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Coral reproduction on the world's southernmost reef at Lord Howe Island, Australia

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ABSTRACT: Despite a recent expansion in the geographic extent of coral reproductive research, there remain many regions in the Indo-Pacific where knowledge is limited. For example, Lord Howe Island is the southernmost reef system in the world (31° S); however, very little is known of the reproductive biology of the coral fauna. Here, aspects of the reproductive biology and the timing of reproduction for 40 of the approximately 65 species that occur on Lord Howe Island are documented. In December 2010, field assessments of the stage of gamete maturity in *Acropora* spp. colonies suggested that 5 species spawned in December 2010 and 11 in January 2011. In January 2012, similar sampling suggested that 12 *Acropora* species spawned in January and 1 in February. In addition, 11 species from 10 genera broadcast spawned gametes from 17:30 to 24:00 h in January 2012, 10 to 12 d after full moon. *Goniastrea favulus* was inferred to spawn prior to 17:00 h, 6 to 12 d after full moon and *Porites heronensis* released brooded larvae. The reproductive biology of 3 other brooding species was examined using dissections and histology monthly for 1 yr from April 2011. Of these, *Seriatopora hystrix* contained planulae between November 2011 and March 2012, *Stylophora pistillata* contained planulae between November 2011 and February 2012. No eggs or planulae were observed in *Pocillopora damicornis*. In conclusion, the spawning patterns on Lord Howe Island are consistent with other locations in the Indo-Pacific: multi-species synchronous spawning episodes occur after full moons, when water temperatures are relatively high.

KEY WORDS: Coral reefs · Larval ecology · Spawning timing · Egg size

INTRODUCTION

Coral reproductive research in the Indo-Pacific has been concentrated historically in regions close to marine research stations in developed countries (see review by Baird et al. 2009b). However, coral reproduction is increasingly recognised as a fundamental process to maintain ecosystem function within coral reefs and, as such, interest in improving our understanding of this process has grown rapidly. In addition, recognition that ecological processes are often context-dependent suggests we should seek to quantify reproductive phenology across a wide geographic extent. Whilst the geographic focus of coral reproductive research has recently expanded to include more remote regions such as India (Raj & Edward 2010), New Caledonia (Baird et al. 2010), the Persian Gulf (Bauman et al. 2011) and Yemen (Baird et al. 2014), reproductive phenology on marginal reefs at the extreme geographical limits of coral distributions has yet to be quantified. Corals on marginal reefs would be expected to be the least con-

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sistent with a broader pattern and, therefore, offer potential to determine the limits of reproductive phenology.

The increased geographical extent across which reproductive phenology has been quantified has altered our understanding of coral reproductive synchrony and the processes that regulate the timing of coral reproduction (Baird et al. 2009b, van Woesik 2010). For example, highly synchronous spawning, both within and among species, is not restricted to higher latitude reefs as earlier hypothesized (Oliver et al. 1988). In particular, multi-species synchronous spawning events (sensu Willis et al. 1985) are now described for >25 locations globally (Baird et al. 2009b, Kongjandtre et al. 2010, Bouwmeester et al. 2011, Permata et al. 2012). In addition, coral reproduction in most regions is highly seasonal, with the vast majority of reproductive activity concentrated in 2 to 3 months each year (Baird et al. 2009a). This trend holds in equatorial locations (e.g. Singapore: Guest et al. 2005; e.g. Kenya: Mangubhai & Harrison 2008) and in regions where breeding patterns had previously been described as aseasonal (e.g. the Red Sea: Shlesinger & Loya 1985) due to incomplete sampling (Hanafy et al. 2010, Bouwmeester et al. 2015).

Despite this recent expansion in the geographic extent of studies on coral reproduction, there remain many regions in the Indo-Pacific where research is limited. For example, Lord Howe Island contains the southernmost reef system in the world (31.53° S, 159.08° E); and is a World Heritage-listed marine protected area in the Tasman Sea, with highly distinctive marine fauna including 9 endemic fish species (Francis 1993) and 47 endemic species of algae (MPA 2010). Lord Howe Island supports a scleractinian fauna of approximately 65 species (Veron 1993); however, almost nothing is known of the reproductive biology of these corals, in particular the timing of spawning and the length of the reproductive season. *Goniastrea favulus* was observed broadcast spawning at approximately 16:30 h 'during mid-January, 1977' (Kojis & Quinn 1981), 6 *Acropora* spp. and *Cyphastrea microphthalma* were observed setting (immediately prior to spawning) or spawning 8 to 9 nights after the full moon, and *Isopora cuneata* planulated 9 nights after the full moon in January 2007 (Harrison 2008). In addition, local tourist operators often run nighttime snorkelling trips to observe corals spawning following the full moon in February (P. Busteed pers. comm.). The reproductive biology of high-latitude corals, such as those on Lord Howe Island, is of particular interest, because these populations are often geographically isolated (Noreen et al. 2009) and therefore replenishment is likely to be highly dependent on local reproductive output or irregular input of propagules from distant upstream reefs (Fellegara et al. 2013, Madsen et al. 2014).

Most broadcast-spawning colonies spawn only once per year (Harrison & Wallace 1990, Baird et al. 2009b). In contrast, oogenic cycles are much shorter in corals that brood larvae (e.g. Stoddart & Black 1985, Permata et al. 2000), and consequently individual colonies can release larvae multiple times per year. For example, individual colonies of *Pocillopora damicornis*, *Seriatopora hystrix* and *Stylophora pistillata* release larvae throughout the year at Palau, whereas at Heron Island, on the southern Great Barrier Reef, breeding is seasonal (see review in Tanner 1996). Similarly, *Isopora palifera* releases planulae throughout the year in Papua New Guinea, but only in the summer months on Heron Island (Kojis 1986).

The highly seasonal nature of coral reproduction has important implications for reef ecology and conservation (Guest 2008). Numerous reef organisms, including many fishes, time their reproductive cycles to benefit from this seasonal abundance of nutrients (Pratchett et al. 2001, McCormick 2003). In addition, knowledge of coral reef phenology allows the use of temporal management strategies that can mitigate the effects of coastal development on coral reefs (Richmond 1997). For example, dredging or discharge of liquid waste from heavy industry can be prohibited during coral spawning, ensuring that the seasonal production of propagules for reef replenishment is not jeopardized (Baird et al. 2011).

In this study, we document the day or month of propagule release for 34 of the approximately 65 coral species on Lord Howe Island. We also document aspects of the reproductive biology of many of these species, including the sexual system, mode of larval development, transmission of *Symbiodinium* spp. and egg size on release.

MATERIALS AND METHODS

Reproductive condition of *Acropora* species

Acropora were sampled 8 to 10 d before full moon on 21 December 2010, and 3 to 5 d after full moon on 9 January 2012. These sampling times were chosen because previous work on Lord Howe Island indicated that *Acropora* spp. spawn 8 to 10 d after full moon (Harrison 2008). Twenty-three *Acropora* spp. were sampled to determine their reproductive condition (for full list of species see Table 1). Three repro-

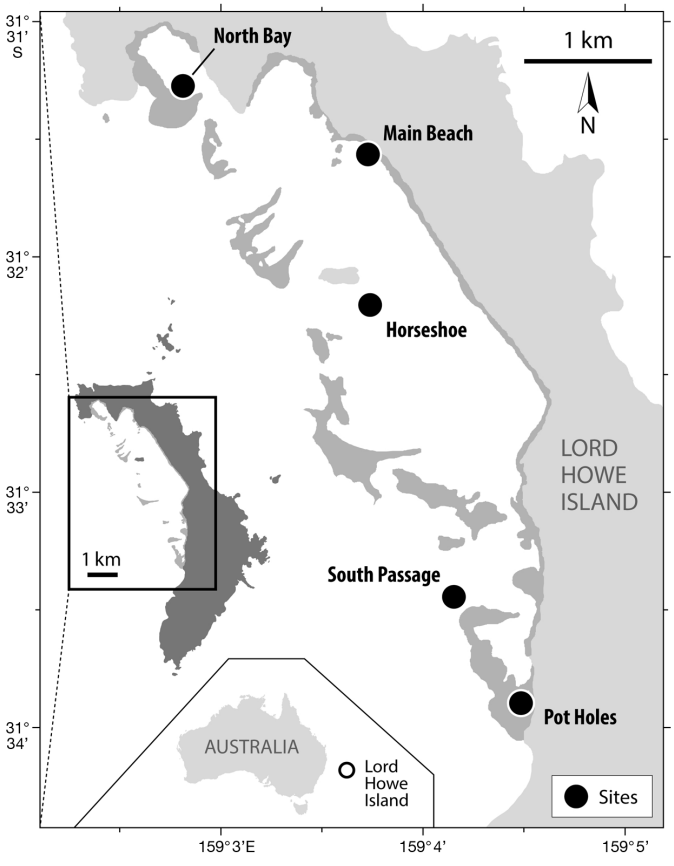

Fig. 1. Map showing the 4 collection sites at Lord Howe Island: North Bay, Horseshoe, South Passage and Pot Holes. All sites were within the lagoon, and the corals were collected 1 to 2 m below tidal datum. Mid-grey shadings are areas of coral reef

ductive conditions were defined (sensu Baird et al. 2002) based on the appearance of the oocytes as observed with the naked eye in the field: (1) mature—oocytes pigmented and assumed to be released within a month; (2) immature—oocytes pale but visible, indicating that they are close to maturity and assumed to be released within 2 mo; and (3) empty—oocytes too small to see or absent, indicating either that the colony has recently released its gametes, or is unlikely to do so for at least 3 mo.

Observations of coral reproductive behaviour in aquaria

Mature coral colonies for spawning observations were collected from 1 to 2 m below tidal datum at 4 sites (North Bay, Pot Holes, Comet's Hole, South Passage) in the lagoon on Lord Howe Island (Fig. 1) between 16 and 20 January 2011 and were stored under the jetty during daylight hours (for species list see Table 2). Colonies were submerged in buckets and transported to the research station each day at 17:30 h, where they were maintained until 08:00 h the following morning, with 1 complete seawater change at 24:00 h. Colonies were inspected approximately every 30 min while at the research station to capture the onset of spawning. Egg colour, whether or not eggs were released in bundles, whether or not eggs contained *Symbiodinium* spp., and the maximum diameter of the spherical eggs were recorded. Egg size was measured to the nearest unit under a dissecting microscope with a stage micrometer and graticule eyepiece at a magnification of ×40 from 2 to 6 h after egg release.

Reproductive biology of species in the family Pocilloporidae

To determine the reproductive condition of 3 species of pocilloporid corals (*Pocillopora damicornis*, *Seriatopora hystrix*, *Stylophora pistillata*), 1 branch, approximately 5 cm long, was collected from each of 5 colonies of each species monthly from April 2011 until March 2012 inclusive in the week before the full moon of each month. The fragments were preserved in 10% seawater formaldehyde and then decalcified in a mixture of 90% water and 10% formic acid and preserved in 70% ethanol. Five polyps were dissected from each branch under a stereo-microscope and the numbers of oocytes and planulae in each polyp were counted. Oocytes and planulae of the Pocilloporidae are readily distinguished under a stereo-microscope on the basis of size: oocytes rarely have a diameter >100 µm (Permata et al. 2000). The type of reproductive tissue was confirmed through histology. Sections of the decalcified branches containing reproductive tissues were embedded in wax following dissections, sectioned at 7 µm thickness, and 3 to 4 sections approximately 50 µm apart were mounted on slides. Slides were stained using Mayer's haematoxylin and Young's eosin-erythrosine (Baird et al. 2011).

Environmental variables associated with coral spawning

Environmental variables hypothesized to serve as proximate cues by which coral synchronise spawning (see review in Baird et al. 2009b) were collated and their association with the timing of spawning on Lord

Howe Island illustrated graphically. This included monthly mean sea-surface temperatures (SST), photosynthetically available radiation (PAR), rainfall and wind speeds. Mean SSTs were calculated for the period 1982–2010 using the NOAA Pathfinder dataset v5.2. SSTs for 2010 and 2012 SSTs were calculated from the on-reef sensor network of the Great Barrier Reef Ocean Observing System and the Australian Institute of Marine Science (http://data.aims.gov.au/gbroos/). Mean monthly PAR was calculated for the period 1999–2010 using data from NASA (MODIS; http://oceancolor.gsfc.nasa.gov/). Mean monthly rainfall and wind speed data were obtained for the period 1999–2010 using data from NASA/NOAA (TMI, www.remss.com/missions/tmi).

Species identifications

Acropora spp. were identified *in situ* or from photographs or microscopic examination of the skeleton following Wallace (1999). Species from other families were similarly identified following Veron (2000). The most recently accepted names for these species were then determined by a search at the World Register of Marine Species (www.marinespecies.org/index.php). Many of the corals on Lord Howe Island are highly distinctive and difficult to place within current morphological species boundaries. Indeed, there are likely to be a number of undescribed species, including at least 4 we examine here that will be described elsewhere.

Table 1. The reproductive condition of 23 *Acropora* spp. on Lord Howe Island in December 2010 and January 2012. Values represent percentage of colonies in each category. Imm.: immature; n: number of colonies sampled

Species	December 2010				January 2012			
	Mature	Imm.	Empty	n	Mature	Imm.	Empty	n
A. aspera					75	25	0	4
A. bushyensis	0	75	25	4				
A. clathrata	7	87	7	15	100	0	0	5
A. muricata					46	0	54	26
A. gemmifera	0	100	0	1				
A. glauca	0	80	20	10	61	0	39	64
A. horrida					25	0	75	8
A. humilis					0	0	100	5
A. hyacinthus	100	0	0	2	0	0	100	1
A. latistella					100	0	0	2
A. loripes					0	0	100	1
A. lovelli	67	33	0	3	45	0	55	11
A. microphthalma	0	50	50	6				
A. nana	0	100	0	3				
A. nasuta					100	0	0	3
A. solitaryensis	0	100	0	5	0	0	100	1
Acropora sp. nov. 1	0	0	100	2	0	0	100	2
Acropora sp. nov. 2					0	0	100	1
A. stoddarti					100	0	0	2
A. tortuosa	0	100	0	2				
A. valida	50	50	0	2	67	0	33	6
A. verweyi					33	0	67	3
A. yongei	32	29	39	28	62	0	38	13
Total	18	58	24	83	54	1	45	158

RESULTS

Stage of oocytes maturity of *Acropora* species

Between 12 and 14 December 2010, 83 colonies were sampled from 13 species (Table 1). Eighteen percent of colonies were mature, 58% were immature and 24% were empty. Four species had at least 1 mature colony and 11 species had colonies that were immature (Table 1). Only 1 species was not gravid (i.e. neither mature nor immature oocytes were detected) at the time of sampling (Table 1). Coral spawning slicks were observed on 29 December 2010 (Fig. 2a), 8 d after full moon.

Between 12 and 14 January 2012, a total of 158 colonies were sampled from 18 species. Fifty-four percent of colonies were mature, 45% were empty and 1 colony was immature (Table 1). Twelve species had at least 1 mature colony and 6 species were not gravid (Table 1). Coral spawning slicks were observed on 19 January 2012 (Fig. 2b), 10 d after the full moon. Extensive field samples on 20 and 21 January 2012 found no *Acropora* colonies with mature oocytes.

Reproductive biology and spawning times of corals maintained in aquaria

Of the 15 species collected for observation in the laboratory, broadcast spawning was observed in 11 species and 1 species, *Porites heronensis*, released planulae that were swimming when first observed at 09:00 h in the morning (Table 2). Broadcast spawning was inferred to occur in *Goniastrea favulus* on the basis of disappearance of mature oocytes from all 5

Fig. 2. Coral spawn slicks at Lord Howe Island: (a) North Bay, 29 December 2010, and (b) Main Beach, 19 December 2012

colonies at some point between initial collection of colonies on 13 January and a subsequent check of reproductive condition on 20 January 2012. We assumed these colonies spawned before 17:00 h when colonies were brought to the laboratory from storage under the jetty for observation. None of the 10 *Acropora* colonies spawned in the laboratory (Table 2); however, neither species had any oocytes in extensive sampling in the field on 20 January 2011. Of the species observed in the aquaria, 5 spawned on 19 January 2012, 10 d after the full moon, 6 on 20 January, and 3 on 21 January (Table 2). *Acanthastrea hillae* spawned 30 min before sunset, *Favites halicora* and 1 colony of *Platygyra daedalea* spawned sometime between 00:00 and 06:00 h the next morning, and the remainder of species spawned between 20:30 and 00:00 h (Table 2). Species observed to broadcast-spawn gametes were hermaphrodites (i.e. both eggs and sperm were apparent in gamete bundles), with the exception of *Goniopora norfolkensis*, in which bundles contained only eggs. Egg diameters on release ranged from a minimum of 284 µm in the 2 *Cyphastrea* species to 484 µm in *A. hillae* (Table 2). Only *P. heronensis* had *Symbiodinium* spp. in its propagules (Table 2).

Reproductive biology of species in the family Pocilloporidae

Oocytes were first observed in 3 out of 5 colonies of *Seriatpora hystrix* in October 2011. Two colonies had oocytes in November, 5 in December and January, and 2 in February. Typically, there were only 1 or 2 oocytes per polyp. Planulae were first observed in

Table 2. Reproductive biology of corals maintained in aquaria at the Lord Howe Island Research Station between 18 and 22 January 2012, 9 to 13 d after the full moon on 9 January 2012. n: number of colonies collected; H: hermaphrodite; G: gonochore; na: no data; 24:00+: spawning occurred between 24:00 and 06:00 h

Family	Species	Site	n	Date spawned in 2012	Colonies spawned	Time of spawning	Gametes in bundles	Egg color	Sex	*Symbiodinium* in propagules	Max. egg diameter (µm)
Acroporidae	*Acropora* sp. nov. 3	South Passage	5	na	0	na	na	Red	na	na	na
Acroporidae	*Acropora glauca*	Horseshoe	5	na	0	na	na	Red	na	na	na
Lobophyllidae	*Acanthastrea hillae*	Pot Holes	1	20 Jan	1	17:35	Yes	Brown	H	No	484
Lobophyllidae	*Echinophyllia aspera*	North Bay	1	19 Jan	1	20:25	Yes	Brown	H	No	440
Merulinidae	*Astrea curta*	North Bay	1	20 Jan	1	24:00	Yes	Red	H	No	352
Merulinidae	*Astrea curta*	North Bay	1	21 Jan	1	24:00	Yes	Red	H	No	352
Merulinidae	*Cyphastrea microphthalma*	North Bay	5	19 Jan	5	21:10	Yes	Brown	H	No	286
Merulinidae	*Cyphastrea* sp. nov.	North Bay	1	20 Jan	1	20:30	Yes	Brown	H	No	286
Merulinidae	*Dipsastrea pallida*	North Bay	1	21 Jan	1	21:00	Yes	Pink	H	No	352
Merulinidae	*Favites halicora*	North Bay	1	20 Jan	1	24:00+	Yes	Orange	H	No	352
Merulinidae	*Goniastrea favulus*	Pot Holes	5	na	5	na	na	Orange	na	na	na
Merulinidae	*Hydnophora exesa*	North Bay	1	19 Jan	1	20:25	Yes	Red	H	No	308
Merulinidae	*Hydnophora exesa*	North Bay	1	19 Jan	1	23:00	Yes	Red	H	No	308
Merulinidae	*Paragoniastrea australensis*	Pot Holes	5	20 Jan	4	22:15	Yes	Red	H	No	374
Merulinidae	*Platygyra daedalea*	North Bay	1	19 Jan	1	23:30	Yes	Red	H	No	352
Merulinidae	*Platygyra daedalea*	North Bay	1	21 Jan	1	24:00+	Yes	Red	H	No	352
Poritidae	*Goniopora norfolkensis*	North Bay	1	21 Jan	1	21:30	Yes	Brown	G	No	462
Poritidae	*Porites heronensis*	Horseshoe	5	18 Jan	1	24:00+	Planula	Brown	na	Yes	na

2 colonies of *S. hystrix* in November 2011. Five colonies had planulae in December; 3, in January; none, in February; and 2, in March. Typically, 1 planula was found in each polyp and very occasionally 2. Oocytes were first observed in all 5 colonies of *Stylophora pistillata* in October 2011. All 5 colonies had oocytes in November; 3 in December; 2 in January and none in February or March. Up to 9 oocytes were observed in a polyp. Planulae were first observed in 3 out of 5 colonies of *S. pistillata* in November 2011. Four colonies had planulae in December and 2 had them in January. Typically 1 or 2 planulae were found in each polyp, although up to 4 planulae were observed in a single polyp. No oocytes or planulae were observed in *Pocillopora damicornis.*

Gametogenic cycles and development of planulae in pocilloporids

Samples for histology were first processed from colonies collected in October 2011 at which time, for *S. hystrix*, both oocytes and spermaries were evident in cross-section (Fig. 3a). Developing larvae were first observed in November 2011, at which point spermaries, oocytes and the developing larvae all co-occur in the same branch (Fig. 3b). The largest oocytes observed were approximately 140 µm (Fig. 3b). Larvae were distinguished by their size (200 to 450 µm in diameter in cross-section; Fig. 3b,c), deep red-staining yolk cells and an epidermis (Fig. 3c,d). Planulae were first observed in November and were distinguished by a well-differentiated gastrodermis and an epidermis with nematocysts and gland cells (Fig. 3e,f). Planulae were approximately 450 to 550 µm in cross-section (Fig. 3e,f).

Environmental conditions during spawning

Spawning at Lord Howe Island coincided with rising SST and occurred prior to the historical peak in SST of 24°C in March and April (Fig. 4a). Coral spawning occurred when PAR was at a maximum (Fig. 4b), monthly rainfall was relatively high (Fig. 4c), and wind speeds were relatively low when compared to other months (Fig. 4d).

DISCUSSION

Here, we documented the month or time of spawning of more than half of the approximately 65 species on Lord Howe Island. Multi-specific synchronous spawning episodes occurred between dusk and midnight, 8 to 12 d after full moons in December and January. Peak reproductive activity most probably occurs in January, because 24 species were either observed or inferred to spawn over a 3 to 4 night period, 8 to 11 d after the full moon in January 2012 and 3 species also released planulae in January 2012. Spawning in December and January coincides with high and rising SST, high PAR, high rainfall and low wind speeds for the location. These spawning patterns are similar to most other locations in the Indo-Pacific (Baird et al. 2009b).

The proportion of *Acropora* spp. colonies and the number of species inferred to spawn in January were similar in both years—58% of the colonies from 11 species in 2010 versus 54% of the colonies from 12 species in 2012 (Table 1)—suggesting that this is the typical pattern. The high proportion of colonies gravid (76%) in December 2010 suggests that reproductive activity is unlikely to be strong in months other than December and January. Nonetheless, 5 of the 23 *Acropora* spp. sampled were not gravid. These 5 species either breed at other times of the year, not at all, or, alternatively, not enough colonies were sampled to detect gravid individuals. High reproductive output in December and January coincides with peaks in coral recruitment to settlement tiles placed between December and March (Harriott 1992).

The sexuality and mode of reproduction of each species are similar to previous records in the Indo-Pacific (Baird et al. 2009b). Novel observations include the first record of the mode of reproduction in *Acanthastrea hillae* and *Cyphastrea* sp. nov., which are both broadcast spawners, and *Porites heronensis*, which is a brooder. *P. heronensis* is highly abundant in the lagoon at Lord Howe Island, and, together with other species known to brood on Lord Howe Island or elsewhere (*Seriatopora hystrix*, *Stylophora pistillata*, *Isopora cuneata*, *P. damicornis*), makes up >60% of the coral cover in the lagoon (Keith et al. 2015). The dominance of brooding species in coral assemblages at Lord Howe Island was first noted by Harriott (1992) who hypothesised that rapid settlement of brooded larvae allows these species to establish populations in isolated locations such as Lord Howe Island. An alternative hypothesis is that internal fertilization (i.e. brooding) is a more successful reproductive strategy than external fertilization (i.e. broadcast spawning) in the sub-tropical waters of Lord Howe Island. In 2 species of broadcast spawners, median larval lifespan was very low: <24 h for both *Paragoniastrea australensis* and *Cyphastrea*

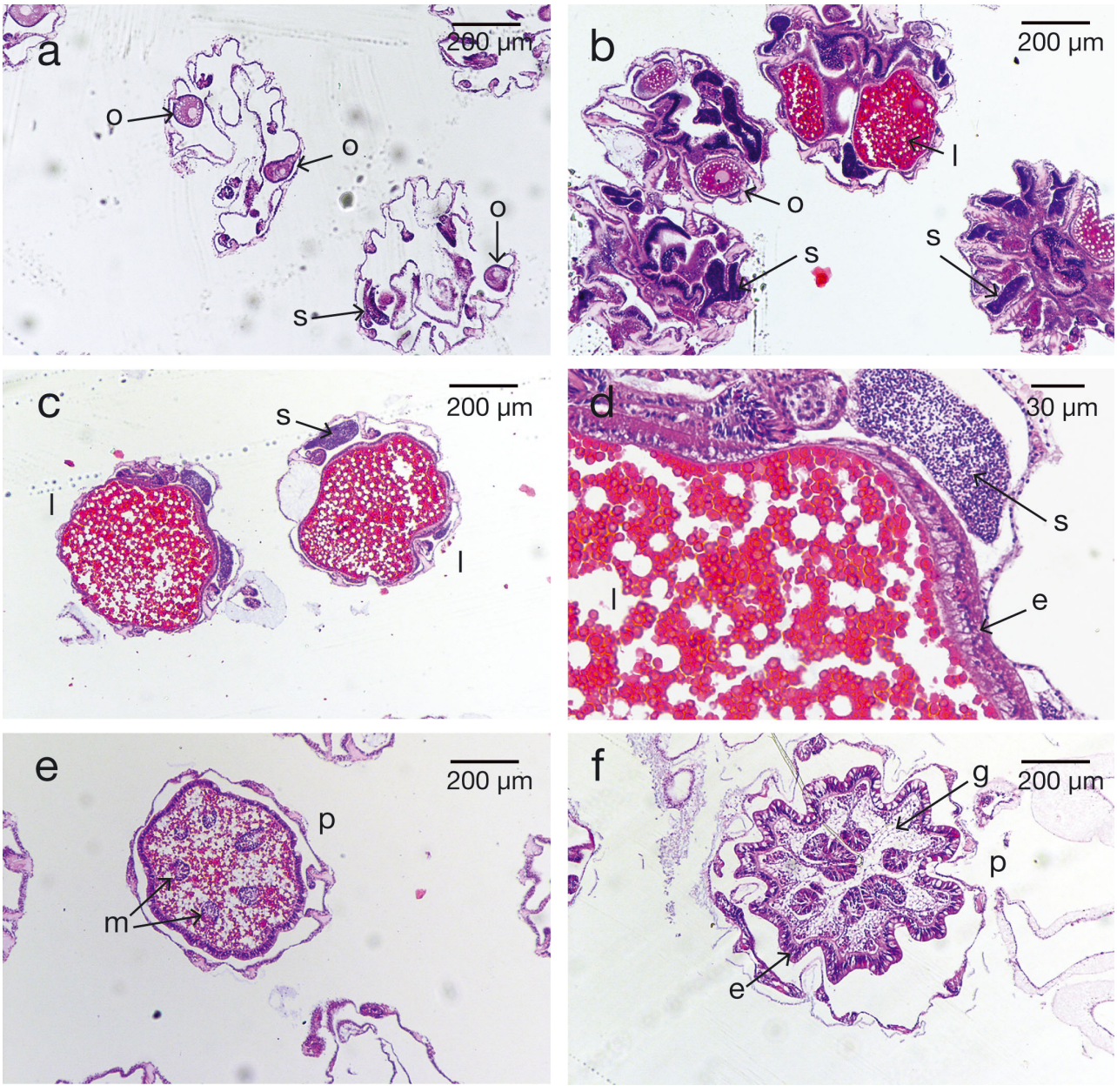

Fig. 3. Gametogenic cycles and development of brooded planulae in *Seriatopora hystrix* at Lord Howe Island: (a) oocytes in polyps in October 2011; (b) oocytes, spermaries and developing larvae in polyps in November 2011; (c) developing larvae, distinguished by their size (~300 µm diameter), deep red-staining yolk cells, and epidermis, and spermaries in adjacent polyps in November 2011; (d) close-up of developing larvae showing epidermis; (e) larvae in polyps with developing mesenteries and epidermis in November 2011; and (f) fully developed planula larvae in a polyp in December 2011. o: oocytes; s: spermaries; l: developing larvae; p: planulae; m: mesenteries; e: epidermis; g: gastrodermis

microphthalma (Woolsey et al. 2014) compared to typical values of >30 d among the larvae of broadcast-spawning species at tropical locations (Graham et al. 2008, Connolly & Baird 2010). This suggests that gametes of these sub-tropical broadcast-spawning corals were either of poor quality or highly sensitive to handling. Poor-quality larvae could be attributed to the marginal environmental conditions experienced in Lord Howe Island waters, such as winter temperatures of 14.4°C (Woolsey et al. 2014). This might have a detrimental effect on the development of gametes in broadcast-spawning species that have an oogenic cycle of between 6 and 14 months (Harrison & Wallace 1990). In contrast, brooding species

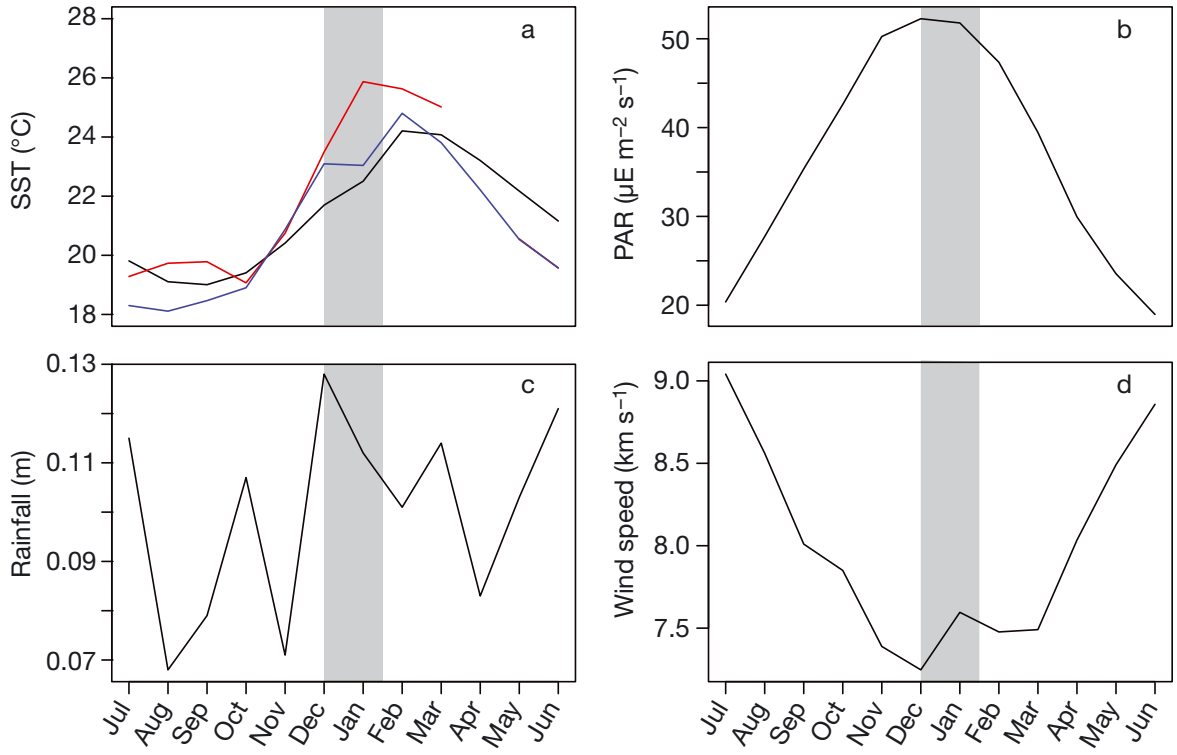

Fig. 4. Environmental variables hypothesised to be involved in synchronising coral spawning: (a) mean monthly sea-surface temperature (SST) for the period 1982–2010 (black line), 2010 (red line) and 2012 (blue line); (b) mean monthly photosynthetically active radiation (PAR); (c) mean monthly rainfall; and (d) mean monthly wind speeds for the period 1999–2010 (data sources are listed in the 'Materials and methods' section). Spawning times are indicated by the grey shading in each panel

have an oogenic cycle of approximately 1 mo, and only breed in the warmer months of the year on Lord Howe Island. Low survivorship of broadcast-spawned propagules is consistent with the low densities of recruits to settlement tiles on the substratum at Lord Howe Island when compared with settlement in tropical locations (Harriott 1992).

Oocytes and larvae were first observed in *Seriatopora hystrix* and *Stylophora pistillata* in October and November, respectively, suggesting an oogenic cycle of approximately 1 mo in these 2 species. Dissections suggested that oocytes were produced monthly and co-occur in the same polyps with developing larvae (Fig. 1b). Planulae are likely to be released shortly after maturity, indicating most colonies will planulate every month over a period of 3 to 4 mo. The length of the reproductive season in these brooders at Lord Howe Island is similar to that at Heron Island but contrasts with the period at more tropical locations where planulation occurs throughout the year (Fan & Dai 1996, Tanner 1996). In contrast, no reproductive activity was observed in *Pocillopora damicornis*: neither oocytes nor planulae were recorded in 300 polyps from a possible 60 colonies over a complete year of sampling. Despite previous conjecture (see citations in van Woesik 1995), this is the first time no reproductive activity has been detected in a scleractinian coral species in the absence of obvious stress. This result is possibly a sampling artefact. If the time to develop from oocyte to planulae is <1 mo then the monthly sampling could have missed the cycle. Indeed, previous estimates of a 2 wk oogenic cycle in *P. damicornis* in Okinawa indicate this is a possibility (Permata et al. 2000). Further work is required to establish whether or not *P. damicornis* is reproductively active at Lord Howe Island.

The patterns of spawning within the coral assemblage at Lord Howe Island indicate that patterns in marginal reef locations are similar to those in locations elsewhere in the Indo-Pacific. This suggests that the selective processes that drive spawning synchrony are the same as those found in other regions of the Indo-Pacific. The highly seasonal nature of coral reproduction at Lord Howe Island and elsewhere means that managing human activities to reduce the threat from processes that affect reproductive success, such as dredging, appears quite feasible once the timing of these events is established.

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