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Synchronous spawnings of 105 scleractinian coral species on the Great Barrier Reef

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Abstract

Following observations of mass spawning of hermatypic corals on the Great Barrier Reef in 1981 and 1982, spawning dates were successfully predicted and documented at five reefs on the Central and Northern Great Barrier Reef in 1983. During the predicted times, 105 species from 36 genera and 11 families were observed to spawn. Of these, 15 species were shown to have an annual gametogenic cycle. All but two of the species observed during mass spawnings shed gametes which underwent external fertilization and development. Synchronous spawning was observed both within and between the five reefs studied, which were separated by as much as 5° of latitude (500 km) or almost a quarter of the length of the Great Barrier Reef. The mass spawning of corals took place on only a few nights of the year, between the full and last-quarter moon in late spring. Maturation of gametes coincided with rapidly rising spring sea temperatures. Lunar and diel cycles may provide cues for the synchronization of gamete release in these species. The hour and night on which the greatest number of species and individuals spawned coincided with low-amplitude tides. Multispecific synchronous spawning, or "mass spawning", of scleractinian and some alcyonacean corals represents a phenomenon which is, so far, unique in both marine and terrestrial communities.

Introduction

Kojis and Quinn (1982b) suggested that the broadcasting of gametes for external fertilization during a brief annual spawning was probably the most common mode of reproduction among scleractinians. This was confirmed by Harrison *et al.* (1984), who showed that more species of coral are known to broadcast gametes than to brood their offspring. Harrison *et al.* (1984) documented spawning in corals on reefs in the central Great Barrier Reef region, and showed that the majority of these broadcasting species spawned together on the same nights. These spawning events were synchronous in that individual colonies and species spawned during only a few hours over several consecutive days every year. Other studies of scleractinian reproduction had pointed to a distinct seasonality of spawning on the Great Barrier Reef (GBR) (Bothwell, 1982; Harriott, 1983); nevertheless, the fact that populations of many widespread and abundant corals spawned together on only the same few lunar nights every year had not previously been documented.

There are a number of well known examples of highly predictable, highly synchronized annual reproductive cycles in marine organisms. Spawning may occur on only one or two nights a year (e.g. in *Eunice viridis*, Korringa, 1957; *Comanthus japonica*, Kubota, 1981) or it may occur with a definite periodicity within a more extended breeding season [*Centrechinus* (*Diadema*) *setosa*, Fox, 1924; *Leuresthes tenuis*, Korringa, 1957; *Neofibularia nolitangere*, Reiswig, 1970; *Clunio marinus*, Neumann, 1981]. These instances all represent spawning events restricted to a single species at a particular time and place. Although a number of species of hydromedusae have been reported to spawn together at Friday Harbour, USA (Miller, 1979), the spawning occurs over an extended period. The mass spawning of corals differs from all the above phenomena in the synchronous spawning of many species in a very brief period of time.

This paper presents findings from an ongoing program to document the mode and timing of coral spawning, and to more fully document the numbers of species involved in the mass spawning of corals on the GBR. Other objectives were to determine whether the mass spawning occurred at reefs in the northern as well as the central region, and to establish the relative timing of spawning in the two regions.

Materials and methods

Study sites

Coral spawning was studied at four sites in the central GBR: Big Broadhurst Reef, Bowden Reef, Magnetic Island

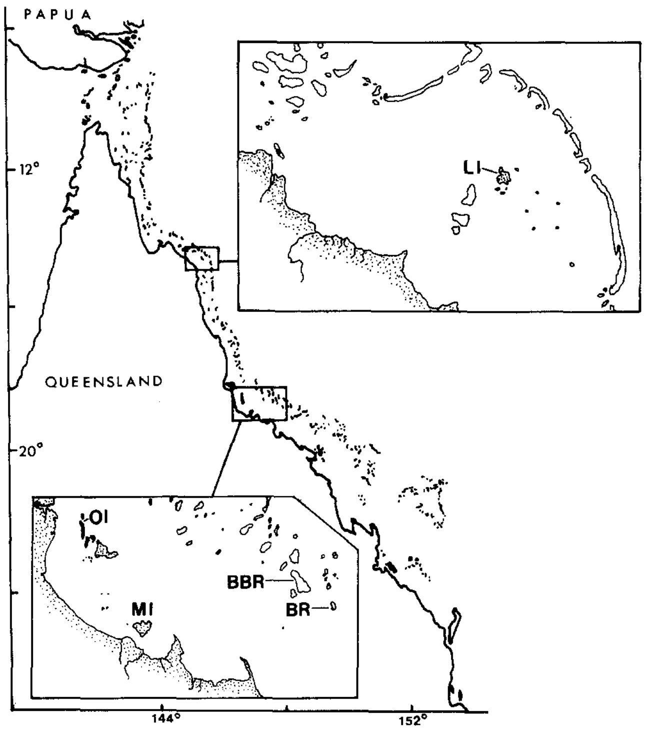

Fig. 1. Map of the Queensland coast, showing study areas. BBR: Big Broadhurst Reef; BR: Bowden Reef; LI: Lizard Island; MI: Magnetic Island; OI Orpheus Island

and Orpheus Island. Observations of coral spawning were also made at Lizard Island in the northern region of the GBR (Fig. 1). Magnetic Island is situated in the shallow (< 10 m) inshore waters of Cleveland Bay, while all the other sites are mid-shelf reefs or islands in deeper (> 20 m) offshore waters.

Gametogenic cycles

Fifteen species of coral were sampled throughout the year at Magnetic Island and Orpheus Island, in order to monitor gametogenic cycles. At both sites, five randomly selected colonies of *Goniastrea aspera, G. favulus* and *Platygyra sinensis* were sampled at monthly intervals between March and November 1983. At Magnetic Island, tagged colonies of 11 species of *Acropora* were sampled at approximately monthly intervals between January and October 1983. These species were *Acropora elseyi* (1 colony), *A. formosa* (7), *A. humilis* (2), *A. hyacinthus* (3), *A. latistella* (2), *A. microphthalma* (1), *A. millepora* (4), *A. nobilis* (2), *A. pulchra* (2), *A. tenuis* (1), *A. valida* (2). In addition, three to five random samples of *A. millepora* and *Galaxea fascicularis* were taken every month between July and November 1983 at Orpheus Island. To determine whether gonads were in a ripe condition, colonies were broken open and examined in the field or brought back to the laboratory and checked under a dissecting microscope. Two criteria were used to determine whether gonads were ripe. These were the presence of pigmentation in the eggs and the presence of testes (Kojis and Quinn, 1981; Babcock, 1984; Harrison *et al.*, 1984). Microscopic examination of smears of squashed fresh testes was used as a final measure of gonad maturity. Motile sperm with condensed heads indicated that spawning would take place within the week (Harrison *et al.*, 1984).

Spawning records

Direct observations of spawning were made at night on undisturbed corals *in situ*, corals moved to underwater observation posts, and corals in aquaria. At night, corals in aquaria were shielded as much as possible from artificial illumination. Frequent brief observations were made using flashlights. Spawning activity was also inferred by several indirect means, including the disappearance of gonads between sequential samples from tagged colonies in the field or in aquaria, the presence of eggs or sperm in aquaria, or the presence of eggs in plankton mesh bags placed over colonies in the field.

Acropora formosa, Goniastrea aspera, G. favulus, Montipora digita and *Platygyra sinensis* were sampled more intensively during the spawning period (i.e., 15 or more colonies of each, Tables 3 and 4), in order to determine whether part of the population delayed spawning until a later period, and what proportion of the population spawned on each day of the spawning period. These species were chosen since they were already the subjects of separate detailed reproductive studies.

Results

Taxonomic and geographic extent of mass spawning

A total of 105 species of scleractinian corals and 7 species of alcyonacean corals, from five geographically distinct reefs, released gametes during a seven-day spawning period (Table 1). Two planulating species of coral were also recorded. In addition to the 105 species which were observed to spawn, 20 species contained mature gonads when sampled during the first few days of the spawning period (Table 2) but for logistic reasons could not be sampled further. Gamete release was observed directly in 80 of the 107 scleractinian species. In the remaining species gamete shedding was inferred from the abrupt disappearance of gametes between sampling periods and the absence of brooded embryos or planulae. Scleractinians participating in the spawning event included 36 genera in 11 families.

Coral spawning was observed on the same nights at reefs in the central and northern Great Barrier Reef region separated by up to 500 km. Fifty species were recorded spawning at more than one reef (Table 1). This included direct observations of spawning in 33 species, 25 of which spawned within one day of each other (Table 8). Mass spawning therefore involved whole populations of many species of coral on widely separated reefs.

Table 1. List of corals recorded spawning in 1983; Data for day and hour of spawning are from direct observation only, except in cases where indirect spawning records are the only ones available. Spawning behaviour: Type I, slow extrusion of gametes; Type II, vigorous ejection of gametes; Type III, passive release of gametes. BBR: Big Broadhurst Reef; BR: Bowden Reef; LI: Lizard Island; MI: Magnetic Island; OI: Orpheus Island. H: hermaphroditic; D: dioecious; s: setting of egg-sperm bundles only, release not observed; –: not recorded

Species	Site of observations	Sexual character	Day of spawning (days after full moon)	Hour of spawning (hours after sunset, h:min)	Type of spawning behaviour	Egg colour
Scleractinia						
Acroporidae						
Acropora aculeus	BR	H	5	2:00	I	–
A. austera	BBR	H	6	–	I	–
A. cerealis	OI, LI, BR	H	4 (OI); 5 (LI); 6 (BR)	3:40 (OI), 3:50 (BR)s	I	–
A. cytherea	BBR	H	6	–	I	–
A. elseyi	MI, BBR	H	15(MI); 6(BBR)	2:30 (MI)	I	pink
A. florida	LI	H	6	3:00	I	pink
A. formosa	MI, LI, BR, OI	H	3 (MI); 4 (OI); 5 (LI); 6 (BR)	2:45 (OI); 3:40 (BR), 2:45 (MI); 1:40 (LI)	I	pink, white
A. gemmifera	LI, BR	H	6 (BR)	3:50 (BR)s	I	–
A. grandis	LI, BR	H	5 (BR)	2:50 (BR)	I	white
A. humilis	MI, LI, BR	H	3 (MI); 6 (BR); 7 (LI)	1:55 (MI); 3:50 (BR)s, 3:15 (LI)	I	pink
A. hyacinthus	MI, LI, BR	H	3 (MI); 5, 6 (LI); 6 (BR)	2:30 (MI); 2:05 (LI) 3:50 (BR)s	I	pink
A. latistella	MI	H	15, 16	–	I	pink, red
A. lutkeni	BBR	H	6	–	I	–
A. longicyathus	MI	H	3	2:20s	I	red
A. loripes	LI	H	6	3:00	I	pink
A. microphthalma	MI	H	3	–	I	red
A. millepora	MI, OI, LI, BR	H	3 (MI); 4 (OI); 6 (BR); 6, 7 (LI)	2:35 (MI); 1:05 (OI), 3:10 (BR); 3:10, 3:45 (LI)	I	cream, pink
A. nasuta	BR,LI, OI	H	4 (OI); 6(BR); 5, 6, 7 (LI)	3:40 (OI); 1:25, 3:15, 3:40 (LI)	I	orange, pink
A. nobilis	MI, BR	H	3 (MI); 6 (BR)	2:25 (MI); 3:40 (BR)	I	cream, pink
A. pulchra	MI	H	3	2:05	I	cream
A. robusta	BBR	H	6	–	I	–
A. sarmentosa	LI	H	7	2:10	I	pink
A. secale	BR, LI	H	5, 7 (LI); 6 (BR)	2:05, 3:40 (LI); 3:50 (BR)s	I	red
A. selago	BR	H	6	–	–	–
A. tenuis	MI, LI, OI	H	3 (MI); 4, 5 (OI); 5, 6 (LI)	0:10 (MI); 1:00 (OI), 1:15, 1:05 (LI)	I	white, red
A. valida	MI, BR	H	3(MI); 6 (BR)	2:25 (MI); 2:25 (BR)	I	red
A. yongei	BBR	H	6	–	I	–
Astreopora myriophthalma	OI, LI, BBR	H	4 (LI); 5, 6 (BBR)	2:05 (LI); 2:10, 2:40 (BBR)	I	pink, purple
Montipora digitata	MI, OI	H	1, 2 (MI); 1, 2 (OI)	1:50 (MI); 2:10 (OI)	I	tan (zooxanthellate)
M. foliosa	MI	H	2	2:25	I	tan (zooxanthellate)
M. hispida	OI	H	4	2:40	I	tan
M. monasteriata	MI	H	1, 2	2:25	I	tan (zooxanthellate)
M. spumosa	MI	H	2	2:15	I	tan (zooxanthellate)
M. tuberculosa	OI	H	5	2:50	I	tan
M. turgescens	BR	H	6	2:25	I	pink
Agaricidae						
Pachyseris rugosa	OI, LI	D	4, 5 (OI)	1:10 (OI)	II	yellow
P. speciosa	MI, OI	D	5, 6, 7 (MI); 5, 6 (OI)	0:10 (MI); 0:40 (OI)	II	yellow
Caryophyllidae						
Euphyllia divisa	OI	D	5	3:30	–	orange
Physogyra lichtensteini	OI	D	4	1:25	Sperm in aquaria	–
Dendrophyllidae						
Dendrophyllia sp.	MI	D	14	–	Planulae in coelenteron	yellow
Tubastrea faulkneri	MI	D	4–7	–	Planulae released	–
Faviidae						
Australogyra zelli	LI, BBR	H	5 (LI, BBR)	3:10 (LI); 4:05 (BBR)	I	pink
Barabattoia amicorum	MI, OI	H	1–?–7 (MI); 3–?–7 (OI)	–	–	green
Caulastrea furcata	OI	H	2	1:25	I	pink
Cyphastrea chalcidicum	MI, BR	H	4, 5 (MI); 5 (BR)	1:55 (MI); 1:45 (BR)	I	pink
C. microphthalma	MI	H	5	2:35	I	–
Echinopora gemmacea	OI	H	4, 5	1:40	I	grey-brown
E. horrida	LI	H	6	3:50 s	–	pink
E. lamellosa	MI	H	6	1:40	I	pink

(continued overleaf)

Table 1 (continued)

Species	Site of observations	Sexual character	Day of spawning (days after full moon)	Hour of spawning (hours after sunset, h:min)	Type of spawning behaviour	Egg colour
Favia favus	OI, LI	H	5 (LI)	1:30 (LI)	II	aqua, red
F. lizardensis	MI, BBR	H	6 (BBR)	–	–	aqua, brown
F. matthai	LI	H	2–?–6	–	–	–
F. pallida	MI, OI, LI, BBR	H	4 (OI); 5 (LI), 6 (BBR)	1:50 (OI); 2:10 (BBR)	II	aqua, brown
F. stelligera	LI, BBR	H	5 (BBR); 6 (LI)	4:20 (LI)s	–	red
F. veroni	OI	H	2–?–8	–	–	grey
Favites abdita	MI, OI, LI, BBR	H	6 (MI); 4 (LI); 4, 5 (OI)	1:50 (MI); 1:55 (OI); 4:10 (LI)	II	pink, red
F. bennettae	OI	H	2–?–8	–	–	tan
F. complanata	OI	H	4, 5	0:55, 2:50	I	tan, red, blue
F. flexuosa	OI, LI	H	5 (LI)	1:55, 2:10 (LI)	I	lavender
F. halicora	MI, LI, OI, BBR	H	6 (MI); 4, 5, 6 (OI); 5 (LI, BBR)	1:15 (MI); 3:20 (OI); 4:30 (LI)	I	cream, red
F. pentagona	MI, OI	H	4, 5 (MI)	1:20 (MI)	I	pink
F. russelli	MI	H	6	1:35	I	–
Goniastrea aspera	MI, OI	H	3, 4 (MI); 4, 5, 6 (OI)	3:25 (MI); 3:10 (OI)	II	green, pink
G. edwardsi	LI, BBR	H	5 (BBR)	3:00–3:50 (BBR)	I	pink
G. favulus	MI, OI	H	3, 4 (MI); 4, 5 (OI)	1:10 (MI); 0:25 (OI)	II	yellow
G. palauensis	MI, LI	H	5 (MI)	2:15 (MI)	I	pink, green
G. pectinata	LI, BBR, BR, OI	H	5 (BR)	2:55 (BR)	I	pink
G. retiformis	OI, LI	H	4, 5 (OI, LI)	2:20, 2:55 (OI, LI)	II	pink
Hydnophora exesa	MI, LI	H	6, 7, 8 (MI)	1:55 (MI)	III	pink
H. rigida	LI	H	3–?–6	–	–	–
Leptoria phrygia	OI, LI, BBR	H	5 (OI, LI)	3:40 (OI, LI)	I	pink, red
Montastrea curta	BBR	H	6	2:40	I	red
M. magnistellata	MI, LI, OI	H	6 (MI); 4, 5 (OI); 5, 6 (LI)	3:10 (OI); 1:15 (MI); 3:10, 5:00 (LI)	I	cream, red
M. valenciennesi	MI	H	3, 4	3:35	II	pink
Moseleya latistellata	MI	H	6	–	II	yellow
Oulophyllia crispa	LI, OI	H	4 (OI); 5 (LI)	2:20 (OI); 1:35 (LI)	II (LI); I (OI)	red
Platygyra daedalea	LI, BR, BBR MI, OI	H	4 (MI); 5 (BR); 5, 6 (OI); 4, 5 (LI); 6, 7 (BBR)	1:25 (MI); 1:10 (OI); 1:10, 1:20 (LI); 3:40 (BR)	I	pink, red
P. lamellina	OI, LI	H	4 (OI)	2:40 (OI)	I	pink
P. pini	BBR, OI, LI	H	5, 6, (OI)	1:15, 1:40 (OI)	I	pink
P. sinensis	MI, OI, LI	H	3, 4 (MI); 4 (OI), 5 (LI)	3:45, 3:25 (MI); 3:25 (LI); 3:10 (OI)	I	pink
Fungiidae						
Fungia fungites	MI	D	5	–0:05	Ejected sperm every 4 min	–
Sandalolitha robusta	BBR	D	5	3:30	I	creamy-yellow
Merulinidae						
Clavarina triangularis	OI	H	6	–	–	creamy-yellow
Merulina ampliata	LI, BR	H	5 (LI); 5, 6 (BR)	1:30 (LI); 2:40 (BR)	I	pink
Mussidae						
Acanthastrea echinata	MI, OI	H	2–?–8 (OI)	–	–	apricot
Lobophyllia corymbosa	OI	H	4, 5	1:10, 1:25	I	pink
L. hemprichii	OI, LI	H	4, 5 (OI)	0:55, 0:40 (OI)	II	tan
Symphyllia radians	LI, BBR	H	5 (BBR)	1:40 (BBR)	–	orange
S. recta	BBR	H	5–?–6	–	–	–
Oculinidae						
Galaxea astreata	MI	H	2–?–6	–	–	pink
G. fascicularis	MI, OI	H	4 (MI); 4, 5 (OI)	2:20 (MI); –0:05 (OI)	I–II, some sperm jets separate	white, pink
Pectiniidae						
Echinophyllia aspera	MI	H	6	2:05	II	yellow
E. orpheensis	OI, BBR	H	5 (OI, BBR)	3:25 (BBR); 3:40 (OI)	I	yellow
Mycedium elephantotus	MI, LI, OI BR, BBR	H	6 (MI); 5, 6 (BBR), 6 (BR); 5 (LI, OI)	3:25 (BBR); 2:25 (BR); 2:55 (LI); 3:40 (OI)	I	pink, yellow
Oxypora glabra	LI	H	1–?–6	–	–	–
O. lacera	OI	H	2–?–8	–	–	–
Pectinia alcicornis	OI	H	5	2:00	I	pink
P. lactuca	BBR	H	6	<2:10	–	pink
P. paeonia	OI	H	5	0:40	I	pink
Poritidae						
Goniopora lobata	OI, LI	D	4, 5 (OI); 5 (LI)	0:40 (OI); 1:15 (LI)	II	brown
G. minor	MI	D	3–?–6	–	–	brown
Goniopora sp. 1 (Veron and Pichon, 1982)	OI	D	2–?–8	–	–	brown

Table 1 (continued)

Species	Site of observations	Sexual character	Day of spawning (days after full moon)	Hour of spawning (hours after sunset, h:min)	Type of spawning behaviour	Egg colour
Goniopora sp.	BR	D	5	1:40	II	–
Porites cylindrica	OI	D	4	2:35 sperm, 2:45 eggs	II, "Epidemic spawning"	tan
P. lobata	OI	D	5	2:40	Diffuse sperm clouds	–
P. lutea	MI	D	3–?–7	–	–	–
P. solida	MI	D	3–?–7	–	–	–
Alcyonacea						
Alcyoniidae						
Alcyonium aspiculatum	OI	–	4	–	–	–
Lobophytum compactum	OI	–	4, 5	–	–	–
L. microlobulatum	OI	–	4	–	–	–
L. hirsutum	OI	–	4	0:40	I	red
Sarcophyton n. sp. 1	OI	–	4	–	–	–
Sinularia c.f. *deformis*	OI	–	4	–	–	–
S. polydactyla	OI	–	4, 5	–	–	–

Table 2. Coral species with mature gonads immediately prior to major spawning period, but for which no subsequent observations or samples could be made. "Last day sampled" refers to number of days after full moon. BBR: Big Broadhurst Reef; LI: Lizard Island; OI: Orpheus Island; H: hermaphroditic; D: dioecious; –: not recorded

Species	Site of observation	No. of colonies	Sexual character	Last day sampled	Egg colour
Acroporidae					
Acropora anthoceris	BBR	1	H	6	–
A. clathrata	BBR	5	H	6	–
A. divaricata	BBR	4	H	6	–
A. monticulosa	BBR	5	H	6	–
A. samoensis	BBR	4	H	6	–
A. subulata	BBR	1	H	6	–
A. valenciennesi	BBR	3	H	6	–
Astreopora sp. 1 (Veron)	LI	1	H	1	purple-brown
Montipora turtlensis	BBR	1	H	–	
Faviidae					
Favites chinensis	LI	1	H	3	–
Montastrea annuligera	BBR	1	H	–	pink
Fungiidae					
Heliofungia actiniformis	LI	1	D	6	pink
Herpetoglossa simplex	OI, BBR	2	D	6 (OI)	–
Herpolitha limax	OI	1	D	6	–
Podabacia crustacea	LI	1	D	5	white
Polyphyllia talpina	OI	1	D	–	–
Mussidae					
Lobophyllia pachysepta	BBR	1	H	–	orange
Siderastreidae					
Coscinarea columna	LI	1	D	3	tan
Thamnasteriidae					
Psammocora contigua	LI	1	D	2	brown
P. digitata	LI	2	D	6	–

Gametogenic cycles

Annual gametogenic cycles were observed in all species sampled throughout the year (*Acropora* spp., *Galaxea fascicularis, Goniastrea aspera, G. favulus, Platygyra sinensis*). Immature oocytes were first visible in dissected samples in late summer (January–February) in *Acropora* species, and in mid-winter (June–July) in other species. Gonad maturation continued until eggs were shed in spring (October or November). The eggs of the faviid species became pigmented four to six weeks prior to the spring spawning, and those of *Acropora* species and *Galaxea fascicularis* approximately three weeks before their release. Egg colour was variable, even within species (Table 1). Pink or red was

Table 3. Magnetic Island coral spawning records, 1983; full moon was 22 October. n = number of colonies sampled. a: spawning observed in the field; b: spawning observed in aquaria; c: spawning inferred from disappearance of gametes between daily samples; d: spawning inferred from disappearance of gametes between field samples two or more days apart; *: sampled but did not spawn; ├—┤: period between samples for "d" and "*"; e: spawning inferred from random field samples made after spawning was observed in other members of the same population; f: spawning inferred from presence of gametes in aquaria; ( ): observed to spawn but some oocytes remained in colony; dash: colonies observed but did not spawn; g: planulation. Data include only species for which evidence of spawning was obtained. Non-spawning colonies have been recorded only when other members of the same population were recorded spawning during the same period. Total no. of species observed = 49; no. of species for which direct spawning observations were made = 27

Species	n	No. of colonies observed on:													
		30 Sept.–	12 Oct.–	23 Oct.	24 Oct.	25 Oct.	26 Oct.	27 Oct.	28 Oct.	29 Oct.	30 Oct.–	5 Nov.	6 Nov.–	18 Nov.–	19 Jan.
Acropora latistella	4	├ 2d	┤									2c, f			
Montipora digitata	25			20c	5a, 5b	–	–	–	–	–	–				
M. spumosa	3				3b	–	–	–	–	–	–				
M. foliosa	4					–	–	–	–	–	–				
M. monasteriata	6			3e	3b	–	–	–	–	–	–				
Acanthastrea echinata	1	├			1d	┤	–	–	–	–	–				
Acropora formosa	20			–	–	10a, 6c, 4e	–	–	–	–	–				
A. humilis	3			├		1a, 2c, 1d	┤	–	–	–	–				
A. hyacinthus	15			–	–	8a, 5c, 2e	–	–	–	–	–				
A. longicyathus	1			–	–	1a	–	–	–	–	–				
A. microphthalma	3			–	–	3c	–	–	–	–	–				
A. millepora	9			–	–	2a, 2c, 1e	–	–	–	–	–			├ 4d ┤	
A. nobilis	12			├		8a, 1d, 3e	1c	┤	–	–	–				
A. pulchra	7			–		3a, 2c, 2e	–	–	–	–	–				
A. tenuis	7			–		3a, 2c, 2e	–	–	–	–	–				
A. valida	7			–		4a, 3c	–	–	–	–	–				
Goniastrea aspera	24					├ 18a	17a, 6d ┤								
G. favulus	21			–		├ 13a	19a, 2d ┤	–	–	–	–				
Montastrea valenciennesi	3				├	1a	1a, 1d, 1*	┤							
Platygyra sinensis	25			–	–	├ 12a	18a, 5d ┤	–	–	–	–				
Cyphastrea chalcidicum	2					├	1a,	1b, 1d ┤	–	–	–				
C. microphthalma	1						1a								
Favites pentagona	6				├		2a, 3d, 1*	┤	–	–	–				
Platygyra daedalea	8				├		2a, 1c, 4d	1b, c	┤ –	–	–				
Barabattoia amicorum	4				├		1d, 3*	1b	┤						
Favia lizardensis	1				├		1d	┤							
F. pallida	6				├		5d, 1*	┤							
Galaxea astreata	6				├		4d, 2*	┤							
G. fascicularis	3				├		2a, 1d	┤							
Goniopora minor	2				├		2d	┤							
Tubastrea faulkneri	2						2g								
Porites lutea	3				├		3d			┤					
P. solida	1				├		1d			┤					
Goniopora palauensis	1						–	1b							
Fungia fungites	1							1b	–	–					
Pachyseris speciosa	3							1b	2b	1b					
Echinopora lamellosa	1							–	1b	–					
Favites abdita	1							–	1b						
F. halicora	1							–	1b						
F. russelli	1						–	–	1b						
Favites sp.	1							├	1d 1b	┤					

Table 3 (continued)

Montastrea magnistella	1						1b
Moseleya latistellata	2						1a, 1e
Echinophyllia aspera	2						2b
Mycedium elephantotus	1						1a
Hydnophora exesa	2			2b	2b		2b
Dendrophyllia sp.	1					1g	
Acropora elseyi	14					3b, 1c, 10e	
Symphyllia recta	1	├── 1d ──┤					

Table 4. Orpheus Island coral spawning records, 1983; full moon was 20 November. Total number of species observed = 48; no. of species for which direct spawning observations were made = 38. For further details see legend to Table 3

Species	*n*	No. of colonies observed on:					
		21. Nov.	22 Nov.	23 Nov.	24 Nov.	25 Nov.	26 Nov.
Montipora digitata	50	43c	50c	4c	–	–	–
Caulastrea furcata	4	–	4a	–	–	–	–
Acropora cerealis	1	–	–	–	1a	–	–
A. formosa	3	–	–	–	2a, 1f	–	–
A. millepora	3	–	–	–	3b	–	–
A. nasuta	2	–	–	–	2a	–	–
Montipora hispida	1	–	–	–	1a	–	–
Physogyra lichtensteini	1	–	–	–	1b	–	–
Oulophyllia crispa	1	–	–	–	1a	–	–
Porites cylindrica	4	–	–	–	4a	–	–
Acropora tenuis	3	–	–	–	2a	–	–
Pachyseris rugosa	5	–	–	–	3b	3b	
Montastrea magnistellata	5	–	–	–	3a	5a	–
Lobophyllia corymbosa	3	–	–	–	1a	2b	–
Goniopora lobata	4	–	–	–	2b	4b	–
Favites abdita	1	–	–	–	1a	1a	–
Echinopora gemmacea	4	–	├────	────	2b ──	2b, 2d ──	──┤
Favia pallida	11	–	├────	────	5a, 2b, 4d ──	────	──┤
Favites complanata	9	–	├────	────	4a, 2b ──	1a, 2b, 3d ──	──┤
Goniastrea favulus	15	–	├────	────	1a, 4b, ──	10d ──┤	
G. retiformis	7	–	├────	────	2a, 2b ──	2a, 2d ──	──┤
Platygyra lamellina	3	–	├────	────	2a, 1d ──	────	──┤
Lobophyllia hemprichii	3	–	├────	────	1b, 2d ──	1a ──	──┤
Galaxea fascicularis	11	–	├────	────	1b ──	3a, 4b, 5d (1) ──	──┤
Favites halicora	6	–	├────	────	2a ──	2f, 2d ──	1b ─┤
Goniastrea aspera	16	–	├────	────	2b ──	2a, 10d ─┤	4b
Platygyra sinensis	18	–	├────	────	4a, 2b ──	10d ─┤	4b
Montipora tuberculosa	1	–	–	–	–	1b	–
Leptoria phrygia	1	–	–	–	–	1a	–
Mycedium elephantotus	1	–	–	–	–	1b	–
Pectinia alcicornis	6	–	–	–	–	3a, 3b	–
P. peonia	4	–	–	–	–	2a, 2b	–
Porites lobata	1	–	–	–	–	1a	–
Pachyseris speciosa	5	–	–	–	–	2b	3b
Platygyra daedalea	2	–	–	–	–	1a	1a
Euphyllia divisa	1	–	├────	────	────	1b, d ──	──┤
Platygyra pini	4	–	├────	────	────	3a, 1d ──	2a ─┤
Echinophyllia orpheensis	3	–	├────	────	────	1a, 2d ──	──┤
Astreopora myriophthalma	2	–	├────	────	────	2d partial ──	──┤
Clavarina triangularis	1	–	–	–	–	–	1b
Favia veroni	1	–	├────	────	────	1d ──	──┤
F. bennettae	1	–	├────	────	────	1d ──	──┤
Favites flexuosa	1	–	├────	────	────	1d ──	──┤
Goniastrea palauensis	1	–	├────	────	────	1d ──	──┤
G. pectinata	2	–	├────	────	────	2d ──	──┤
Acanthastrea echinata	1	–	├────	────	────	1d ──	──┤
Oxypora lacera	2	–	├────	────	────	2d ──	──┤
Goniopora sp. 1	1	–	├────	────	────	1d ──	──┤

most common, although colours ranged from brown to aqua, and in some cases pigment was absent and eggs appeared white. In dissections of fresh specimens collected throughout the year, testes containing spermatids were observed only in the four to six weeks prior to the October or November spawning. Motile sperm were not detected in freshly prepared squashes until approximately one week prior to spawning.

Of the corals studied only two species were observed to release or contain planulae. Colonies of *Tubastrea faulkneri* released large (2 mm long) bright orange planulae in aquaria over a few days; these were largely benthic and immobile. Mobile planulae were found in the coelenteron of *Dendrophyllia* sp.

Lunar day of spawning

Two discrete multispecific spawning periods were recorded in the spring of 1983; an early inshore spawning in October at Magnetic Island, and a later offshore spawning exactly one lunar month afterwards in November at the other four reefs.

At all five reefs, the third to the sixth nights after the full moon were the major nights of spawning activity, both in terms of the number of species and the number of colonies observed to spawn. At least 87 of the 105 species recorded spawned on these nights (Table 1, Fig. 2). Peak spawning occurred on the third to the fifth nights after the full moon at Magnetic and Orpheus Islands, but on the fifth and sixth nights after the full moon at the three other reefs (Tables 3–7). Only a few species were recorded to spawn on the first and second nights, or seventh and eighth nights after full moon. In contrast, *Acropora latistella* spawned just after new moon at Magnetic Island (Table 3). *A. elseyi* also spawned after the new moon at Magnetic Island (Table 3), but spawned after the full moon at Big Broadhurst Reef (Table 6).

Hour of spawning

Release of gametes in the synchronous multispecific spawning event began around sunset and continued for approximately four hours (Table 1). The time of spawning (hours after sunset) was generally consistent within each population and between populations at different sites. In 17 of the 33 species observed at more than one reef, populations spawned within an hour of each other on the same lunar day (Table 8). The time of release was also consistent from year to year. For example, at Magnetic Island *Acropora tenuis* spawned 20 min after sunset in 1982 (Harrison et al., 1984), and 10 min after sunset in 1983 (Table 8); *Platygyra sinensis* spawned 3 h 40 min after sunset in 1982 (Babcock, unpublished data), and 3 h 25 min after sunset in 1983 (Table 8). Some species showed a range of spawning times within a population (e.g. *Galaxea fascicularis*, Table 8) and between populations (e.g. *Acropora formosa* and *A. humilis*, Table 8).

Spawning synchrony within populations

In the five detailed population studies (involving *Acropora formosa, Goniastrea aspera, G. favulus, Montipora digitata,* and *Platygyra sinensis*), all colonies sampled from a single reef were found to release gametes over one to three consecutive nights (Tables 3 and 4). In a further 22 species, at least five colonies were recorded spawning during one to three consecutive nights on one reef (Tables 3–7).

Although populations of most coral species at each site spawned during only one spawning period, one species was observed to have a split spawning period which took place in two consecutive months (*Acropora latistella*). A similarly divided spawning period was inferred in other species from the absence of gametes in part of the population prior to the observed spawning at the site, or from the presence of maturing gametes in a few colonies some days after the rest of the population had spawned (*Acropora millepora, A. nasuta, A. tenuis, Astreopora myriophthalma, Barabattoia amicorum, Favia pallida, Favites pentagona, Galaxea fascicularis, G. astreata, Montastrea valenciennesi*, Tables 3–7). Another type of split spawning period was apparent within one colony of *Galaxea fascicularis* (Table 4) which was observed spawning in the field, yet at the end of the spawning period the colony still contained significant numbers of gametes.

A greatly extended spawning period was observed in *Hydnophora exesa* which released eggs singly in aquaria over several nights at Magnetic Island (Table 3). Sequential samples of the same two colonies over a period of 22 d

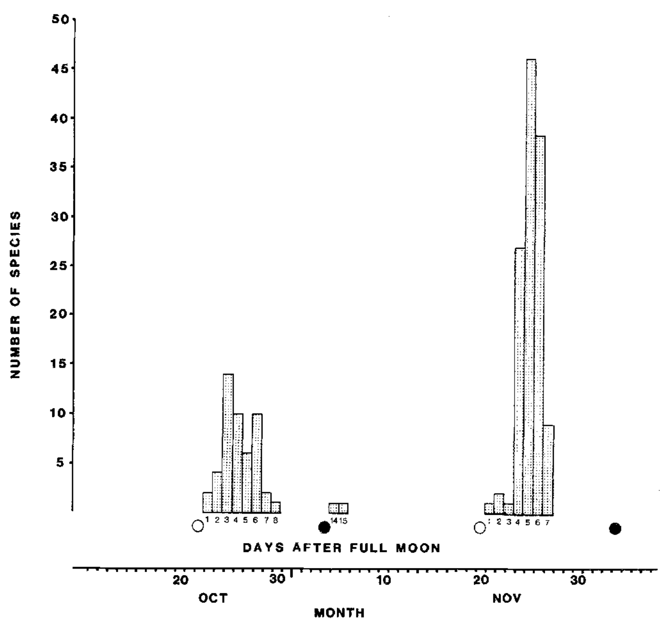

Fig. 2. Frequencies of coral spawnings in 1983. Number of coral species observed spawning on each day is given. Only those species for which the exact day of spawning could be determined have been included. Bottom abscissa gives date of spawning; intermittent abscissa, showing days after full moon, has been drawn only for those days on which sampling or observations were carried out (see Tables 3–7). open circles: full moon; filled circles: new moon

Table 5. Bowden Reef coral spawning records, 1983; full moon was 20 November. Total no. of species observed = 19; no. of species for which direct spawning observations were made = 19. For further details see legend to Table 3

Species	*n*	No. of colonies observed on:		
		22–24 Nov.	25 Nov.	26 Nov.
Acropora aculeus	2	–	1a	–
A. grandis	1	–	1a	–
Cyphastrea chalcidicum	1	–	1a	–
Goniastrea pectinata	2	–	2a	–
Platygyra daedalea	1	–	1a	–
Goniopora sp. 1	1	–	1a	
Merulina ampliata	8	–	3a	5a
Acropora nobilis	8	–	3a	5a
A. cerealis	5	–	–	5a
A. formosa	5	–	–	5a
A. gemmifera	2	–	–	2a
A. humilis	1	–	–	1a
A. hyacinthus	1	–	–	1a
A. millepora	2	–	–	2a
A. nasuta	2	–	–	2a
A. secale	1	–	–	1a
A. selago	3	–	–	3a
A. valida	1	–	–	1a
Montipora turgescens	1	–	–	1a

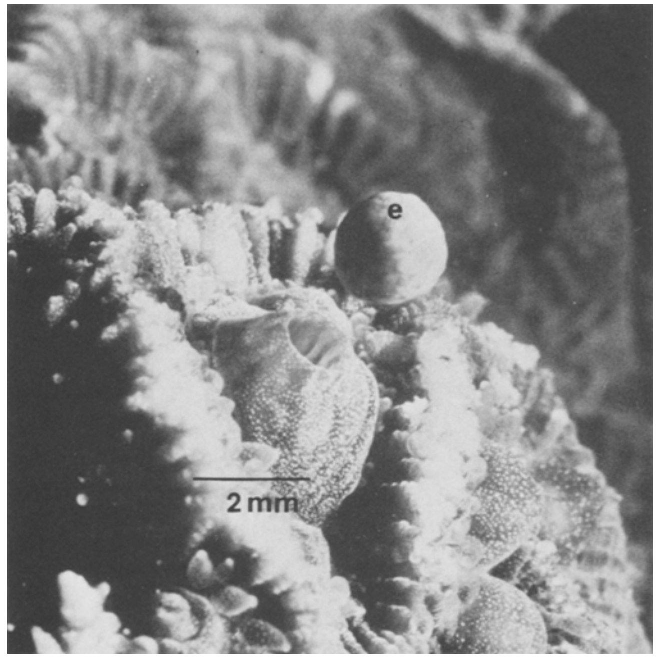

Fig. 3. *Goniastrea palauensis.* Type I spawning behavior, immediately following the release of egg-sperm bundle. e: egg-sperm bundle. (Aquarium photo)

showed a progressive decrease in the numbers of gametes at each sampling.

Spawning behaviour

Three types of spawning behaviour were observed in corals participating in mass spawning (Table 1). The most common type of spawning behaviour (Type I, Table 1) was the slow release of gamete bundles through the polyp mouth which took place throughout the colony over a period of 5 to 50 min (*Acropora* spp., *Platygyra* spp.). In hermaphroditic colonies the eggs and sperm within each polyp were packaged into one or more compact egg-sperm bundles (Type I, Table 1, Fig. 3). The packaging process took 20 to 60 min to be completed, during which time the bundle was visible in the pharynx or under the distended oral disc of each polyp. We have termed this stage of the process the "setting" of the egg-sperm bundle. Videotape recordings of an *Acropora elseyi* colony spawning showed the egg-sperm bundle being rotated under the distended oral disc of each polyp. Rotation of the bundle continued during the final release phase as the polyp mouth opened and the bundle was slowly released from the polyp.

In Type II spawning behaviour, the gametes were ejected from the polyp via rapid contractions over all or part of the colony after a short period of setting. This process was repeated once or several times in quick succession (*Goniastrea aspera, Echinophyllia aspera*) or in a regular cyclic fashion (*Fungia fungites*). Gametes were ejected in a variety of forms: as egg-sperm bundles (*G. aspera*) or separately as eggs and sperm clouds (*G. favulus, Lobophyllia hemprichii*). An intermediate spawning behaviour (Types I–II) was observed in *Galaxea fascicularis*, which slowly released egg-sperm bundles together with separate jets of sperm.

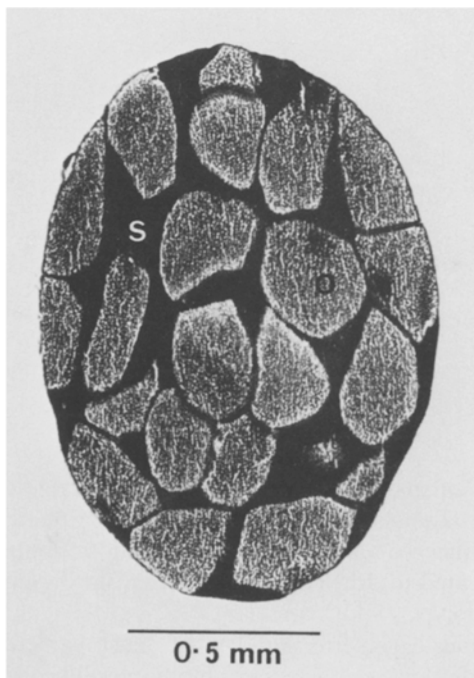

Fig. 4. *Platygyra sinensis.* Histological section (5 μm) of freshly spawned egg-sperm bundle. Note that none of the oocytes have been fertilized. o: oocytes; s: sperm

Table 6. Big Broadhurst Reef coral spawning records, 1983; full moon was 20 November. Total no. of species observed = 37; no. of species for which direct spawning observations were made = 34. For further details see legend to Table 3

Species	*n*	No. of colonies observed on:				
		23 Nov.	24 Nov.	25 Nov.	26 Nov.	27 Nov.
Sandalolitha robusta	1	–	–	1b		
Australogyra zelli	1	–	–	1b		
Favia stelligera	1	–	–	1a		
Favites halicora	1	–	–	1b		
Goniastrea edwardsi	3	–	–	3a		
Echinophyllia orpheensis	1	–	–	1b		
Astreopora myriophthalma	2	–	–	1b	1b	
Platygyra daedalea	3	–	–	├──	1b ──	1b, 1d┤
Mycedium elephantotus	2	–	–	1a	1a	
Symphyllia radians	2	–	├──	1a, 1d ──	┤	
Favia lizardensis	2	–	–	├1d ──	──	1b┤
Platygyra pini	3	–	├──	2d ──	┤	1b
Favia pallida	1	–	–	–	1b	
Montastrea curta	1	–	–	–	1b	
Pectinia lactuca	1	–	–	–	1f	
Favites abdita	1	–	–	–	1b	1b
Goniastrea pectinata	1	–	–	├──	1d ──	┤
Leptoria phrygia	2	–	–	├──	2d ──	┤
Symphyllia recta	2	–	–	├──	2d ──	┤
Acropora secale	1	–	–	–	1b	
A. loripes	1	–	–	–	1b	
A. longicyathus	1	–	–	–	1b	
A. tenuis	1	–	–	–	1b	
A. elseyi	1	–	–	–	1b	
A. cerealis	1	–	–	–	1b	
A. florida	1	–	–	–	1b	
A. yongei	1	–	–	–	1b	
A. millepora	1	–	–	–	1b	
A. lutkeni	1	–	–	–	1b	
A. hyacinthus	1	–	–	–	1b	
A. cytherea	1	–	–	–	1b	
A. nasuta	1	–	–	–	1b	
A. austera	1	–	–	–	1b	
A. gemmifera	1	–	–	–	1b	
A. humilis	1	–	–	–	1b	
A. robusta	1	–	–	–	1b	
A. valida	1	–	–	–	1b	

A third type of spawning behaviour (Type III, Table 1) was apparent in *Hydnophora exesa*. In this species, gametes were neither squeezed out or forcibly ejected from the polyp, but appeared to drift passively out from the gaping mouth of each polyp.

The eggs and egg-sperm bundles of most gamete-spawning corals species, whether hermaphroditic or dioecious, were buoyant and floated to the surface layers of the sea. The spawning of *Goniastrea favulus* was unique among the corals observed in that the eggs were contained in a sticky mucous envelope and were negatively buoyant. The eggs of *Astreopora myriophthalma* also appeared to sink after separating from buoyant egg-sperm bundles. The buoyant nature of the reproductive products of the majority of species probably increased the rate of fertilization by concentrating gametes at the surface. After the egg-sperm bundles reached the surface they broke apart, releasing the eggs and sperm. No sign of fertilization was observed prior to the fragmentation of the egg-sperm bundles (Fig. 4). The first signs of fertilization were not observed until approximately 2.5 h after spawning, and the larvae did not become strongly mobile until approximately 36 h old.

Discussion

Our results, including those of Harrison *et al.* (1984) show that at least 109 species of scleractinians and 7 species of soft corals broadcast gametes in multispecific spawning episodes. We have now documented the mode and timing of reproduction for species belonging to 11 of the 15 families of hermatypic scleractinians on the GBR. These spawning observations encompass about one-third of the 340

Table 7. Lizard Island coral spawning records, 1983; full moon was 20 November. Total no. of species observed = 42; no. of species for which direct spawning observations were made = 27. For further details see legend to Table 3

Species	*n*	No. of colonies observed on: 22 Nov.	23 Nov.	24 Nov.	25 Nov.	26 Nov.	27 Nov.
Favites abdita	1	–	–	1b	–	–	–
Astreopora myriophthalma	5	–	├──	1b	1d, 3d*	──┤	–
Goniastrea retiformis	1	–	├──	1b	1b, 1d	──┤	–
Platygyra daedalea	4	–	├──	1b	3b, 2d	──┤	–
Acropora cerealis	1	–	–	–	1f	–	–
A. grandis	2	–	–	├──	1d, 1*	──┤	–
Favia favus	1	–	–	–	1b	–	–
Favites halicora	1	–	–	–	1b	–	–
Leptoria phrygia	1	–	–	–	1b	–	–
Oulophyllia crispa	1	–	–	–	1b	–	–
Mycedium elephantotus	1	–	–	–	1b	–	–
Australogyra zelli	1	–	–	–	1b	–	–
A. formosa	2	–	├──	──	1b, d; 1d ──┤	–	–
A. gemmifera	2	–	├──	──	1d, 1* ──┤	–	–
A. humilis	9	–	├──	──	1d, 6* ──┤	–	2b
Favia matthai	1	├──	──	──	1d	──┤	–
F. pallida	2	–	├──	──	1b, d; 1d	──	──┤
Favites flexuosa	2	–	├──	──	2b, 1d	──┤	–
Goniastrea edwardsi	3	–	–	├──	3d	──┤	–
G. pectinata	1	–	–	├──	1d	──┤	–
Platygyra lamellina	3	–	├──	──	3d	──┤	–
P. pini	2	–	├──	──	2d	──┤	–
P. sinensis	3	–	├──	──	1b, 3d	──┤	–
Merulina ampliata	2	–	├──	──	1b, 1d, 1e	──┤	–
Lobophyllia hemprichii	2	–	├──	──	2d	──	──┤
Symphyllia radians	1	–	–	├──	1d	──┤	–
Oxypora glabra	1	├──	──	──	1d	──┤	–
Goniopora lobata	3	├──	──	──	1b, d, 2d	──┤	–
Acropora nasuta	9	–	├──	──	1b, d; 2d, 6*	1b ──┤	4b
A. florida	2	–	├──	──	2d	1b ──┤	–
Favia stelligera	1	–	├──	──	1d	1b ──┤	–
Acropora tenuis	4	–	├──	──	2b	1b, 3d, 1* ──┤	–
Montastrea magnistellata	2	–	–	├──	1b, 2d	1b, ──┤	–
Acropora hyacinthus	5	–	├──	2*	2b	1b ──┤	–
A. loripes	5	–	├──	──	──	1b, 5d ──┤	–
Echinopora horrida	1	–	├──	──	──	1b, d; 1* ──┤	–
Pachyseris rugosa	1		├──	──	1*	1d ──┤	–
Hydnophora exesa	1	–	├──	──	1d, (partial) ──┤		–
H. rigida	1	–	├──	──	1d, (partial) ──┤		–
Acropora millepora	4	–	├──	──	──	1b, 1d, 1* ──┤	2b
A. sarmentosa	2	– –	├──	──	──	1b, 1d, 1* ──┤	2b
A. secale	3	–	–	–	2b	–	1b

species which occur on the Great Barrier Reef (J. Veron, personal communication), or over 50% of the species listed by Done (1982) as constant or frequent in coral communities across the central GBR.

In addition to the fifteen species whose gametogenic cycles were monitored in the present study, eighteen species recorded in the mass spawning have been reported to have annual gametogenic cycles terminating in a brief reproductive period (Marshall and Stephenson, 1933; Robertson, 1981; Kojis and Quinn, 1982a, b, and personal communication; Harriott, 1983; Heyward and Collins, 1985; Wallace, 1985). For the remainder of the species involved, it is unlikely that they could have spawned at other times of the year, therefore annual gametogenic cycles are assumed. Random samples taken at other times of the year from a wide range of coral species failed to detect ripening of gonads on this massive scale in these or other species not recorded in this paper. It is possible that the total number of species involved in these mass spawnings is even greater than we have so far recorded.

Proximate factors implicated in synchronous spawning

The synchrony, predictability and brevity of the mass coral spawning appear to be linked to successive environmental

Table 8. Species observed spawning at more than one reef in 1983. Day column gives the day after the full moon, hour column shows hour:min after sunset at which spawning occurred. Where more than one colony was observed, median values are given (negative sign indicates spawning before sunset). F: field observation; A: aquarium observation; S: setting of egg-sperm bundles only, release not observed

Species	Magnetic		Orpheus		Lizard		Bowden		Big Broadhurst	
	day	h	day	h	day	h	day	h	day	h
Acroporidae										
Acropora cerealis			4F	3:40	5A		6F	3:50s	6A	
A. elseyi	15A	2:30							6F	
A. formosa	3F	2:45	4F	2:45	5A	1:40	6F	3:40		
A. humilis	3F	1:55s			7A	3:15	6F	3:50s	6A	
A. hyacinthus	3F	2:40			5A	2:05	6F	3:50s	6A	
					6A	3:20				
A. millepora	3F	2:35	4A	1:05	6, 7A	3:10	6F	3:10	6A	
A. nasuta			4F	3:40	5A	1:25	6F			
					6A	3:15				
					7A	3:40				
A. nobilis	3F	2:25s					6F	3:40		
A. secale					5A	1:25	6F	3:50s	6A	
					7A	3:40				
A. tenuis	3F	0:10	4, 5F	1:00	5A	1:15			6A	
					6A	1:05				
A. valida	3F	2:55					6F	2:25	6A	
Astreopora myriophthalma					4A	2:05			5A	2:10
									6A	2:40
Montipora digitata	1, 2F	1:50	1, 2F	2:10						
Agaricidae										
Pachyseris speciosa	5, 6, 7A	0:10	5, 6A	0:40						
Faviidae										
Australogyra zelli					5A	3:10s			5A	4:10
Cyphastrea chalcidicum	4F	1:55					5F	1:45		
Favia pallida			4F	1:50	5A	3:40			6A	2:10
F. stelligera					6A	4:20s			5F	
Favites abdita	6A	1:50	4, 5F	1:55	4A	4:10			6, 7A	
F. halicora	6A	1:15	4, 5, 6F	3:20	5A	4:30			5A	4:50
Goniastrea aspera	3, 4F	3:25	4, 5, 6F	3:10						
G. favulus	3, 4F	1:10	4, 5F	0:25						
G. retiformis			4, 5F	2:20	4, 5A	2:20				
				2:55		2:55				
Leptoria phrygia			5F	3:40	5A	3:40				
Montastrea magnistellata	6A	1:15	4, 5F	3:10	5A	5:00				
					6A	3:10				
Oulophyllia crispa			4F	2:20	5A	1:35				
Platygyra daedalea	4F	1:25	5, 6F	1:10	4, 5A	1:20	5F	3:40	6, 7A	
P. sinensis	3F	3:25	4F	3:10	5A	3:25				
	4F	3:45								
Merulinidae										
Merulina ampliata					5A	1:30	5, 6F	2:40		
Oculinidae										
Galaxea fascicularis	4F	1:25	4, 5F	–0.05 to 2:30						
Pectinidae										
Echinophyllia orpheensis			5F	3:40					5A	3:25
Mycedium elephantotus			5F	3:20	5A	2:55	6F	2:25	5, 6F	3:25
Poritidae										
Goniophora lobata			4, 5A	0:40	5A	1:15				

cues which operate on increasingly fine time scales: annual sea temperature patterns, monthly lunar or tidal cycles, and diel light cycles.

Sea water temperatures along the GBR show a distinct seasonal variation which may influence gametogenic cycles. Mass spawning occurs in the period between mid-October and early December after a rapid spring rise in sea temperature between late August and September (Fig. 5). The possible importance of temperature in determining timing of the spawning season is supported by the dif-

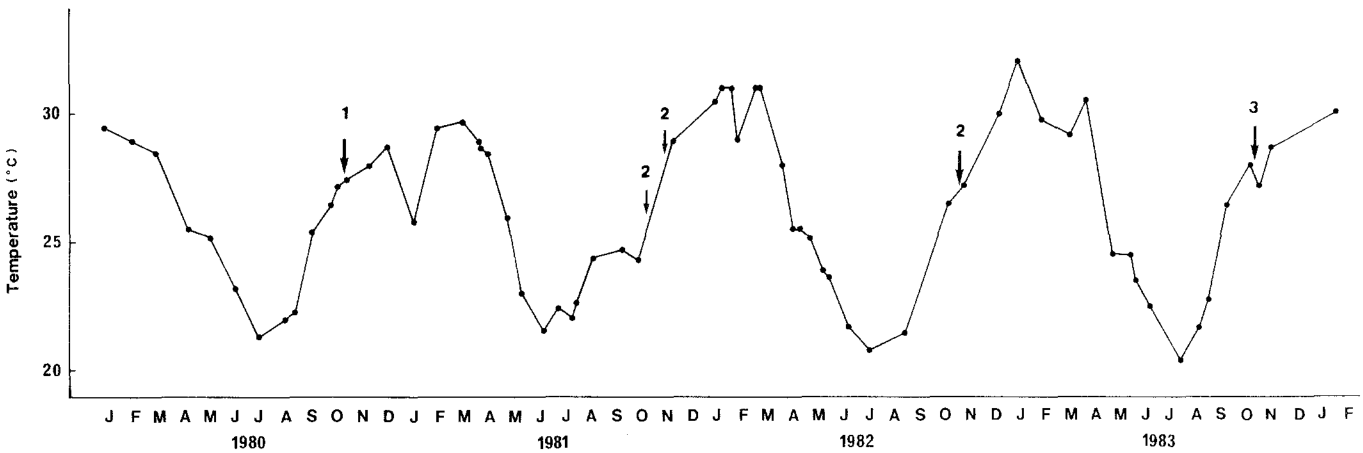

Fig. 5. Annual temperature variation at Magnetic Island 1980–1983, recorded at 3 to 5 m depth. Arrows indicate observed spawning periods. 1: Babcock (1984); 2: Harrison *et al.* (1984); 3: present study

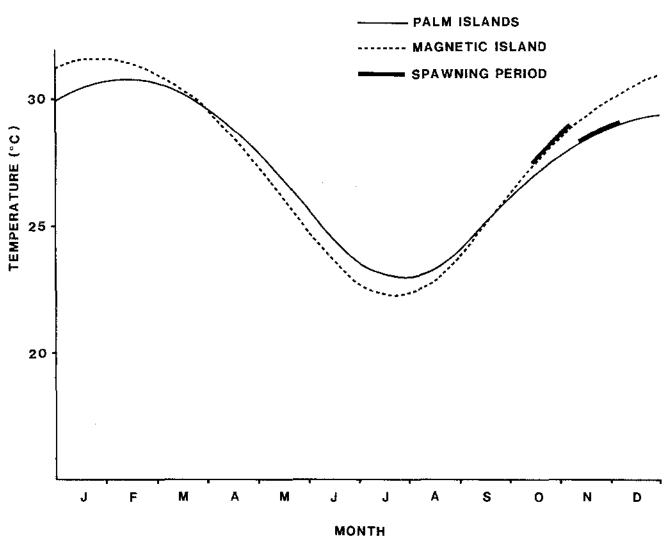

Fig. 6. Average annual temperature variation at Magnetic Island during 1979–1983 and Palm Islands (Orpheus Island and Eclipse Island) during 1979–1984, recorded at 2 to 5 m depth. Temperatures were plotted and curves fitted by eye

ferences in the month of spawning at the inshore and offshore reefs. In 1982, spawning at Magnetic Island took place early in November, while at Big Broadhurst Reef and Orpheus Island, it occurred one lunar month later, in early December (Harrison *et al.,* 1984). The same pattern was observed in 1983, with Magnetic Island populations spawning one month earlier than those at offshore reefs (Big Broadhurst, Bowden, Lizard and Orpheus). Sea temperatures began to rise earlier and more rapidly in the shallow (maximum depth 10 m) inshore waters around Magnetic Island than they did further offshore at Orpheus Island in the Palm Island Group (Fig. 6). This earlier warming may accelerate the maturation of gonads. Changes in temperature have previously been associated with annual periodicity of spawning in other marine invertebrates (Orton, 1920; Korringa, 1947; Campbell, 1974; Grigg, 1979) as well as scleractinians (Kojis and Quinn, 1981).

All the corals recorded in this paper exhibited lunar periodicity in reproductive behaviour. Most species spawned after the full moon and two species spawned after the new moon (Fig. 2). Only one species, *Acropora elseyi,* spawned at both the new and full moons. Our observations of mass spawning in corals suggest that the release of gametes occurs after nightfall following the first full moon subsequent to the maturation of gonads. Lunar periodicity has been well documented in brooding corals (Abe, 1937; Atoda, 1953; Lewis, 1974; Rinkevich and Loya, 1979; Richmond and Jokiel, 1984) and in gamete-releasing species (Kojis and Quinn 1981, 1982a, b; Harriott, 1983; Babcock, 1984; Harrison *et al.,* 1984). A wide range of other marine organisms also display distinct lunar periodicity in their reproductive behaviour (Korringa, 1957; Johannes, 1978; Kubota, 1981). In particular, the spawnings of *Comanthus japonica* (Kubota, 1981) and *Eunice viridis* (Caspers, 1984) are similar to many corals in that they occur on only a few days once a year.

It has been shown that the timing of the release of planulae in races of *Pocillopora damicornis* at Hawaii can be manipulated by means of artificial moonlight (Jokiel *et al.,* 1985). This does not prove the existence of an endogenous lunar rhythm, but indicates that moonlight is an entraining factor. Other factors such as pressure (Naylor and Atkinson, 1972) and water motion (Neumann, 1978) may act as "Zeitgebers" for a tidal rhythm, but they have not been demonstrated in coelenterates.

Spawning tends to occur after a specific period of darkness, ranging from a few minutes to over four hours after sunset (Tables 1 and 8). It appears likely that the final sequence of events leading to the release of gametes is set in motion by the onset of darkness, once the gametes are fully differentiated. Babcock (1984) showed that for *Goniastrea aspera* in aquaria, the hour of spawning could be controlled by manipulating the light-dark cycle. Similar mechanisms using diel changes in light appear to be widespread in coelenterates, (Campbell, 1974; Honnegger *et al.*, 1980; Yoshida *et al.*, 1980).

Possible causal factors of synchronous spawning

Successful synchronization of gamete release within populations, however it is achieved, maximizes the probability of achieving fertilization. While temperature, moonlight and sunlight may be used by corals as cues to synchronize spawning, they are not necessarily the forcing functions which ultimately determine the time when spawning will take place. For example, moonlight can be used to predict the tidal regime. This use of one signal to gain information on another, perhaps less easily detectable factor, has been shown to exist in a number of arthropod species (Tevis and Newell, 1962; Hoffman, 1978). The significance of the precise time during the lunar/tidal cycle at which coral spawning occurs may be related to the need to avoid predation while still producing a high concentration of gametes in order to maximize fertilization. Spawning at night minimizes predation by visual feeders such as planktivorous fish species.

It is also possible that the timing of spawning is related to the advantage of reduced dispersal of gametes prior to fertilization. On the nights following the full moon, low tide falls between late afternoon and midnight on the GBR. The difference between this low tide and the following high tide is small (0.5 m), resulting in an extended period of slack water (Fig. 7), during which the majority of coral species were observed to spawn. Thus, it is possible that the timing of spawning is ultimately due to the advantage of increased fertilization during periods of low water motion and low water volume.

Evidence which supports the importance of low tides as a factor in determining the timing of spawning can be obtained from *Goniastrea favulus*. This species spawns during daylight (16.00–18.00 hrs) at Heron Island (Kojis and Quinn, 1981), but after dark (18.25–20.50 hrs) on reefs near Townsville. In both cases, however, spawning occurs around low tide. Tides in the Townsville region always occur one half hour or more later than those at Heron (Maxwell, 1968). Spawning during low tide has been postulated as a mechanism for increasing the concentration of gametes in other animals (McDowall, 1969). Tide heights themselves appear not to trigger the final events leading to spawning since corals kept in aquaria still spawn at the appropriate time as determined by the light dark cycle, even when that cycle is artificially manipulated (Babcock, 1984).

The interspecific synchrony of coral spawning on the GBR is the most significant and unusual aspect of the mass spawning phenomenon. This synchrony may be the result of species responding independently to physical factors in order to maximize reproductive success. The buoyant properties of egg-sperm bundles, modes of reproduction, and larval development (Heyward and Babcock, 1985) of most of the species involved in the mass spawning are very similar; therefore, the physical constraints which determine optimal spawning times for each species are also likely to be similar.

It has also been suggested (Harrison *et al.*, 1984) that the chances of survival of planktonic larvae would be increased during synchronous multispecific spawning by satiating predators and filter-feeders. A number of planktivorous fish species have been observed eating coral eggs, including species of *Abudefduf*, *Neopomacentrus*, and *Pomacentrus*, which picked off egg-sperm bundles as they were released. This activity was observed only during the crepuscular period, when there was still sufficient light for

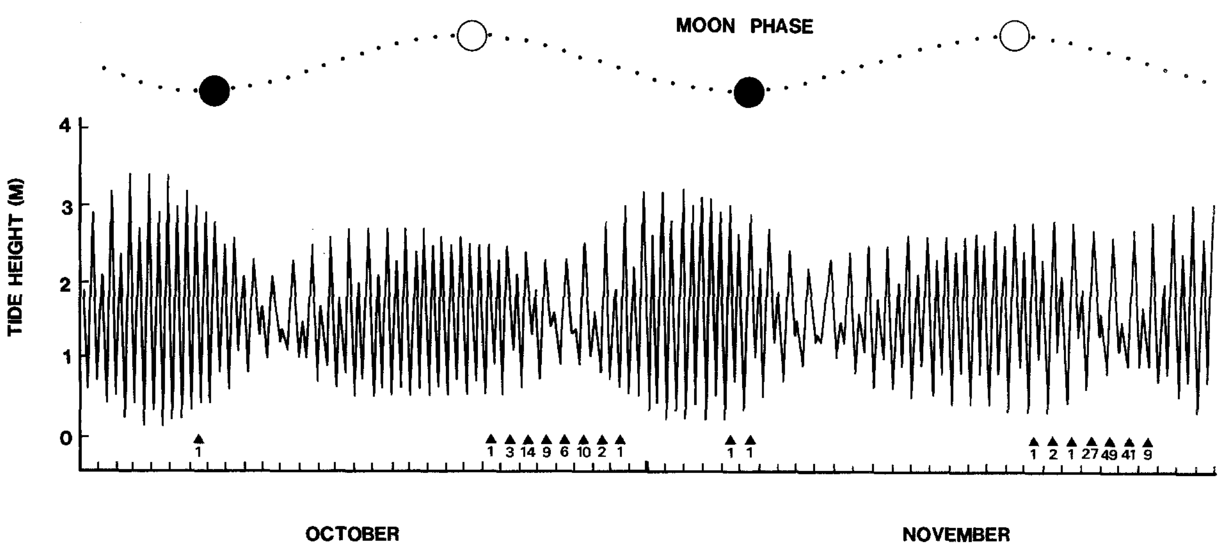

Fig. 7. Tidal cycle, October and November 1983 for Townsville area. Triangles indicate days on which corals were known to have spawned. Numbers beneath triangles indicate number of species from all five reefs which were known to have spawned on those days

visual feeding. It may be significant that the majority of corals spawn during the period of darkness between sunset and moonrise, on the third to sixth nights after full moon.

It is not yet known whether the mass spawning of corals observed on the GBR occurs in other parts of the world. The phenomenon does not appear to occur in the Red Sea, where coral species spawn over a period of several months, and during a variety of different lunar phases (Shlesinger and Loya, 1985). In the Caribbean Sea, some corals appear to spawn together (*Acropora* spp.), but a greater number spawn or planulate at various times throughout the year (Szmant-Froelich *et al.*, 1984). Slicks of coelenterate larvae have been reported from Bermuda (Butler, 1980) which appear to be similar to slicks observed as a result of coral spawning on the GBR. Variation in physical factors, such as tidal amplitude and annual sea temperature range, which may determine the most favourable spawning period, appears to be more pronounced on the GBR (Maxwell, 1968) than in the Red Sea (Shlesinger and Loya, 1985), or Caribbean Sea (Olhorst, 1980). This may more sharply define the period of time during which conditions are optimal for reproductive success on the GBR, thereby concentrating the reproductive season of many corals into a relatively brief period of time.

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