N), the proportion of colonies mature was evenly split between the full moons in April (18%) and May (22%) (Fig. 2a). A small proportion of colonies were also immature in May, suggesting that these colonies would have spawned in June (Fig. 2a). At Akajima (26°N), the first mature colonies were detected in May (42% Fig. 2b) and a further 3% of colonies were mature in June (Fig. 2b). At Oku (28°N), 60% of colonies were mature in June (Fig. 2c). A further 10% of colonies had immature oocytes indicating at least one other spawning event in July (Fig. 2c). In the Amakusa Islands (31°N), 85% of colonies were empty (Fig. 2d),

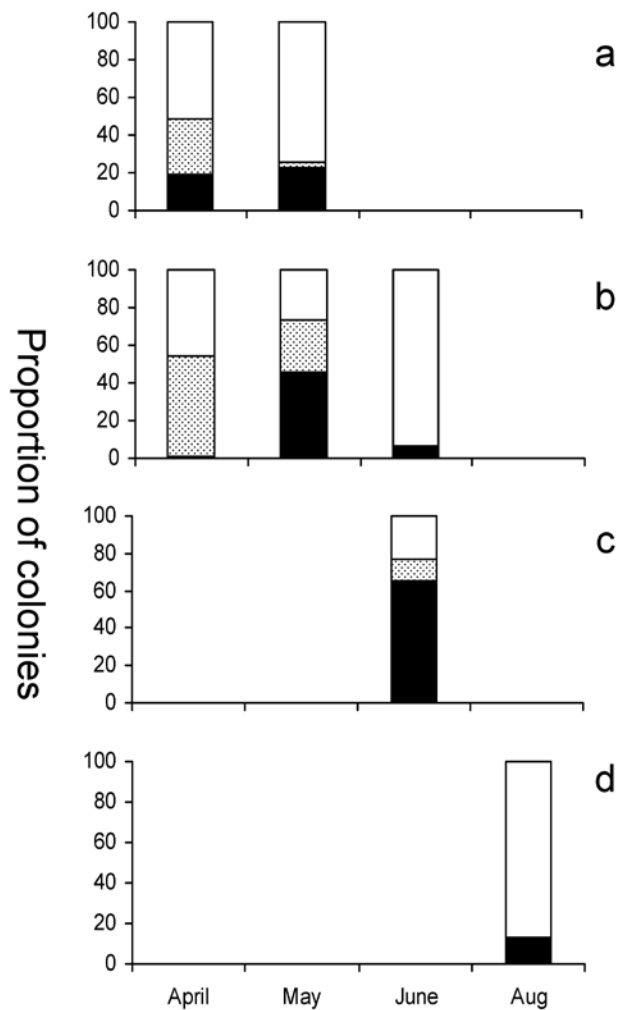


**Fig. 1** (a) The proportion of *Acropora* colonies with mature, immature or no visible oocytes in November 2004. (b) The proportion of *Acropora* species with at least one mature colony at four mid-shelf regions on the Great Barrier Reef (Far North=12°S, Cooktown=14°S, Townsville=18°S, Capricorn Bunker Group=22°S). Black sections are the proportion of colonies with mature oocytes, shaded sections are the proportion of colonies with immature oocytes and white sections are the proportion of colonies with no oocytes observed

suggesting that sampling in August missed the peak in reproductive activity which most likely occurred in July. Nonetheless, 15% of colonies retained mature oocytes in August (Fig. 2d).

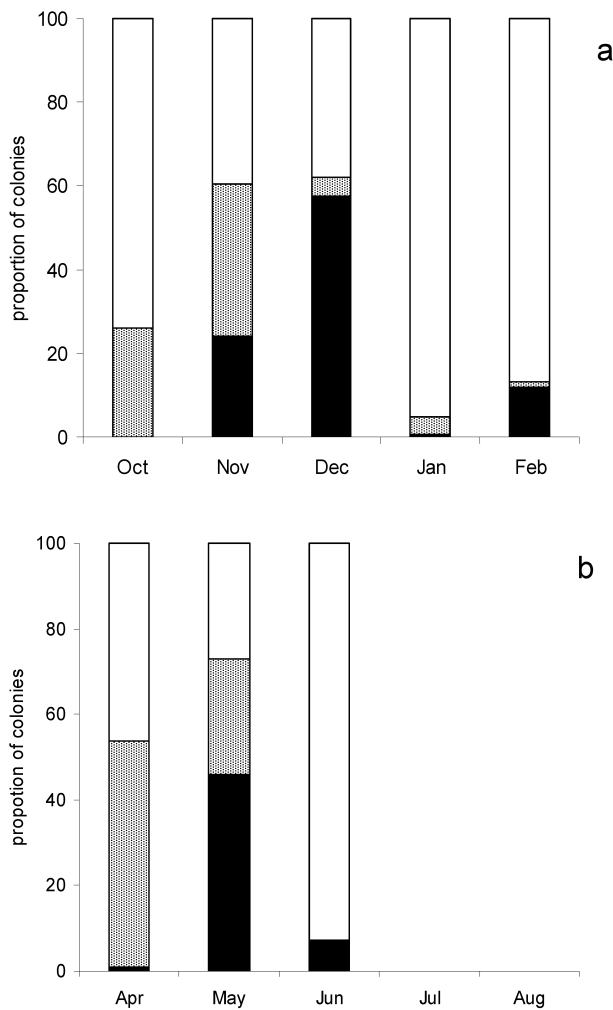
#### Seasonal patterns of reproduction in *Acropora* assemblages GBR vs. Japan

Despite the profound difference in the timing of peak reproductive activity among regions between the GBR and Japan, at any one location the seasonal patterns in



**Fig. 2** Proportion of *Acropora* colonies with mature, immature or no visible oocytes from April to August 2000 at four municipalities in Japan (a) Sekesei lagoon 22°N; (b) Akajima 26°N; (c) Oku 28°N; (d) Amakusa 31°N. Black sections are the proportion of colonies with mature oocytes, shaded sections are the proportion of colonies with mature eggs and white sections are the proportion of colonies with immature oocytes and white sections are the proportion of colonies with no gametes present

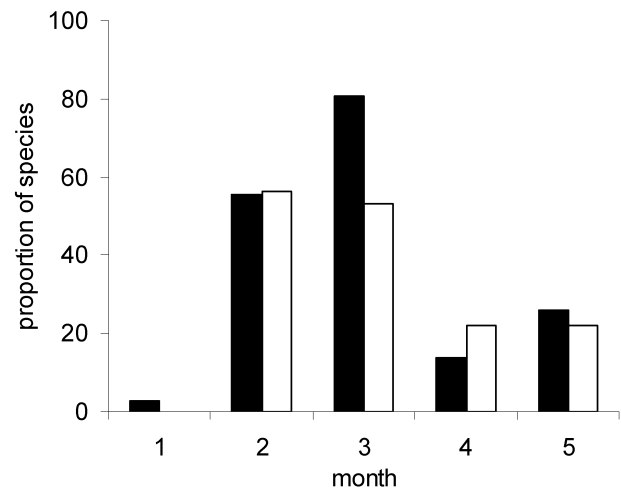
reproductive synchrony are remarkably similar. On reefs off the Whitsundays some colonies were mature every month (Fig. 3a). Mature colonies were first detected in October when 1% of colonies were mature. Spawning activity increased to 22% in November and peaked in December when 60% of colonies were mature (Fig. 3b). In addition, a small proportion of colonies were mature in both January (1%) and February (12%). Similarly, some colonies were mature in every month sampled (April, May, June) at Akajima (Fig. 3b). The high proportion of



**Fig. 3** The proportion of *Acropora* colonies with mature, immature or no visible oocytes during each month of sampling at Akajima, Japan and four mid-shelf reefs in the Whitsunday section of the GBR Marine Park in 2003. Black sections are the proportion of colonies with mature oocytes, shaded sections are the proportion of colonies with immature oocytes and white sections are the proportion of colonies with no oocytes observed

colonies that did not mature in the three months of sampling at Akajima (approximately 50%) strongly suggests that some further reproductive activity in this assemblage occurs later in the season (Fig. 3b).

The seasonal patterns in the proportion of species spawning were also strikingly similar, with 60 to 80% of species mature in the 2<sup>nd</sup> and 3<sup>rd</sup> months of sampling and at least some species had mature colonies before every full moon in both regions (Fig. 4), with the exception of April at Akajima.



**Fig. 4** The proportion of species in the *Acropora* assemblage with at least one mature colony during each month of sampling at Akajima (white bars: data from Table 1 in Hayashibara et al. 1993) and on 4 mid-shelf reefs in the Whitsunday section of the GBR Marine Park in 2003 (black bars). First month of sampling on the GBR was October, in Japan April

## Discussion

### Coral spawning synchrony on the GBR vs. Japan

The timing of peak reproductive activity was less synchronised across the Japanese Archipelago when compared to regions over a similar latitudinal range on the GBR. In Japan, peak reproductive activity occurred one month later in the season for every 2–3° further north (Fig. 2). This result confirms previously established patterns in the timing of spawning within Japan (Hayashibara et al. 1993; van Woesik 1995; Nozawa et al. 2006; Mezaki et al. 2007). However, this is the first study to have sampled all regions with the same methods in the same season. In contrast to this step-like pattern in Japan, on the GBR peak reproductive activity at all regions sampled in 2004 coincided with the November full moon, confirming earlier work documenting the geographical scale of spawning synchrony (Oliver et al. 1988; Hughes et al. 2000; Baird et al. 2002). The regions sampled in Japan are further from the equator, ranging from 22–31°N, than the regions sampled on the GBR (12–22°S). Nonetheless, the Kuroshio current in the northern hemisphere means that the environments in each of the regions are broadly

similar, with strong reef development at all locations in Japan, except Amakusa (31°N). Further south, in the Philippines (16°N), many colonies of *Acropora* are mature in March (Vincentuan et al. 2007), suggesting a further offset in the beginning of the reproductive season as sites in the northern hemisphere become progressively closer to the equator. In contrast, the geographical extent of the November spawning in the southern hemisphere extends far beyond the GBR including reefs from the Coral Sea (Baird et al. 2001), Melanesia (Baird et al. in press) and French Polynesia (Carroll et al. 2007). However, a similarly disjunct pattern in the time of peak spawning to that in Japan is apparent if the latitudinal transect on the GBR was extended further down the east coast of Australia. In Moreton Bay, peak reproductive activity occurs in December (Fellegera et al. unpublished data) and in both the Solitary Islands (30°S) and Lord Howe Island (31°S) peak spawning in *Acropora* assemblages is in January (Wilson and Harrison 2003; Harrison 2008).

#### **Seasonal patterns of reproduction in *Acropora* assemblages GBR vs. Japan**

The season patterns of spawning synchrony were remarkably similar at reefs off the Whitsunday Islands, Australia and in Akajima Island, Japan. Reproductive activity in the *Acropora* assemblage peaked early in the spring at both locations. However, mature colonies were detected at both locations in each of 5 consecutive months (Figs. 3 and 4). Consequently, the reproductive season of the *Acropora* extends for at least 5 months in both these locations. While an extended reproductive season is an accepted feature of Japanese coral assemblages (Hayashibara et al. 1993), the reproductive season on the GBR is presumed to be far shorter (Harrison and Booth 2007; Mangubhai and Harrison 2008, but see Wallace 1999 and Wolstenholme 2004). Our data clearly demonstrate that, at least in these *Acropora* assemblages in 2003, there is nothing unusual about the length of the reproductive season on the GBR.

The ultimate factor driving spawning synchrony is the need to maximize fertilization success. However, the proximate cues remain elusive. In many locations one prominent cue is provided by rapid changes in seawater temperature. For example, there is a clear disjunction in

the beginning of the reproductive season between inshore and offshore reefs in the central GBR (Willis et al. 1985). Inshore reefs typically spawn one month earlier than the offshore reefs examined here, when shallow inshore waters warm more rapidly at the start of spring (Willis et al. 1985). However, van Woesik et al. (2006) have recently questioned the primacy of temperature in driving the timing of gamete release, suggesting rather, that spawning synchrony is often driven by seasonal variation in solar insolation. One prominent pattern observed in Japan is that most colonies mature on or around the full moon after water temperatures have reached 26°C, and this is similar to patterns in the Atlantic (van Woesik et al. 2006). However, solar insolation is also likely to vary seasonally among these regions and a detailed analysis of the correlation between various environmental parameters and the time of spawning is required to determine the most probable cues.

High levels of spawning synchrony over a large spatial scale on the GBR are possibly driven by high levels of genetic connectivity among populations caused by high reef density, resulting in high levels of dispersal, and large reef area resulting in large effective population sizes (Ayre and Hughes 2004). One potential consequence of high gene flow among populations over a wide latitudinal scale is a reduced capacity for adaptation to local environmental regimes. Consequently, in the southern GBR, corals are potentially releasing gametes at less than optimal temperatures for larval development and survival. Certainly, recruitment rates of spawners are typically an order of magnitude lower in the southern GBR when compared to the central GBR (Hughes et al. 1999, 2002), supporting the idea that conditions may not be optimal for larval survivorship. Nonetheless, southern areas support vibrant reefs, and recover equally well from disturbance (Emslie et al. 2008).

In conclusion, spawning among these regions was more synchronous with respect to the timing of peak reproductive activity on the GBR than in Japan. However, there was a prolonged period of reproductive activity observed at individual locations on both the GBR and in southern Japan. Indeed, spawning at any given location on the GBR is much less synchronous than previously recognised, with some spawning occurring after every full moon in

spring and summer at many reefs.

## Acknowledgements

AHB thanks the Japanese Society for the Promotion of Science for a Postdoctoral Fellowship to Japan in 2001–2002 and a GIAR to support field work in Japan. Work in Australia was supported by the Australian Research Council. We thank J. Eagle, R. van Woesik and one anonymous reviewer for valuable comments on the manuscript. J Eagle also produced all the figures.

## References

- Ayre DJ, Hughes TP (2004) Climate change, genotypic diversity and gene flow in reef-building corals. *Ecol Lett* 7: 273–278
- 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
- Baird AH, Guest JR, Willis BL (2009) Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. *Annu Rev Ecol Syst* 40: 531–571
- Baird AH, Kospartov MC, Purcell SW (in press) Highly seasonal reproduction of *Acropora* in New Caledonia. *Pac Sci* 64
- Baird AH, Marshall PA, Wolstenholme J (2002) Latitudinal variation in the reproduction of *Acropora* in the Coral Sea. *Proc 9th Int Coral Reef Symp*: 385–389
- Baird AH, Sadler C, Pitt M (2001) Synchronous spawning of *Acropora* in the Solomon Islands. *Coral Reefs* 19: 286–286
- Carroll A, Harrison PL, Adjeroud M (2006) Sexual reproduction of *Acropora* reef corals at Moorea, French Polynesia. *Coral Reefs* 25: 93–97
- Emslie MJ, Cheal AJ, Sweatman H, Delean S (2008) Recovery from disturbance of coral and reef fish communities on the Great Barrier Reef, Australia. *Mar Ecol Prog Ser* 371: 177–190
- Glynn PW, Ault JS (2000) A biogeographic analysis and review of the far eastern Pacific coral reef region. *Coral Reefs* 19: 1–23
- Guest JR, Baird AH, Goh BPL, Chou LM (2005) Reproductive seasonality in an equatorial assemblage of scleractinian corals. *Coral Reefs* 24: 112–116
- Hanafy MH, Aamer MA, Habib M, Baird AH, Roupheal AB (2010) Mass spawning of corals in the Red Sea. *Coral Reefs* DOI 10.1007/s00338-009-0552-2
- Harrison PL (2008) Coral spawn slicks at Lord Howe Island, Tasman Sea, Australia; the world's most southerly coral reef. *Coral Reefs* 27: 35–35
- Harrison PL, Booth DJ (2007) Coral reefs: Naturally dynamic and increasingly disturbed ecosystems. In: Connell SD, Gillanders BM (eds) *Marine ecology*. Oxford University Press, London, pp 316–377
- Harrison PL, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky Z (ed) *Coral reefs*. Elsevier, Amsterdam, pp 133–207
- Harrison PL, Babcock RC, Bull GD, Oliver JK, Wallace CC, Willis BL (1984) Mass spawning in tropical reef corals. *Science* 223: 1187–1188
- 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 TP, Baird AH, Dinsdale EA, Harriott VJ, Moltischniwsykyj NA, Pratchett MS, Tanner JE, Willis BL (2002) Detecting regional variation using meta-analysis and large-scale sampling: Latitudinal patterns in recruitment. *Ecology* 83: 436–451
- Hughes TP, Baird AH, Dinsdale EA, Moltischniwsykyj NA, Pratchett MS, Tanner JE, Willis BL (1999) Patterns of recruitment and abundance of corals along the Great Barrier Reef. *Nature* 397: 59–63
- Hughes TP, Baird AH, Dinsdale EA, Moltischniwsykyj NA, Pratchett MS, Tanner JE, Willis BL (2000) Supply-side ecology works both ways: The link between benthic adults, fecundity, and larval recruits. *Ecology* 81: 2241–2249
- Kenyon JC (2008) *Acropora* (Anthozoa: Scleractinia) reproductive synchrony and spawning phenology in the northern Line Islands, Central Pacific, as inferred from size classes of developing oocytes. *Pac Sci* 62: 569–578
- Levitan DR, Fukami H, Jara J, Kline D, McGovern TM, McGhee KE, Swanson CA, Knowlton N (2004) Mechanisms of reproductive isolation among sympatric broadcast-spawning corals of the *Montastraea annularis* species complex. *Evolution* 58: 308–323
- Mangubhai S, Harrison PL (2008) Asynchronous coral spawning patterns on equatorial reefs in Kenya. *Mar Ecol Prog Ser* 360: 85–96
- Mezaki T, Hayashi T, Iwase F, Nakachi S, Nozawa Y, Miyamoto

- M, Tominaga M (2007) Spawning patterns of high latitude scleractinian corals from 2002 to 2006 at Nishidomari, Otsuki, Kochi, Japan. *Kuroshio Biosphere* 3: 33–47
- Nozawa Y, Tokeshi M, Nojima S (2006) Reproduction and recruitment of scleractinian corals in a high-latitude coral community, Amakusa, southwestern Japan. *Mar Biol* 149: 1047–1058
- Oliver J, Babcock RC (1992) Aspects of the fertilization ecology of broadcast spawning corals: Sperm dilution effects and in situ measurements of fertilization. *Biol Bull Mar Biol Lab Woods Hole* 183: 409–417
- 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: 803–810
- 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 versus the Great Barrier Reef. *Science* 228: 1333–1335
- Shlesinger Y, Goulet TL, Loya Y (1998) Reproductive patterns of scleractinian corals in the northern Red Sea. *Mar Biol* 132: 691–701
- van Woessik R (1995) Coral communities at high latitude are not pseudopopulations: evidence of spawning at 32°N, Japan. *Coral Reefs* 14: 119–120
- van Woessik R, Lacharaise F, Koksals S (2006) Annual cycles of solar insolation predict spawning times of Caribbean corals. *Ecol Lett* 9: 390–398
- Vicentuan K, Guest J, Baria M, Cabaitan P, Dizon R, Villanueva R, Aliño P, Edwards A, Gomez E, Heyward A (2008) Multi-species spawning of corals in north-western Philippines. *Coral Reefs* 27: 83–83
- Wallace CC (1985) Reproduction, recruitment and fragmentation in nine sympatric species of the coral genus *Acropora*. *Mar Biol* 88: 217–233
- Wallace CC (1999) *Staghorn corals of the world*. CSIRO, Collingwood, Australia
- Willis BL, Babcock RC, Harrison PL, Oliver JK (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
- Wilson JR, Harrison PL (2003) Spawning patterns of scleractinian corals at the Solitary Islands - a high latitude coral community in eastern Australia. *Mar Ecol Prog Ser* 260: 115–123
- Wolstenholme JK (2004) Temporal reproductive isolation and gametic compatibility are evolutionary mechanisms in the *Acropora humilis* species group (Cnidaria; Scleractinia). *Mar Biol* 144: 567–582

Received: 19 September 2009

Accepted: 13 October 2009

© Japanese Coral Reef Society