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REPORT

Multi-species spawning synchrony within scleractinian coral assemblages in the Red Sea

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Abstract Early work on coral reproduction in the far northern Red Sea suggested that the spawning times of ecologically abundant species did not overlap, unlike on the Great Barrier Reef where many species spawn with high synchrony. In contrast, recent work in the northern and central Red Sea indicates a high degree of synchrony in the reproductive condition of *Acropora* species: over 90 % of species sampled in April/May contain mature gametes. However, it has yet to be determined when most *Acropora* release their gametes. In addition, there is a lack of data for other ecologically important scleractinian species such as merulinids and poritids. Here, we document the date and time of spawning for 51 species in the central Red Sea over three consecutive years, and the month of spawning for an additional 17 species inferred from the presence of mature gametes. Spawning occurs on nights around the full moon, the spawning season lasts at least 4 months from April until July, and observations are consistent with the few other records from the Red Sea. The number of *Acropora* species spawning was highest in April with 13 species spawning two nights before the full moon in 2011, 13 species spawning on the night of the full moon in 2012, and eight species spawning four nights after the full moon in 2013. The total number of species spawning was high in April, May, and June and involved 15–19 species per month in 2012. Only four species spawned in July 2012. Few regions worldwide have been similarly sampled and include the Philippines, Okinawa in Japan, and Palau, where spawning patterns are very similar to those in the central Red Sea and where corals spawn on nights around the full moon over a period of 3–4 months. In particular, in all four locations, *Acropora* are among the first species to spawn. Our results add to a growing body of evidence indicating that multi-species spawning synchrony is a feature of all speciose coral assemblages.

Keywords Coral reefs · Larval ecology · Reproduction · Saudi Arabia · Multi-species spawning

Introduction

Knowing when corals spawn is fundamental to understanding the factors that regulate populations, such as rates of recruitment and patterns of connectivity. Most broadcast spawning scleractinian coral species have colonies with a single annual gametogenesis cycle and high levels of

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spawning synchrony within populations (Harrison and Wallace 1990). The first multi-species spawning events were documented on the Great Barrier Reef (GBR) in Australia, where over 130 species from many families were documented to spawn over a few nights between the full and last quarter moon in late spring (Harrison et al. 1984; Willis et al. 1985; Babcock et al. 1986). For many years, multi-species spawning events were thought to be restricted to the GBR (Shlesinger and Loya 1985; Oliver and Willis 1987; Harrison and Wallace 1990; Richmond and Hunter 1990). However, multi-species spawning events have now been documented in at least 24 other locations around the globe (Baird et al. 2009a).

Geographical and latitudinal variation in the length of reproductive seasons is also a point of some controversy (Mangubhai and Harrison 2008, 2009; Baird and Guest 2009). For example, van Woesik (2010) assumed that the reproductive season on the GBR lasted only 2 months, leading to the erroneous conclusion that the length of the reproductive season in corals was driven by annual wind regimes. Recent work on the GBR has demonstrated that some species within the genus *Acropora* breed every month between October and February (Baird et al. 2009b) indicating a reproductive season of at least 5 months for this genus. This work, combined with historical records of *Acropora* spawning as early as September (Wallace 1985) and as late as March (Wolstenholme 2004) on the GBR, indicates that extended breeding seasons for corals are not restricted to low latitudes (Baird and Guest 2009). Controversies about seasonality and synchrony stem largely from the fact that coral assemblages have only been sampled adequately enough to determine the length of the reproductive season in very few locations. Notable exceptions include work from Okinawa, Japan (Heyward et al. 1987; Hayashibara et al. 1993; Kinzie 1993), Singapore (Guest et al. 2002, 2005a), the Persian Gulf (Bauman et al. 2011), and Palau (Penland et al. 2004). All these studies reveal an extended reproductive season in corals in addition to regular multi-species spawning events.

The Red Sea has been described as a marine biodiversity hotspot because it is species-rich and has high levels of endemism (Veron 2000; Hughes et al. 2002). However, many aspects of the biology and ecology of the region remain poorly understood (Berumen et al. 2013). In particular, the reproductive biology of scleractinian corals has received relatively little attention. Reproductive surveys and night-time observations in Eilat, Gulf of Aqaba, northern Red Sea, suggested the absence of multi-species synchronous spawning with 21 of the dominant species reproducing in different months and at different times throughout the lunar cycle (Shlesinger and Loya 1985; Shlesinger et al. 1998). Except for two species which spawned in April, the reproductive season lasted from June to September (Shlesinger and Loya 1985; Shlesinger et al. 1998). Due to the lack of similar work in the rest of the Red Sea, it was assumed for many years that the temporal reproductive isolation of corals was representative of the entire Red Sea (Richmond and Hunter 1990; Mangubhai and Harrison 2008), reinforcing the hypothesis that multi-species synchronous spawning was restricted to certain regions, such as the GBR (Harrison and Wallace 1990; Richmond and Hunter 1990). However, recent work on the Egyptian coast in the northern Red Sea revealed 85 % or more of *Acropora* colonies had mature oocytes in April 2008 and in April 2009. Subsequent sampling revealed the absence of oocytes in all but one of these species, indicating that spawning had occurred sometime in the previous couple of weeks (Hanafy et al. 2010). This was later confirmed when ten *Acropora* species were observed spawning synchronously in situ on the same night in April 2011 on the Saudi Arabian coast in the central Red Sea (Bouwmeester et al. 2011). Nonetheless, there are very few other observations on the timing of gamete release for scleractinian corals in the Red Sea.

In this study, we document the month and time of spawning for 51 coral species based on in situ observations in the central Red Sea. We then compare spawning patterns in the Red Sea to those in the Philippines, Okinawa in Japan, and Palau to determine whether there are consistent geographical patterns in terms of the timing of spawning within a season among coral taxa.

Materials and methods

Study sites and sampling design

The stage of gametogenesis of 37 species from 21 genera was examined from April to July 2011 at Al Fahal (22°13′26.51″N, 38°58′10.12″E), a mid-shore reef in the central Red Sea 12 km off the coast of Thuwal (Fig. 1). In parallel, night-time observations were conducted from April to June 2011 and April to July 2012 at Al Fahal or, when weather conditions did not allow boat access to the reef (May 2011, June and July 2012), at Dreams Beach Reef (21°45′24.43″N, 39°3′7.05″E), a fringing reef north of Jeddah with a similar coral assemblage. In 2013, night-time observations were conducted in April only, during a 10-d biodiversity expedition on mid- and offshore reefs off the coast of Thuwal, each night on a different reef.

In situ seawater temperatures were recorded hourly with a HOBO Water Temp Pro v2 logger installed at the depth of approximately 0.7 m on a mooring between Thuwal and Jeddah (21°58′45.48″N, 38°50′41.28″E) from April to May in 2011 and on the reef edge in Al Fahal from December 2011 to August 2013.

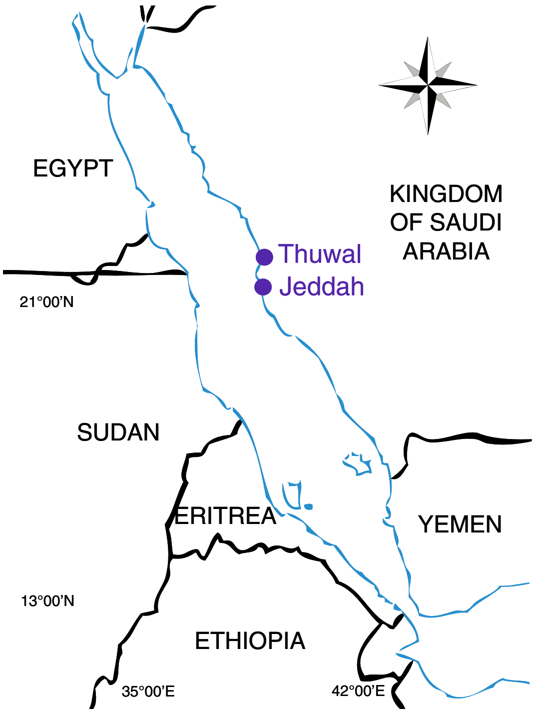

Fig. 1 Map of sites in the Red Sea where surveys were conducted: Thuwal (Al Fahal Reef, 10 km off the coast) and Jeddah (Dreams Beach Reef, fringing reef)

Examination of gamete maturity with in situ observations and histology

As a general rule, broadcast spawning corals spawn gametes within a month of the eggs becoming visibly pigmented (Harrison et al. 1984). Oocytes of *Acropora* species when observed in situ can be classified as mature or immature based on colour (Baird et al. 2002). However, when immature, oocytes of species other than *Acropora* are generally too small to be visible. In this case, gamete maturity can be determined by histological examination. Therefore, to determine the spawning window, 37 coral species were sampled (see Table 1 for number of samples collected per species) and taken back to the laboratory for histology. Coral species were sampled between one and three times from April to July 2011 and colonies of two *Porites* species again in October and November 2011. Except for *Porites*, for which the same colonies were sampled repeatedly, originally as part of a different research project, colonies were selected randomly. The development of gametes is usually highly synchronous between polyps within a colony (Harrison and Wallace 1990), so one fragment is sufficient to assess the reproductive condition (Baird et al. 2011). Fragments of approximately 10 cm^2 containing several polyps from the centre of each colony (colonies >25 cm diameter) were collected on SCUBA with a hammer and a chisel and fixed in 10 % seawater formalin for at least 24 h. Coral tissue was decalcified in 5 % hydrochloric acid, wax-embedded, sectioned, and stained with H&E using the procedure described in Baird et al. (2011). Each colony was then classified into one of four stages of oogenesis or spermatogenesis (Baird et al. 2011). Mature gametes (stage IV) were assumed to be released around the following full moon and stage III gametes around the subsequent full moon. No predictions were made when stages I or II of gametogenesis were observed.

Coral spawning observations

Broadcast spawning scleractinian corals generally release gametes around the full moon in the spring as sea surface temperatures are rising (Willis et al. 1985; Baird et al. 2009a). Following the appearance of mature oocytes in surveys of the reproductive condition in the *Acropora* (Baird et al. 2002), night-time surveys commenced three nights before the full moon and continued until six nights after the full moon (Electronic Supplementary Material, ESM, Fig. S1). Reproductive data from histology and from in situ examinations of gamete maturity in 2011 suggested that many species spawn between April and July. Therefore, in 2012, we increased the duration each night and the number of nights around each full moon, spent surveying corals for spawning behaviour. Each month, surveys lasted 5–9 nights in 2011, 6–11 nights in 2012, and 9 nights in 2013. Surveys were done on SCUBA starting 30 min after sunset for 2 h in 2011 and for 4 h in 2012 (sunset times varied between 18:40 hrs in April and 19:10 hrs in July). In May 2011 and in June and July 2012, the surveys were conducted from Dreams Beach Reef in Jeddah. All scleractinian corals were carefully examined while following a random diving path between the reef edge and a depth of 10 m looking for setting behaviour of polyps which generally precedes the release of gametes (Babcock et al. 1986).

On nights during which *Acropora* species spawned, all *Acropora* colonies were regularly monitored throughout the night, and spawning behaviour was described using the following categories: no activity, setting (defined by egg–sperm bundles appearing under the oral disc of the polyps), or spawning (release of gametes). In 2012, 73 mature *Acropora* colonies (19 species) were tagged at random prior to the first night-time spawning surveys in order to check whether some colonies were spawning more than once and these colonies were followed in April and May. Coral colonies were identified to species in the field when possible, otherwise from field photographs or from bleached samples observed under a stereo microscope. *Porites* colonies were identified to species after imaging with a scanning electron microscope. Coral species were

Table 1 Stages of gametogenesis on various dates relative to the full moon (FM) throughout the spawning season in 2011 and inferred month of spawning

Species	Date sampled	Field observations	Stage of oogenesis	Oocyte size	Stage of spermatogenesis	Inferred month of spawning	Number colonies	Sexuality [H/G]
Poritidae								
Goniopora columna	May FM − 6	–	III	300	No	June	1♀	G
*Porites monticulosa**	April FM − 16	–	No		No	–	10	G
	May FM	–	No		No	–	10	
	June FM − 8	–	No		No	–	10	
	Oct FM − 8	–	III–IV	74	III–IV	Nov.	4♀, 5♂	
	Nov FM + 16	–	No		No	–	10	
*P. nodifera**	May FM	–	IV	360	IV	May	4♀ 3♂	G
	June FM − 8	–	III–IV		III	June	1♀, 1♂	
	Oct FM − 8	–	No	–	No	–	8	
	Nov FM + 16	–	No	–	No	–	8	
Acroporidae								
Astreopora listeri	May FM − 6	–	II–III	185	–	–	1	H
A. myriophthalma	May FM − 6	–	–	–	III	June	1	H
	May FM + 14	Big cream eggs	IV	500	IV	June	2	
	June FM + 10	–	No	–	–	–	1	
Montipora efflorescens	May FM − 6	–	III	280	II	June/July	1	H
M. tuberculosa	May FM − 6	–	No	–	No	–	1	H
	June FM + 10	–	II	75	–	–	1	
	July FM − 9	–	No	–	No	–	1	
Agariciidae								
Pavona varians	April FM − 5	–	IV	250+	No	April	1♀	G
Clade XI								
*Coscinaraea monile**	April FM − 5	–	IV	240	–	April	1	–
	July FM − 9	–	III–IV	180	–	July	1	
Clade XIV								
*Blastomussa loyae**	June FM + 10	–	III–IV	320	–	July	1	–
Diploastreidae								
Diploastrea heliopora	May FM − 6	–	III	250	–	May/June	1	G
	May FM + 14	–	No	–	No		1	
	June FM + 10	–	No	–	No		1	
Merulinidae								
Cyphastrea chalcidicum	May FM + 14	–	IV	265	IV	June	1	H
	July FM − 9	–	II	110	–	–	1	
*C. kausti**	May FM − 6	–	III	230	II–III	June	1	H

Table 1 continued

Species	Date sampled	Field observations	Stage of oogenesis	Oocyte size	Stage of spermatogenesis	Inferred month of spawning	Number colonies	Sexuality [H/G]
C. serailia	May FM − 6	–	III	200	–	June	1	H
Echinopora forskaliana	April FM − 5	–	II	140	–	–	1	H
	May FM − 6	–	III–IV	230	–	May	1	
	June FM + 10	–	III	200	–	July	1	
E. gemmacea	April FM − 5	–	IV	400	–	April	1	H
	May FM + 14	–	III	200	II–III	June	2	
	July FM − 9	–	III	160	II–III	July	1	
*E. hirsutissima**	June FM + 10	–	IV	250	IV	July	1	H
*Favia albidus**	July FM − 9	–	III	200	–	July	1	–
F. helianthoides	May FM − 6	–	III	305	III	May/June	1	H
*F. maritima**	June FM + 10	–	III	300	–	July	1	–
*F. rotundata**	May FM + 14	–	III	320	–	June	1	–
	July FM − 9	–	No	–	No	–	1	
Favites abdita	May FM − 6	Red eggs	IV	300	IV	May	2	H
	July FM − 9	–	No	–	No	–	1	
*F. paraflexuosa**	May FM − 6	–	II–III	200	–	June	1	–
Goniastrea aspera	June FM + 10	–	II–III	160	–	July	1	H
G. pectinata	May FM + 14	Red eggs	III	190	III	June	1	H
	July FM − 9	–	III–IV	280	III	July	1	
Favia stelligera	June FM + 10	–	III	200	–	July	1	H
*Leptoria phrygia**	April FM − 5	Light green eggs	III	215	III	May	1	H
Montastrea cf. *curta**	May FM − 6	–	III–IV	200+	–	May	1	–
Oulophyllia bennettae	April FM − 5	–	II–III	110	–	May	1	H
Oulophyllia crispa	June FM + 10	–	IV	250	IV	July	1	H
	July FM − 9	–	No[a]	–	No	–	1	
Platygyra acuta	May FM + 14	Pink eggs	III–IV	235	–	June	1	H
Platygyra crosslandi	April FM − 5	Pink eggs	–	–	–	April	1	H
Platygyra sinensis	May FM − 6	–	II	80+		–	1	H
Hydnophora microconos	April FM − 5	–	III	200+	II	May	1	H
	May FM + 14	–	No	–	No	–	1	
	June FM + 10	–	IV	200+	IV	July	1	
Lobophylliidae								
Lobophyllia corymbosa	April FM − 5	Red eggs	–	–	–	April	1	H
*Symphyllia erythraea**	May FM + 14	–	no	–	No	–	1	–
	July FM − 9	–	III–IV	220	–	July	1	

Table 1 continued

Species	Date sampled	Field observations	Stage of oogenesis	Oocyte size	Stage of spermatogenesis	Inferred month of spawning	Number colonies	Sexuality [H/G]
Echinophyllia aspera	June FM + 10	–	III	200	III	July	1	H

Dates sampled were 2 April (April FM − 16), 13 April (April FM − 5), 11 May (May FM − 6), 17 May (May FM), 31 May (May FM + 14), 7 June (June FM − 8), 25 June (June FM + 10), 6 July (July FM − 9), 4 October (Oct FM − 8), and 26 November (Nov FM + 16). Size of oocytes (maximum size observed) is in μm. Sexuality is defined as hermaphroditic (H) or gonochoric (G). For gonochoric species, the number of male (♂) and female (♀) colonies is indicated

* New records

[a] Stretched empty mesenteries

classified into molecular-based clades following Fukami et al. (2008), Huang et al. (2011), and Arrigoni et al. (2012).

Biogeographical comparison of spawning patterns

In order to compare the spawning patterns in the Red Sea to other regions of the globe, we identified a number of studies from the literature with comparable data: i.e. at least 3 months of in situ spawning observations in a given year. These data are available for surprising few locations and include observations in 1987, 1990, and 1991 from Okinawa (Heyward et al. 1987; Hayashibara et al. 1993; Kinzie 1993), observations in 2002/2003 from Palau (Penland et al. 2004), and observations in 2007 from the Philippines (Vicentuan et al. 2008; Guest et al. unpublished data). We included Red Sea spawning observations for 2011 and 2012. For each year and each location, the number of species spawning per month and the families (or genera in the case of abundant groups) involved were compared.

Results

Spawning month inferred from histology and in situ examination of gamete maturity

Histology and in situ examinations of the stage of gamete maturity in 37 coral species from eight clades in spring 2011 (Fig. 2) suggest a reproductive season from April to July (Table 1), a period during which sea surface temperatures increase rapidly, rising from 24.7 to 33.5 °C in 2012 and from 26.1 to 32.3 °C in 2013 (ESM Fig. S2). Of these 37 species, five were predicted to spawn on or around the April full moon, along with 12 out of 18 *Acropora* species (72 out of 110 colonies), which were observed in situ to have mature gametes. Four additional species were predicted to spawn on or around the May full moon, five in June, and seven in July. No gametes were observed in ten colonies of *Porites monticulosa* between April and June. However, immature gametes were observed in these same colonies in October and no gametes were present at the end of November, suggesting *P. monticulosa* released gametes on or around the November full moon. Stage III gametes in histological sections suggest an additional 15 species spawned between May and July (Table 1).

Spawning times based on in situ observation of gamete release

Over the three reproductive seasons, 51 species from eight clades were observed to spawn in situ: 22 species from four clades in 2011, 42 species from eight clades in 2012,

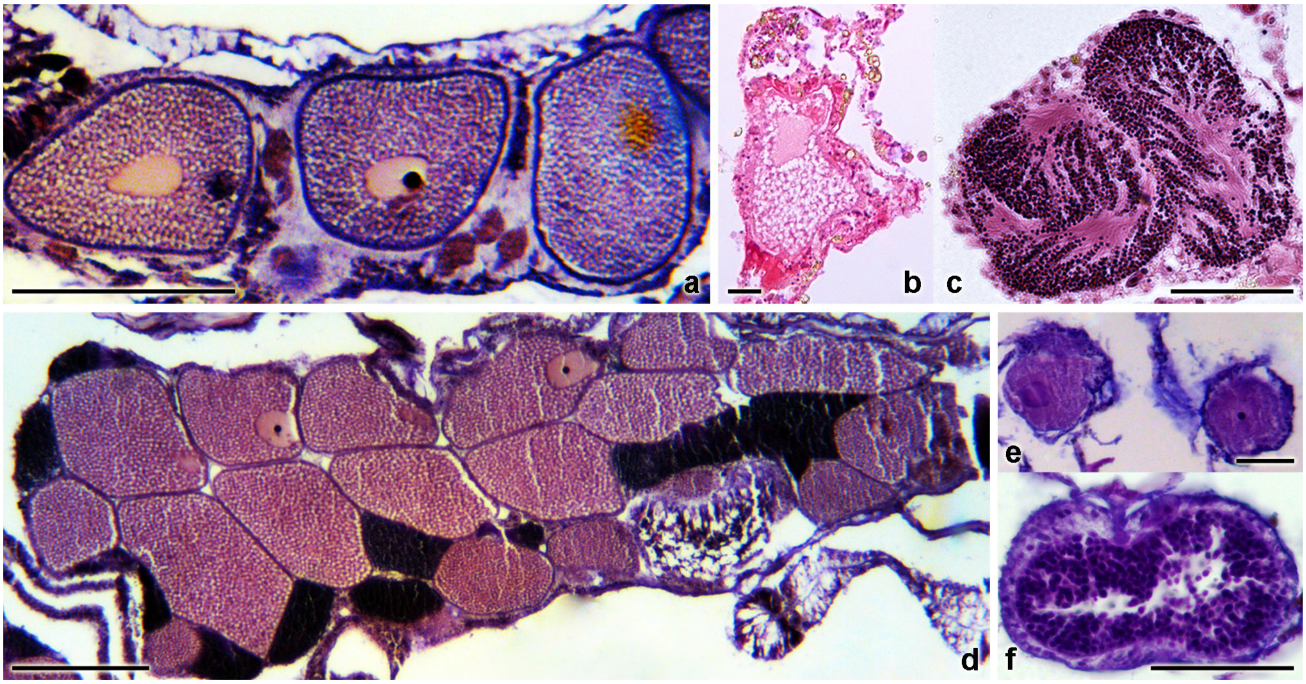

Fig. 2 Stages of gametogenesis of some scleractinian corals throughout the reproductive season in 2011. **a** Stage II–III oogenesis in *Favites paraflexuosa* on 11th May, **b–c** *Porites nodifera* on 17th May showing, **b** stage III–IV oogenesis and **c** stage IV spermatogenesis with visible spermatozoa tails, **d** *Echinopora hirsutissima* on 25th June showing stage IV gametogenesis with a tight aggregation of mature gonads already forming bundles, **e–f** *Porites monticulosa* on 4th October showing, **e** stage II oogenesis, and **f** stage II–III spermatogenesis. The *scale bar* represents 200 μm in **a**, **d**; and 50 μm in **b**, **c**, **e**, **f**

and 13 species from three clades in April 2013. These observations include the first spawning records for ten species (Table 2; ESM Fig. S3g–i). The time and number of colonies spawning, the length of the setting period during which gamete bundles were visible in the mouth of the polyps, the form under which gametes were released, and the sex of the species on the basis of gamete release are presented for each species in Table 2. Spawning was observed in each month from April to June in 2011 and from April to July in 2012, and over a period of one to seven consecutive days within each month (ESM Fig. S1). The number of species spawning at the same time on any one night ranged from one species on the night following the July full moon in 2012 to 13 species both on four nights before the April full moon in 2011 and on the night of the April full moon in 2012. Spawning was observed as early as three nights before the full moon in July 2012 until seven nights after the full moon in June 2012, and over 15 colonies of *Pocillopora verrucosa* spawned 1 d before the new moon in 2011 and in 2012. Except for *P. verrucosa* which spawned in the morning between 08:40 hrs and 09:20 hrs, all species spawned in the 5-h following sunset, between 19:20 hrs and 23:45 hrs (Table 2).

Fifteen *Acropora* species spawned in 2011 and 16 in 2012. All *Acropora* species released egg/sperm bundles and most spawned in April. In 2011, on the 16 April (two nights before full moon), 13 out of 16 *Acropora* species (57 tagged colonies) spawned. In 2012, on the 6 April (full moon night), 13 out of 20 *Acropora* species (64 tagged colonies) spawned. In 2013, six species (nine colonies) spawned on the 25 April (full moon night) and eight (17 colonies) on the 29 April. In 2011 and 2012, a few colonies from six species which had already spawned in April spawned again in May. Finally, two species spawned in June (Table 2).

Four species of *Porites* were observed to spawn throughout May–June 2012 and April 2013. Male and female *Porites* colonies slowly released sperm or eggs starting between 21:35 hrs and 23:25 hrs. Sperm clouds were thick and dense and visible for up to 2–3 h. In June 2012, two neighbouring colonies of *P. solida* were observed to release what looked like bundles between 20:40 hrs and 21:00 hrs.

Biogeographical comparison of spawning patterns

Spawning in the first months of the reproductive season was dominated by *Acropora* species in the central Red Sea, north-western Philippines, and Okinawa. In Palau, where at least two distinct reproductive seasons exist, the first month of August–September reproductive season was also dominated by *Acropora* species. Furthermore, it is on the first spawning night of the reproductive season that most of the

Table 2 List of corals seen spawning in situ

Species	Spawning month	Spawning day	Hour of spawning	Number colonies	Setting duration	Gametes released	Sexuality
Dendrophylliidae							
*Turbinaria stellulata**	June 2012	5	20:20	1	No	E	G
Poritidae							
*Porites columnaris**	May 2012	0, 1	21:45–22:00 (S)	1♂, 3♂	No	S + E	G
P. lobata	May 2012	1	21:35–23:15 (S)	1	No	S + E	G
P. lutea	May 2012	0, 1, 2, 3	21:15–23:15 (S)	4♂2♀, 12♂6♀, 10♂11♀, 3♂4♀	No	S + E	G
	April 2013	2, 3	22:05–23:20 (E)	4♂, 2♂			
*P. solida**	June 2012	4, 5	20:40–21:00	2, 2	No	B	?
Euphylliidae							
Galaxea fascicularis	June 2012	6, 7	20:05–21:20	2, 2	No	S + B	GD
	July 2012	−1		1			
Acroporidae							
Acropora anthocercis	April 2011	−2	22:40–23:10	1	3:00	B	H
	April 2012	0, 1		2, 1			
A. eurystoma	May 2012	3	19:20	2	Yes	B	H
*A. downingi**	April 2012	0	22:30–22:35	7	2:30	B	H
	April 2013	4		2			
A. gemmifera	April 2011	−2	22:45–23:30	12	2:45	B	H
	April 2012	0, 1		3, 1			
A. hemprichii	April 2012	0, 1	22:40	2, 1	2:10	B	H
	May 2012	3		1			
	April 2013	4		2			
A. humilis	June 2011	2		21	1:40	B	H
	May 2012	3		4			
	June 2012	2, 3, 5, 7	21:10–21:40	2, 1, 1, 1			
A. hyacinthus	April 2011	−2	22:45–23:45	12	1:40	B	H
A. lamarcki	April 2011	−2	22:40–23:10	5	2:40	B	H
	April 2012	0		6			
	April 2013	0		2			
A. loripes	April 2013	4	22:30–22:50	3	1:10+	B	H
A. lutkeni	May 2011	0, 1	21:00–22:15	7, 4	2:00	B	H
	June 2011	2		1			
	April 2012	0, 1		1, 1			
	May 2012	3		5			
A. maryae	April 2012	0	(between 19:50 and 20:40)	1	Yes	B	H
A. microclados	April 2011	−2	22:50–23:00	2		B	H
	May 2011	0		1			
A. parapharaonis	April 2011	−2	22:30	1	0:45+	B	H
	April 2013	4		1			
A. pharaonis	April 2011	−2	22:25–23:00	2	2:25	B	H
	April 2012	0		3			
	April 2013	0, 4		1, 2			
A. plantaginea	April 2011	−2		3	2:50	B	H
	May 2011	0		2			
	April 2012	0, 1, 3		5, 1, 1			
	April 2013	−3, 0, 4	22:30–22:45	1, 2, 1			
A. polystoma	April 2011	−2	(after 22:15)	3	1:30+	B	H

Table 2 continued

Species	Spawning month	Spawning day	Hour of spawning	Number colonies	Setting duration	Gametes released	Sexuality
A. samoensis	April 2011	−2	22:45–22:55	2	2:15	B	H
	April 2012	0, 1		4, 1			
A. secale	May 2012	3	21:50	1		B	H
A. selago	April 2011	−2	(after 22:10)	1		B	H
A. squarrosa	April 2012	0	22:40–22:50	2	2:00+	B	H
A. valida	April 2011	−2	22:00–22:40	1	2:20	B	H
	May 2011	0, 1		12, 2			
	April 2012	0, 1		4, 1			
	May 2012	3		4			
	April 2013	0		2			
*A. variolosa**	April 2011	−2	22:45	1	2:00	B	H
	April 2012	0, 1		3, 1			
	April 2013	0, 4		2, 6			
A. verweyi	May 2011	0	20:20–20:30	1	Yes	B	H
Montipora efflorescens	June 2012	1, 2	20:45–21:25	2, 1	0:30	B	H
	July 2012	−3, 0, 1, 2		1, 1, 3, 6			
M. tuberculosa	June 2011	2	20:20–20:25	1	n/a	B	H
M. turgescens	June 2012	1	20:05	1	Yes	B	H
Pocilloporidae							
Pocillopora verrucosa	May 2011	NM-1	8:40–9:15	20+	No	S + E	H
	May 2012	NM-1	8:55–9:20	15+			
Diploastreidae							
Diploastrea heliopora	May 2011	4	22:20–22:35 (S)	4♂1♀	No	S + E	PD
	June 2012	3	+ 23:00 (E)	1			
Merulinidae							
Cyphastrea microphthalma	May 2012	1, 2	20:50–21:05	3, 2	0:10	B	H
*Echinopora hirsutissima**	May 2011	5	22:25–23:30	1	No	B	H
	April 2012	2		15+			
	June 2012	2, 3, 4		1, 1, 1			
	April 2013	2, 3		3, 2			
Favia matthaii	July 2012	2	22:20	1	No	B	H
F. speciosa	June 2012	2, 3	20:40–20:45	1, 1	No	B	H
F. veroni	June 2012	2	22:30	1	No	B	H
Favites abdita	April 2013	1, 2	23:00–23:10	1, 1	No	B	H
*F. paraflexuosa**	June 2012	2	22:55	1	No	B	H
F. pentagona	June 2012	5	20:35	1	No	B	H
*F. spinosa**	June 2012	3	21:30	1	No	B	H
Goniastrea edwardsi	May 2011	4, 5	21:30–23:15	10+, 10+	0:30	B	H
	May 2012	4		1			
	June 2012	4, 5		5+, 1			
	July 2012	−3		1			
G. retiformis	April 2012	2, 3	22:15–23:20	30+, 7+	0:20	B	H
	May 2012	1, 2, 4	22:15–22:50	22+, 1, 3			
	April 2013	1, 2		10+, 10+			
Favia stelligera	May 2011	5	22:00–23:00	5+	0:30	B	H
	April 2012	6		5+			
	June 2012	4, 5, 6, 7		2, 10+, 10+, 4			
Leptoria phrygia	June 2012	4	22:20	1	No	B	H

Table 2 continued

Species	Spawning month	Spawning day	Hour of spawning	Number colonies	Setting duration	Gametes released	Sexuality
Platygyra sinensis	April 2012	6	20:20	1	n/a	B	H
Lobophylliidae							
*Acanthastrea brevis**	June 2012	5, 6, 7	21:05–21:35	5+, 1, 1	No	B	H
Echinophyllia aspera	June 2012	5	21:10	1	No	B	H
*Oxypora crassipinosa**	June 2012	5	21:15	1	No	B	H

Spawning day: day(s) before (–) or after the full moon; NM, new moon. Number colonies: number of colonies observed to participate in the spawning per day; for gonochoric species, the number of male (♂) and female (♀) colonies is indicated. Setting duration: h:min; No, no setting observed before gamete release; Yes, setting observed but duration not recorded; n/a, data not available. Gametes released: form of release of gametes: *B* egg–sperm bundles, *S* sperm, *E* eggs. Sexuality: *H* hermaphroditic, *G* gonochoric, *GD* gynodioecious, *PD* polygamodioecious

* New records

Acropora species spawn, as observed in the central Red Sea, in Okinawa, and in Palau. In the Philippines, only *Galaxea fascicularis* spawned in the first month (April) of the reproductive season; however, two *Acropora* species were observed to spawn in situ in March in 2006, and parallel surveys on the synchrony of maturation of gametes suggest that >50 % of the *Acropora* assemblage and at least 21 species spawn either in March or in April (Guest et al., unpublished data). *Montipora* species spawn towards the end of the reproductive season in the Red Sea, in the Philippines, and in Palau in its August–September season, but throughout the entire season in Okinawa (except for 1990). Most *Porites* species spawn in May in the central Red Sea (except for two neighbouring colonies of *P. solida* spawning in June) and spawn either in June (1991) or in July (1990) in Okinawa. In Palau, *Porites* species spawn in the April–May reproductive season. Merulinids spawn throughout the reproductive season in the Red Sea, in the Philippines, and in Okinawa, but only in the April–May reproductive season in Palau. Lobophylliidae spawn at the end of the reproductive season in the central Red Sea and in the Philippines but at the beginning of the reproductive season in Okinawa. Euphylliidae, represented in each location by *Galaxea fascicularis*, seem to spawn several times in the reproductive season in the central Red Sea, the Philippines, and Okinawa.

Discussion

Over three reproductive seasons, 51 species from eight clades were observed to spawn on the reef. Additionally, the month of spawning could be inferred from the presence of mature gametes for an additional 17 species. These observations include novel data on reproductive biology of 20 species from six clades. We conclude that the spawning season in the central Red Sea occurs in the spring from April to July, coinciding with rapidly rising sea surface temperatures. Furthermore, in contrast to early work from the Gulf of Aqaba, numerous species spawned synchronously on at least one night during the mass spawning period in each year, contradicting the earlier belief that multi-species spawning is absent from the Red Sea.

Some phylogenetic trends were evident in the time of spawning. Most *Porites* colonies spawned in May in 2012 (fourth lunar month) and in April in 2013 (fourth lunar month), most *Acropora* colonies spawned in April, *Montipora* colonies spawned in June and July, species from the family Lobophylliidae all spawned in June, whereas the Merulinidae spawned throughout the reproductive season. Most coral species spawn at a predictable time each year (Willis et al. 1985). The month of spawning in the central Red Sea was generally consistent although some taxa occasionally shifted by one solar month between years. For example, *Diploastrea heliopora* spawned in May in 2011 (fifth lunar month) and in June in 2012 (fifth lunar month). Similarly, *A. humilis* spawned in June in 2011 (sixth lunar month) and both in May and June in 2012 (fourth–fifth lunar month). Additionally, *A. lutkeni* spawned in May and June in 2011 (fifth–6th lunar month) but in April and May in 2012 (third–fourth lunar month). In some years, depending on when the moon cycle falls, some spawning can be shifted to the next lunar cycle or split over two consecutive moon cycles (Baird et al. 2009a). In 2012, the full moon was 11–12 d earlier in the month and this could have caused some species to spawn on the following full moon. Similarly, the nights of the moon cycle during which spawning occurs in the central Red Sea are not as predictable from one year to the next as they are in other regions such as the Caribbean (Levitan et al. 2011) or the GBR (Willis et al. 1985), where corals are very regular, spawning on the same moon night year after year. For example, in the central Red Sea, *A. humilis* spawned between two and seven nights after the full moon

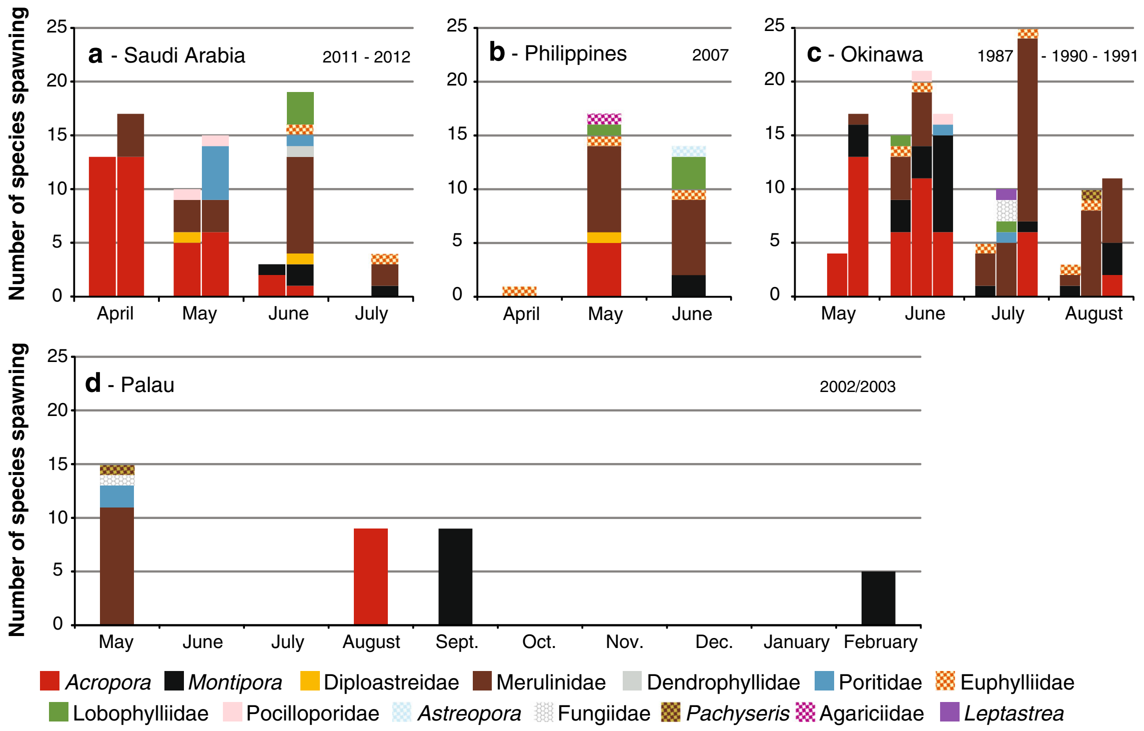

Fig. 3 Number of species observed to spawn each month for different genera or clades, for the following locations and years: **a** Saudi Arabia, central Red Sea, 2011 (*left column*) and 2012 (*right column*); **b** north-western Philippines, 2007; **c** Okinawa, 1987 (*left*), 1990 (*centre*), 1991 (*right*); **d** Palau, 2002/2003

depending on the month (Table 2). The other species observed to spawn over at least 2 months or observed over consecutive years (e.g. *Goniastrea edwardsii*, *Echinopora hirsutissima*, and *Favia stelligera*) rarely spawned on the same night before or after the full moon (Table 2). This could be due in some cases to variation in the location of observations (e.g. in 2013), but this pattern was also observed in coral species from a single location.

The vast majority of *Porites* species are gonochoric, although a few populations have low numbers of hermaphroditic colonies (Baird et al. 2009a; Guest et al. 2012). The *Porites* species observed to spawn in the central Red Sea released either sperm or eggs, suggesting that they are gonochoric. However, one *Porites* species, *P. solida*, spawned a month later than most other species and was observed to release what appeared to be bundles because they were much larger than the typical size of mature eggs in the *Porites*. The bundles were not sampled, and therefore, it is not known whether they contained eggs only or eggs and sperm. Further histological work will be necessary to confirm the sexuality of this species in the Red Sea. While most poritids spawned early in the season, *P. monticulosa* most likely spawned in November, based on the stage of maturity of gametes in samples at this time (Table 1). This is the only species in the Red Sea to date which is reproductively active outside the main spawning season from April to July. Some *Porites* species spawn out of the main breeding season in other parts of the world, such as in Western Australia (Stoddart et al. 2012). A number of common species were not observed to spawn, in particular, species from the families Agariciidae and Fungiidae. Many of these species probably spawn very late at night, or early in the morning or even during the daytime. For example, the agaricid *Pavona gigantea* releases its gametes in the late afternoon in the Galapagos Islands (Glynn et al. 1996), and an unidentified *Pavona sp.* releases sperm in the morning in the Gulf of Thailand (Plathong et al. 2006). In addition, many fungiids release gametes very early in the morning in Okinawa, Japan (Loya et al. 2009), and some, such as *Herpolithia limax*, release gametes during daylight hours (Y Loya pers. comm).

Observations from the central Red Sea are consistent with recent work from the northern Red Sea (Hanafy et al. 2010). Gamete maturation of the *Acropora* species in Hurghada and Marsa Alam in the north-western Red Sea indicates that 95 % of the assemblage was mature in mid-April and the first week of May (Hanafy et al. 2010). If these species behave like *Acropora* in other regions of the globe, they will spawn in synchrony sometime around the full moon, as indeed, the data presented here demonstrate (Table 2). In addition, the length of the reproductive season in the central Red Sea is similar to Eilat (Shlesinger and Loya 1985; Shlesinger et al. 1998). The putative absence of multi-species spawning in Eilat may be due to the fact that only a small proportion of the assemblage from often distantly related clades was sampled (Guest et al. 2005b). If the entire *Acropora* assemblage were sampled, it is probable that multi-species spawning would be observed.

The reproductive patterns in the central Red Sea are likely to hold in the southern Red Sea. Indeed, in the Farasan Islands (16°40′N, 42°00′E), coral spawn slicks have occurred at the time of the full moon, once in March but usually in April (Gladstone 1996). In the Gulf region, located approximately 1500 km east of the Red Sea, spawning observations and reproductive surveys suggest a reproductive period of 2–3 months, in April, May, and June (Fadlallah 1996; Bauman et al. 2011). The Red Sea and the Gulf display similar reproductive patterns with spawning happening in the same months although the length of the reproductive season might be longer in the central Red Sea, which is not surprising given the much greater species diversity.

The spawning patterns in the central Red Sea are similar to the few other similarly well-sampled regions in the Indo-Pacific, with spawning concentrated in a four- to 10-d period on or around the full moon and many species spawning in synchrony on some nights (Table 2). However, a biogeographical comparison of spawning patterns suggests few strong phylogenetic trends in the timing of spawning, except for the *Acropora* which dominate the first spawning day and month in the Red Sea, the Philippines, Okinawa, and Palau (Fig. 3). It is not clear why *Acropora* species release gametes earlier in the season than other genera. *Acropora* species are generally more sensitive to thermal stress than species from other clades (Marshall and Baird 2000; Furby et al. 2013), and perhaps, spawning early in the spring is an adaptation to avoid the peak in sea temperatures which typically occur later in the season (ESM Fig. S2).

The present study provides the first records of multi-species synchronous spawning in the Red Sea, supporting the hypothesis that multi-species spawning synchrony is a feature of all speciose coral assemblages (Guest et al. 2005b; Baird et al. 2009a). Reproductive data are still missing on an important proportion of species and conducting reproductive surveys as well as night-time observations in different habitats to cover a broader range of species will help increase the number of species observed to spawn.

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